Degenerative joint disease (DJD) in non-human primates and its relationship to locomotor adaptation and support use

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ABSTRACT

This thesis examines degenerative joint disease (DJD) in non-human primates with the aim to detect potentially contributing factors to its presence. Locomotor behaviour has received little attention in studies on DJD in non-human primates as a potential causal factor, despite the great locomotor diversity of the order and the link between human bipedalism and DJD.

The main goal was to explore the relationship between the disease and the stress exerted on joints, mainly as a result of locomotion. Locomotor adaptation and locomotor strategy were considered alongside with non-locomotor factors (principally body mass and age) as causal factors for joint degeneration. DJD was recorded for the main weight-bearing joints of 35 taxa of non-human primates, representing a wide variety of locomotor adaptations (vertical clingers and leapers, slow arboreal quadrupeds, leapers, quadrupeds, knuckle-walkers and suspensory primates). These taxa move according to different locomotor strategies, such as different speeds (fast and slow moving species) or different patterns of habitat use (arboreal, terrestrial or semi-arboreal species), which led to interactions with supports of different levels of compliance.

The primate taxa studied showed different patterns of DJD expression, which were partially determined by locomotor behaviour. Primates of different locomotor adaptations showed different distribution patterns of DJD according to the levels of stress exerted on different joints or body compartments as a result of locomotion. Moreover, the adoption of different locomotor strategies was coupled with variability of DJD. Other factors, such as body mass or age showed significant correlations with DJD severity exhibiting different coefficients at different joints and body compartments, suggesting that their effect on DJD expression was likely to be important but only in combination with other factors. Multivariate analyses confirmed this conclusion, demonstrating the important effect of mechanical factors in variability of the early development of DJD, as well as a consistent effect of age, especially correlated with an increase in DJD severity and variability.

DJD in non-human primates is clearly a multifactorial phenomenon, where stress related to locomotion plays an important role. A new perspective in the study of DJD was presented, providing a good basis for future studies from which other areas could benefit, such as sports medicine, evolutionary primatology or captive care studies.

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CHAPTER 1: GENERAL INTRODUCTION

Degenerative joint disease (DJD) has often been reported in the archaeological record, affecting anatomically modern humans as well as their ancestors (Cook et al., 1983; Trinkaus, 1985; Degusta, 2002; Weiss and Jurmain, 2007; Aufderheide and Rodríguez-Martín, 2011). However, the aetiology of the disease is unclear, often being defined as an idiopathic disorder (Rogers et al., 1987; Martin et al., 1998; Aufderheide and Rodríguez-Martín, 2011). DJD in anatomically modern humans has been related to bipedalism, as a result of greater pressures generated by the habitual orthograde behaviour characteristic of humans, ultimately relating DJD to locomotor adaptation (Cook et al., 1983; Hutton, 1987; Jurmain, 1989; Knüsel et al., 1997). However, the link between locomotor adaptation and DJD has been a rare approach in studies concerning DJD in other mammals (Baker and Brothwell, 1980; DeRousseau, 1988; Johannsen, 2006).

The present research aims to gain a better understanding of the nature of DJD. The main focus is on how locomotor behaviour can shape joint degeneration. Non-human primates were the chosen sample of study because they exhibit a great range of locomotor behaviours (Hunt et al., 1996; Schmidt, 2011; Elton et al., 2016). Furthermore, DJD has been previously reported within this order (DeRousseau, 1985, 1988; Jurmain, 1989, 2000; Rothschild and Woods, 1992, 1993; Rothschild and Rühli, 2005; Nuckley et al., 2008), making non-human primates good subjects of study, as they could provide insight on DJD mechanisms also applicable to humans.

The potential role of locomotion as a causal factor of DJD in non-human primates has received little attention. Only one study treated locomotor behaviour as an explanatory factor for DJD development, comparing two species of different locomotor adaptations (DeRousseau, 1988). Instead, most of the previous studies on DJD in non-human primates aimed to report and describe the disease in order to define its aetiology, often drawing similarities with the human expression of DJD, using phylogeny and infectious processes as proxies (Rothschild and Woods, 1992; Rothschild and Rühli, 2005). However, most studies failed to present a consistent model of DJD prevalence across primates as well as consistent causality, suggesting that the disease is likely to be a multifactorial phenomenon.

The present study explores DJD from a functional point of view, where its development was hypothesised to be linked to the amount of mechanical stress born by a joint. Bone morphology and bone remodelling are greatly influenced by mechanical load and stress (Ruff et al., 2006; McFarlin et al., 2008; Stephens et al., 2016). Therefore, it was assumed that development of DJD was unlikely to be an exception. Consequently, different factors that would define the system of forces acting on joints and the associated stress were considered as potential determinants of DJD.

Locomotor adaptation was considered as one of the main drivers of DJD associated to locomotor behaviour and mechanical stress. The positioning of the body of a primate during locomotion determines the angle of incidence of the forces and the corresponding loads acting on the skeleton associated with locomotion (e.g., Demes et al., 1995; Larson, 1998; Schmitt, 1998, 2006; Schmitt and Hanna, 2004; Granatosky et al., 2017). Therefore, it is expected that primates that shared locomotor adaptation would experience similar systems of forces, compared with primates of different locomotor adaptations, and this could lead to different patterns of DJD expression.

Further differences among species with the same locomotor adaptation were expected. Primates can perform different locomotor strategies, even if they share the same locomotor adaptation. These strategies are often coupled with differences in the magnitude of the forces exerted and supported during locomotion, particularly affecting the support reaction forces (SRF). For instance, support choice during locomotion may entail SRF of greater or lesser magnitude, directly affecting the intensity of the load born by the joints (Schmitt, 1998, 2003a; Schmitt and Hanna, 2004). Similarly, SRF is also modulated by locomotor speed (Bertram, 2004; Schmitt and Lemelin, 2004; Hanna et al., 2006). Therefore, differing locomotor strategies may result in different levels of DJD as a result of the varying mechanical stress associated to each of the strategies considered. In this thesis, habitat (and support) use and speed were studied as two of the main strategies that could entail variability of DJD expression.

The two main factors that reflected mechanical stress related to locomotor behaviour studied in this thesis were locomotor adaptation and locomotor strategy. However, other factors that are not a direct consequence of locomotor behaviour could also determine stress on a joint. Body mass was included as a non-locomotor factor related to mechanical stress. Despite the fact that primates of different body mass tend to perform different types of locomotion (Fleagle and Mittermeier, 1980; Gebo and Chapman, 1995a; Fleagle, 2013), the potential effect of body mass on joint degeneration is rather straightforward. This study focuses on the weight-bearing joints of the primate skeleton and thus, these were expected to be directly affected by the magnitude of the weight they bear. The force of weight is directly related to body mass and, therefore, the joints of larger primates would experience greater weight, compared to smaller primates. Consequently, body mass was studied as an important factor of mechanical nature that could potentially entail different patterns of DJD expression.

The potential effect that locomotion and other mechanically related factors could have on DJD expression in weight-bearing joints is important but cannot be considered in isolation. The primate body exhibits a set of morphological adaptations that can help deal with some of the forces briefly described. For instance, differences in musculature arrangements and function not only allow certain movementes, but have a determining role in the coupling of the action-reaction forces on the weight-bearing regions of the primate body (Larson, 1998; Schmitt, 1998). Moreover, musculature may also have a significant effect in terms of dealing with the stress, serving as a potential minimizer of load on joints (Biewener, 1990; Thorpe, 1997). Further structures may also be present in a joint that help deal with stress, such as the intervertebral discs of the spine or the menisci and ligaments of the knee joint (Norkin and Levangie, 1992; Gosling et al., 2008; Gebo, 2014). Skeletal differences could also play an important role, such as different joint dimensions, elongated skeletal elements (Gebo and Sargis, 1994; Nakatsukasa, 1994; Schmidt, 2011) or even different morphologies of the bony elements in the surrounding area of a joint that diminish stress (Schmitt, 2003b). Functional adaptation plays a key role in the efficiency of a joint to deal with forces and the associated stress and should not be overlooked in the study of DJD.

Previous research on non-human primates pointed out that DJD was unlikely to respond to only one factor. It is plausible that other factors, not necessarily related to mechanical stress, could significantly contribute to DJD development.

Consequently, age and sex were also considered in terms of DJD prevalence among primates.

The present study uses a holistic approach to examine the expression of DJD in non-human primates, integrating information of different nature in the study of DJD. Even though the materials used were skeletal remains of non-human primates and the data collected were purely osteological, information on locomotion, ecology, anatomy, physiology and biomechanics was used in order to achieve a better understanding of DJD in primates. The results obtained may have implications and provide greater insights into the study of extant and extinct primates, including humans and their ancestors, potentially providing information on how a primate would have moved and what type of habitat it would have exploited.

1.1 Objectives and hypotheses

This piece of research explores the nature of DJD in non-human primates to determine which would be the main drivers of its expression, with particular focus on locomotor behaviour. However, other factors are also considered and their combined action as DJD causal factors is investigated. As a result, three main objectives were pursued in the present research.

Objective A: Assess the role of mechanical stress as a driver of DJD

In this study it is projected that DJD is the result of mechanical stress acting on a joint. Therefore, different mechanically related factors were considered: locomotor adaptation, locomotor strategy and body mass, the latter being a factor that is not directly related to locomotor behaviour but is closely related to the forces acting on the joints, ultimately, shaping the loads that these joints would bear. As a result, some of the main research questions addressed in this research involved these three factors (Q1, Q2 and Q3).

Q1: Do primates with different locomotor adaptation exhibit different patterns of DJD expression?

> H_0: All primates exhibit similar patterns of DJD expression, regardless of their locomotor adaptation.
>
> H_1: Primates of different locomotor adaptation exhibit different patterns of DJD expression.

Q2: Do primates that perform different locomotor strategies associated with SRF of different magnitude exhibit different patterns of DJD expression?

> H_0: There are no differences in DJD expression among primates that perform different locomotor strategies.
>
> H_1: There are differences in DJD expression among primates that perform different locomotor strategies, with those species performing strategies associated to greater SRF showing greater severity levels of DJD.
>
> H_2: There are differences in DJD expression among primates that perform different locomotor strategies, with those species performing strategies associated to lower SRF showing greater severity levels of DJD.

Q3: Do larger sized primates exhibit greater severity levels of DJD than smaller sized primates?

> H_0: All primates exhibit similar levels of DJD, showing no apparent connection between body mass and DJD expression.
>
> H_1: Larger species exhibit greater levels of DJD than smaller primates, showing a connection between body mass and DJD expression.
>
> H_2: Smaller species exhibit greater levels of DJD than larger primates, showing a connection between body mass and DJD expression.

Objective B: Assess the role of non-mechanically related factors as drivers of DJD

It is unlikely that only mechanically related factors would determine DJD expression in the primate skeleton, especially considering results from previous research, where no causation of the disease was clear when considering only one factor. As a result, the effect of non-mechanically related factors, such as age and sex, were taken into account (Q4). Age has been a common factor associated with DJD, as the disease could be aggravated by repetitive cumulative use of the joint. Sex could entail differences in body mass due to dimorphism (DeRousseau, 1988) as well as hormonal differences (Ethier and Simmons, 2008).

Q4: Are non-mechanically related factors related to DJD expression?

> H_0: Non-mechanically related factors are not related to DJD expression.
>
> H_1: Age is related to DJD expression, contributing to its expression.
>
> H_2: Sex is related to DJD expression, contributing to its expression.

Objective C: Assess the combined role of all the factors as drivers of DJD

The potential factors that could be involved in DJD development have been considered separately up until this point. The final stage of this study was to see to what extent all of the aforementioned factors contributed to DJD development and to see if there were any additive effects among such factors in terms of DJD expression for non-human primates (Q5).

Q5: Are more than one of these factors involved in variability of DJD expression in non-human primates?

> H_0: DJD expression relates to a single causal factor.
>
> H_1: DJD expression relates to several causal factors, all of them mechanically related.
>
> H_2: DJD expression relates to several causal factors, none of them mechanically related.
>
> H_3: DJD expression relates to several causal factors, both mechanically and non-mechanically related.

1.2 Outline of the thesis

This thesis is divided in three distinct sections. The first section includes chapters two, three and four and presents the context necessary to start assessing DJD in non-human primates. The second section consists of chapter five, which presents the materials recorded and the methodology used to obtain the necessary information in order to assess the three main objectives and the corresponding questions. The third section includes chapters six through nine and presents all the results obtained with the corresponding discussions in each of the chapters. The first of these chapters provides an overview of DJD distribution and suggests different factors that could be linked to its expression. These factors are treated separately in the following two chapters, composing the more exploratory portion of the isolated variables. This section culminates in the last of the results and discussion chapters, which brings together all factors, investigating the multifactorial context of DJD. This section is followed by a tenth chapter, where a general discussion and the conclusions are presented. There are two appendices with further data at the end.

Section 1: Context

Chapter 2: *Weight-bearing joints, growth and degeneration*. This chapter presents the osteological background. It includes basic information on bone composition, metabolism and joint maintenance principles as well as definitions of the main weight-bearing joints in non-human primates. Principles on DJD are found in this chapter with a brief summary of the research published on DJD in non-human primates. A final section deals with skeletal growth and ageing, important in this thesis from a methodological perspective.

Chapter 3: *Primates in context*. This chapter presents the primatological background, defining primates, their taxonomy and origin. A general overview on the ecology of extant primates is presented, elaborating on forest architecture and the implications for moving primates. Variability of locomotor behaviour is presented, providing definitions of the main locomotor adaptations seen in primates and some morphological aspects related to locomotion are introduced.

Chapter 4: *Biomechanics of primate locomotion*. This chapter presents the principles of mechanics applied to primatology and, particularly, to the study of primate locomotion. It introduces the characteristics of the primate quadrupedal gait and the mechanics of the limbs during quadrupedalism, including the definition of load and SRF as well as the mechanisms of reduction of forces adopted by primates. The mechanical effect of body size and speed is further developed in this chapter, as well as the effect of support use on SRF.

Section 2: Materials and methods

Chapter 5: *Materials and methods*. This chapter introduces the materials recorded for this thesis, presenting the joints recorded, the list of taxa considered and their provenance. The methodology used to record DJD is presented as well as the rationale for determination of support deformability based on support use information gathered from the literature. The equations developed for body mass estimation are introduced as well as the formulae used for the calculations of pressure on the shoulder and knee joints. Lastly, the method used for assessment of relative age is presented.

Section 3: Results and discussion

Chapter 6: *Distribution of DJD across the primate skeleton*. This chapter describes the distribution of DJD across the primate skeleton, evidencing some deviations from a generalised primate pattern of DJD distribution and presenting possible factors that may have contributed to this variability. It is established that differences in locomotor behaviour, body mass and longevity may contribute to DJD development. These factors are evaluated separately in the following two chapters.

Chapter 7: *Locomotor behaviour and DJD: a mechanical approach to joint degeneration*. This chapter presents a comparison of the distribution of DJD among groups of primates based on different aspects of locomotor behaviour. Locomotor adaptation and locomotor strategies showing differences in speed and in habitat use were tested as sources of variability in DJD. These analyses conclude that general locomotor behaviour and locomotor strategy are important factors involved in joint degeneration. However, not all the variability observed in DJD across primates could be explained by differences related to locomotion.

Chapter 8: *Effect of body mass and age on DJD*. This chapter focuses on the effects of body mass and age on DJD, the other two factors recognised as potential causes of DJD development in chapter 6. Significant correlations with DJD were found for both of these factors. Sex, as a modulator of body mass, did not seem to be related to differences in DJD expression. The potential effect of both body mass and age seemed to be significant but only partial explanatory factors.

Chapter 9: *Models of DJD development at the limbs of quadrupeds and suspensory primates: a multivariate approach.* This last chapter of results and discussion brings together the variables treated in the previous two chapters in an attempt to obtain statistical models to observe the relationships between variables in relation to DJD development in two groups of primates. These models confirmed the multivariate nature of DJD and exhibited some of the main interactions between variables involved in joint degeneration, highlighting the importance of both mechanically and non-mechanically related factors.

Chapter 10: *General discussion and conclusion*. This last chapter summarises all the conclusions reached in chapters six through nine in order to assess the main objectives presented in this introduction. A synopsis of the main findings is provided and ideas for future research are presented.

CHAPTER 2: WEIGHT-BEARING JOINTS, GROWTH AND DEGENERATION

2.1 Bone: composition, metabolism and maintenance

Bone has two main functions in the skeleton concerning locomotion. Firstly, bones of terrestrial vertebrates provide support and stability bearing the forces resulting from gravity and from the interactions with the surrounding environment and, secondly, bones act as levers and transform the forces produced by the muscles into movement (Thorpe, 1997; Fleagle, 2013).

The capacity of a bone to bear external forces is determined by its internal structure and its overall morphology (DeRousseau, 1988; Fajardo and Müller, 2001; Ethier and Simmons, 2008). Therefore, differences in bone morphology among primates (external and internal) are found according to different mechanical requirements (Houssaye et al., 2016). As a biomaterial, bone is light and strong, it can adapt to its functional demands and it repairs itself (Humphrey and Delange, 2004).

The type of bone that gives support and strength to the epiphyses is trabecular bone, where the trabeculae are arranged to withstand compressive or tensile stress (Frost, 1990; Currey, 2003; Ruff et al., 2006). It is found in the vertebrae and the epiphyses of the long bones (Martin et al., 1998; Ethier and Simmons, 2008; White et al., 2012), giving strength but at the same time providing a greater area for metabolic reactions (Waldron, 2008). The mechanical properties of trabecular bone are complex and mainly depend on the spatial disposition of the trabeculae as well as on the properties of the bone matrix (Ruff et al., 2006). Arrangements of the trabeculae differ depending on the mechanical requirements of each specific bone, and, despite the fact that the functional adaptability of trabecular bone is not yet fully understood, there is at least some response to loading (Currey, 2012). This is observed in primates, despite the lack of correlation with all primate loading models (Fajardo and Müller, 2001; Schilling et al., 2013; Stephens et al., 2016).

2.1.1 Bone tissue

Bone is a connective tissue and, as such, it consists of a cellular portion embedded into an extracellular matrix (e.g., Norkin and Levangie, 1992; Humphrey and Delange, 2004). The matrix is characterised by a combination of an organic component (mainly collagen) that gives the tissue flexibility and an inorganic component (hydroxyapatite and other ions), which gives strength to the bone. Differences in the proportion between these two fractions determine the mechanical properties of bone (Currey et al., 2001; Currey, 2012).

There are a good number of studies concerning bone tissue composition in humans (e.g., Humphrey and Delange, 2004; Ethier and Simmons, 2008; Ross and Pawlina, 2011). Other studies in different mammals (e.g., Bonewald, 2011; Houssaye et al., 2016) and non-human primates (Burr, 1980; Fajardo and Müller, 2001; Ryan and Ketcham, 2002; Carlson and Pickering, 2004; Schilling et al., 2013; Stephens et al., 2016) show a few differences in terms of bone basic composition and reactivity. For example, there is interspecific variability in the structure of the trabecular bone in primates related to locomotor behaviours (Fajardo and Müller, 2001; Ryan and Ketcham, 2002). Other factors, such as bulk bone mineral density (BMD) and hormonal regulation, or bone volume fractions also show interspecific variability (Ryan and Ketcham, 2002; Carlson and Pickering, 2004; Bonewald, 2011). However, despite these differences, bone reactivity to strain and stress is similar so that the basic structural and mechanical properties are the same across most primate species (Burr, 1980; Fajardo and Müller, 2001).

2.1.2 Bone remodelling and pathology

Bone, as any living tissue, is in constant activity. Remodelling processes consist of bone removal and new bone depositions in order to repair defects on the tissue, adapt to strain or release calcium if necessary for other metabolic processes. This process is known as bone turnover and is divided in four stages: activation, resorption, reversal and formation and is conducted by the cellular portion of bone tissue (Waldron, 2008).

Some types of bone pathology are coupled with the disruption of the normal balance of bone turnover, so bone is either formed or lost, leading to a disease of erosive or proliferative nature (Waldron, 2008). This is often accompanied by abnormal tissue formation, such as inflammatory or tumour tissue, which may replace normal bone depositions (Aufderheide and Rodríguez-Martín, 2011).

Alterations of the remodelling cycle of bone produce changes in the density of the bone as a result of excessive bone loss or production. There is a positive correlation between strength of the tissue and bone density (Ethier and Simmons, 2008) and, therefore, any type of loss or production of bone tissue may entail significant variation in mechanical properties, increasing the risk of fracture and other possible degenerative processes (Waldron, 2008), such as degenerative joint disease (DJD).

2.1.3 The rate-of-living theory: metabolic rate, body mass, lifespan and bone turnover

Bone remodelling is a metabolism-dependant process that relies on cellular activity and, therefore, differences in metabolic rate might have an important effect on the prevalence of metabolic disorders of bone remodelling among different species of vertebrates. Bone turnover rates have not been established for all non-human primates. However, higher metabolic rates could potentially entail an acceleration of bone remodelling and, therefore, degenerative changes would be expected to be faster. This is an important consideration for this thesis, as it is based on a comparative study including different species with different lifespans (Harvey and Clutton-Brock, 1985; Pickering et al., 2015) and, possibly, variable metabolic rates.

Prior research has established a significant influence of mechanical input concerning bone remodelling (Biewener, 1991). However, metabolically driven remodelling is also an important factor in bone turnover and this type of bone remodelling occurs regardless of the surrounding conditions and level of activity (Bouvier and Hylander, 1996). Therefore, overall levels of bone turnover are determined by different factors among which are mechanical stress and metabolically driven remodelling but other factors that also play a significant role are still poorly understood (McFarlin et al., 2008).

The overall metabolic rate of an animal is in general terms influenced by several factors, including environmental temperature and level of activity (Genoud, 2002; Hanna et al., 2008). The basal metabolic rate (BMR) is free of these extrinsic factors and is often measured as oxygen consumption. The surface area of the lungs scales isometrically (in the same proportion) to body size (Conroy, 1990), consequently correlating basal metabolic rate and body size. In fact, BMR of mammals is mainly determined by body mass, following a specific equation, known as the Kleiber's equation (Martin, 1990; Genoud, 2002):

$$BMR = kW^{0.75}$$

Equation 2.1

(where k is the allometric coefficient and W the weight).

The BMR of the primate species for which such data are available fall within the range observed for mammals and its variability depends mainly on differences in body mass. However, the amount of mass-independent variability of BMR is considerable (Genoud, 2002). Furthermore, strepsirhines and haplorhines (see Chapter 3) exhibit lower BMR than expected considering their body mass, despite the haplorhines being closer to their expected levels, suggesting that BMR may undergo adaptive changes (Müller, 1985). Several explanations for the lower BMR in primates have been proposed. Firstly, it has been argued that the lower BMR of primates may be an adaptation to hot climates, as lowering their overall BMR decreases their body temperature, avoiding overheating (Müller, 1985; Kurland and Pearson, 1986). Other hypotheses work around differences in dietary habits, stating that species feeding on meat, nuts or grass tend to have higher metabolic rates (Kurland and Pearson, 1986). However, this relationship between BMR and dietary quality was found to be non-significant among primates (Ross, 1992). Only partial information is available concerning BMR among primates and further research is needed in order to better understand the mass-independent variability of BMR among the order (Genoud, 2002). However, what seems to be consistent is that primate values of BMR are generally lower than would be expected only considering body mass, although they are still within the mammal range and are mainly influenced by body mass.

Bigger animals, according to Kleiber's equation, tend to exhibit lower BMR. This, coupled with the observation that bigger animals have longer lifespans, led to the **rate-of-living theory** of ageing, which establishes that individual's with faster metabolisms live shorter lives than individuals with slower metabolisms (Hulbert et al., 2007). This could be a result of the free radical production coming with normal oxygen consumption, as such radicals damage biomolecules that lead to ageing processes (Pérez-Campo et al., 1998). Therefore when metabolism is faster, so is the consumption of oxygen and the production of free radicals, accelerating ageing.

Molecular data have shown that, however approximate, the rate-of-living theory of ageing is not perfectly precise in terms of explaining maximum lifespan. Especially as the fatty acid composition of the cell membrane varies among species and contributes towards differences in metabolic rates, ultimately modulating the maximum lifespan of an animal (Hulbert et al., 2007). Furthermore, increased proteasome and immunoproteasome activity in skin-derived fibroblasts of non-human primates has also been linked to longer lifespans (Pickering et al., 2015). These examples show that, despite BMR being a well-studied factor in relation to lifespan, the maximum lifespan of a species is partially determined by further molecular factors and not all of them are fully understood.

DJD is often associated with advanced age (DeRousseau, 1985; Rogers et al., 1987; Lovell, 1990; Knüsel et al., 1997; Weiss and Jurmain, 2007). Therefore, it would be logical to assume that animals that live longer would exhibit higher prevalence and/or greater severity of DJD towards older ages in comparison with animals with shorter lifespan. Based on the rate-of-living theory smaller animals live shorter but their BMR is much higher than the BMR of larger animals, also applicable to primates even though their BMR is lower than would be expected from their size (Genoud, 2002). Considering that bone turnover rate is partially determined by metabolic processes, differences in BMR could be reflected in differences in bone turnover and, therefore, bone maintenance cycles would be accelerated in smaller primates, compensating for the shorter lifespans in terms of cumulative bone resorption-formation along the animal's life.

Burr (1992) studied bone turnover in macaques and humans with the aim of establishing if these non-human primates were good osteological models for humans at a microscopic level. He observed that, not only did bone turnover in macaques during growth not depend on body weight, but it was much slower than in humans. These findings question the direct relationship between BMR and bone turnover in primates. However, there is no clear relationship for the whole of the skeleton, as only the femur was assessed and, moreover, comparisons during growth are not the best suited to draw generalisations, as ontogeny occurs in different patterns for different regions of the body, and such patterns also differ among primates (Garber and Leigh, 1997; Marroig and Cheverud, 2001; Mitteroecker et al., 2004; Ruff et al., 2013; Burgess et al., 2016). In addition, differences in development can be determined by genetic, behavioural and environmental factors (Ruff et al., 2013).

Nutritional studies have pointed out that food restriction in both humans and macaques slows skeletal growth and development, ultimately, decreasing the rate of bone turnover (Lane et al., 1995). In fact, differences in dietary intakes can affect turnover rates not only at a skeletal level, but also at a molecular level. For example, in an experiment with n-3 fatty acid deficient rhesus macaques, who do not synthesise enough docosahexaenoic acid (a phospholipid present in the cerebral cortex and retina), after dietary introduction of fatty acids for the n-3 deficient macaques, the turnover rate producing such phospholipid increased as soon as one week after ingestion (Connor et al., 1990). These results show that turnover rates can be highly influenced by dietary habits and restrictions. Considering that human and non-human primates differ in dietary habits with consequences on micronutrient intakes (Milton, 2003), differences in turnover rates could be due to these differences in nutrient intakes, making humans a not very good species for comparative purposes in order to understand primate metabolic processes.

This thesis is a comparative study among primates that includes very different species, thus facing differences in lifespan among the different groups of primates considered. It is possible that bone turnover rates differ among primate species in relation to differences in mechanical stress or body mass and consequently to different BMR and lifespan. However, this relationship is unclear, as there seem to be many factors contributing to differences in lifespan as well as in bone turnover rate. It is for this reason that comparisons among all the taxa considered were avoided in this study and different sub-samples were treated and analysed independently, in order to compare taxa of similar lifespans and, thus, neutralise the potential differences in DJD expression that come from differences in lifespan and bone turnover rate.

2.2 Weight-bearing joints: function and morphology

2.2.1 Types of joints: joint design and function

Joints serve a dual function: enhancing mobility and providing stability to the skeleton. The morphology of a joint determines its function (Ruff, 1988; Whitehead et al., 2005; Fleagle, 2013; Dunham et al., 2017). Hence, joints that serve a single function tend to be simpler in design than those joints that serve a more complex purpose. In general terms, joints can be classified as synarthrodial and diarthrodial joints (Norkin and Levangie, 1992).

Synarthrodial joints are connected by interosseous fibrous or cartilaginous connective tissue. These joints can be immoveable (fibrous joints), such as a cranial suture, or partially moveable (cartilaginous joints), such as the pubic symphysis or the intervertebral joints. In **diarthrodial (or synovial)** joints the articular facets are not joined by connective tissue but are covered in hyaline cartilage. The epiphyses of the bones lie within a joint capsule and are submerged in synovial fluid, which reduces friction between the articular facets (Norkin and Levangie, 1992).

Diarthrodial joints are designed primarily for mobility although many of them also provide stability, as stability is first needed in order to perform any movement (Ankel-Simons, 2007). Furthermore, joints are continuously subjected to forces that result from habitual movements and activities producing stress, the intensity of which shapes the particular morphology of the joint and associated structures (Badoux et al., 1974). Consequently, diarthrodial joints have accompanying structures that help deal with intense mechanical stress. For instance, ligaments or tendons of the surrounding musculature avoid separation of the elements by passive tension and aid in absorbing potentially damaging shock and store energy (Alexander, 1991; Thorpe, 1997; Aerts, 1998). There are also structures within some joints, like articular disks that prevent excessive compression (Norkin and Levangie, 1992; Aiello and Dean, 2006; Schwartz, 2007; Gebo, 2014).

The mechanical stress acting on joints is sometimes coupled with strain (defined as changes in the shape of the load-bearing structure). The nature of loads (stress) varies depending on the **magnitude** of the force and the **area** onto which this force is applied. Thus, a joint can be subjected to tensile stress (produced by two forces of similar magnitude acting along the same plane but in opposite directions), compressive stress (produced by two forces acting along the same plane towards each other) or shear stress (produced by two forces acting in opposite but parallel directions to each other) (Fig. 2.1) (e.g., Badoux et al., 1974; Norkin and Levangie, 1992; Humphrey and Delange, 2004). The overall function of a joint depends on the function of each of the bones forming it and of the forces each bears. Therefore, the malfunction or disruption of one of the parts of the joint (due to injury, age or disease) has an effect on its overall performance. As a consequence, joints with several elements that bear different types of forces are more likely to suffer modifications than simpler joints, as they are subject to more wear and tear (Norkin and Levangie, 1992).

Figure 2.1 Representation of the different types of forces, stress and strain. On the left there is a representation of: a) tensile forces (horizontal centred arrows) with the corresponding strain (represented in a dotted line, ΔL) and b) compressive forces (arrows) with the corresponding compressive strain (dotted line, ΔL). On the right there is a representation of shear forces (arrows) and the corresponding strain (modified from Norkin and Levangie, 1992)

The anatomy of an animal is highly influenced by body size, which plays a key role in ecological adaptation (Fleagle, 2013). Primates in particular vary considerably in size across species and it would be logical to assume that larger individuals have larger joints. Considering that stress depends on the force applied to an area, the effect of differing body size would be neutralized by the differing joint size. This would only apply if body and joint size scaled isometrically. However, this is not the case, as joint morphology responds to a multifactorial context where locomotion and interaction with the environment are two of the main drivers of adaptation for joints and for the postcranial musculoskeletal system as a whole (e.g., Diogo and Wood, 2013; Fleagle, 2013; Kardong, 2015; Molnar et al., 2017).

The shape of a joint is therefore partially determined by the forces it must bear resulting from the animal's activity, but it also varies depending on the movement a joint must perform. For example, orangutans have relatively small femoral and tibial diaphyses for their body mass, which indicates a lesser degree of use of the hindlimbs compared to other primate species thus decreasing the mechanical stress on the bones. However, the relative size of the hindlimb joints is larger than expected compared to other species, which responds to the need of a greater joint excursion, particularly at the hip, where great levels of abduction are performed (Ruff, 1988). Furthermore, locomotor adaptation is strongly influenced by a species' habitat exploitation (Napier, 1976; Fleagle, 2013) and these differences in locomotor adaptation are reflected in differences in skeletal morphology (more on Chapter 3).

2.2.2 The vertebral column

The vertebral column or spine, with its corresponding ligaments and associated musculature form the central body axis of vertebrates, becoming a vital biomechanical component of the locomotor apparatus (Badoux et al., 1974). The body's central axis in terrestrial quadrupeds has a propulsive role, but also a weight-bearing one. A compromise between the propulsive and weight-bearing character of the spine is reflected in its morphology. In fact, the vertebral column at the moment of birth is a system of rigid diaphyses with several adaptive zones and the final shape of the epiphyses is determined by the intensity of stress produced by

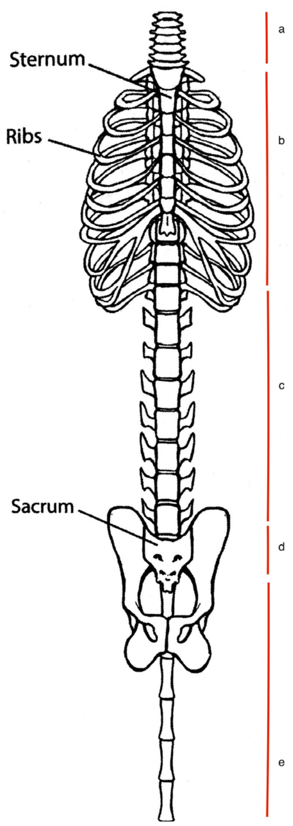


Figure 2.2 Representation of the different parts of the primate spine: a) cervical vertebrae, b) thoracic vertebrae, c) lumbar vertebrae, d) sacral vertebrae and e) caudal vertebrae (modified from Gebo, 2014)

gravitation and locomotion during growth (Badoux et al., 1974).

The spine is not arranged as a straight line. Due to its weight-bearing character, it is subjected to forces resulting from gravity. Terrestrial mammals support their weight on the area formed by the outer margins of their feet. Therefore, contrary to what is seen in humans (bipeds), who must keep their centre of gravity within a very small area of support and need a double curvature of the spine to keep balance, non-human primates have a very long single curvature (kyphosis) in order to withstand the forces resulting from gravity (Thorpe, 1997).

The primate spine includes five distinct regions, exhibiting morphological and functional differences: cervical, thoracic, lumbar, sacral and caudal (of variable extend and number of elements) (Fig. 2.2) (Aiello and Dean, 2006; Ankel-Simons, 2007; Fleagle, 2013; Gebo, 2014). The spine is thus composed of an aggregation of vertebrae; each of which comprises a system of several joints. Synarthrodial joints are found between vertebral bodies. These joints provide limited motion with adjacent vertebrae sharing a cartilaginous structure, an intervertebral disc that deals with high compressive forces (Fig. 2.3). The apophyseal joints, projecting articulations between adjacent vertebrae, are highly mobile synovial joints (Fig. 2.3) (Norkin and Levangie, 1992). This system of joints makes the spine stable and flexible simultaneously. The degree of movement of the spine is controlled by the positioning of the three points of articulation between two adjacent vertebrae (the vertebral body and the two apophyseal joints) (Ankel-Simons, 2007).

Figure 2.3 Representation of the different parts of a vertebra of a macaque (left), with the different joints: vertebral bodies (in the image also called centrum) and the apophyses (articular facets in the image). On the right there is a representation of movements allowed between vertebral bodies and the direction of forces (arrows) (modified from Gebo, 2014 and Norkin and Levangie, 1992)

The **cervical region** is rather conservative in terms of morphology and number of vertebrae in most mammals (Conroy, 1990; Fleagle, 2013). The vertebral bodies are square and are saddle-shaped cranially and caudally (Fig. 2.4) (Ankel-Simons, 2007). With the exception of the first two cervical vertebrae (atlas and axis), which act as pivoting points for the movements of the head, the arrangement of the cervical spine allows some dorsal sagittal bending but very little or no ventral bending and no rotation (Norkin and Levangie, 1992; Ankel-Simons, 2007). The apophyses are located laterally rather than dorsally to the adjacent vertebral bodies, which limits the range of movement for this region (Schwartz, 2007; Gebo, 2014). An exception is *Tarsius* sp., where the apophyseal joints lie dorsally in parallel with the adjacent vertebral body, which allows extensive neck rotation, as they are able to perform rotations of nearly 180º (Ankel-Simons, 2007; Gebo, 2014).

The cervical region is followed caudally by the **thoracic region**. The bodies of the thoracic vertebrae are typically heart-shaped and are characterised by the presence of the articular facets for the ribs (Fig. 2.4). Differently to the cervical vertebrae, the apophyses are located dorsally to the adjacent vertebral body. Therefore, seen from a cranial or a caudal view the apophyses are flat above the vertebral body, with the exception of the first thoracic vertebra, where the cranial apophyses are cervical-like (Ankel-Simons, 2007; Schwartz, 2007). The particular positioning of the apophyses is what enables the spine to perform the rotational movement, always accomplished at the thoracic spine, making this one of the most mobile regions of the vertebral column (Fleagle, 2013). However, rotation does not always occur throughout the rib-bearing vertebrae. The caudal apophyses of one particular thoracic vertebra (often the last rib-bearing vertebra, but it can be a more cranial one in some primate species) experience a change in orientation. They angle steeply to the mid-sagittal plane, so the articular facets face the adjacent vertebral body laterally and it entails an important functional change. This happens abruptly and the vertebrae positioned caudally from this *transitional thoracic vertebra* do not perform rotational movements anymore, but instead they are able to perform dorso-ventral sagittal bending (Ankel-Simons, 2007). Thus, it is possible to differentiate between the morphological thoracic vertebrae (rib-bearing vertebrae) and functional thoracic vertebrae (those able to perform rotational movement).

Figure 2.4 Representation of the different types of vertebrae of a macaque as a non-human primate example (cervical, thoracic, lumbar, sacral and caudal) (after Gebo, 2014)

The vertebrae of the **lumbar region** lack rib attachments but have very large transverse processes in order to accommodate the deep back muscles in charge of spine extension and flexion (Fig. 2.4) (Fleagle, 2013). These transverse processes form from the vertebral bodies in most primate species; however, in apes, large cebids and some fossil lemurs they arise from parts of the vertebral arches (Ankel-Simons, 2007; Fleagle, 2013). The lumbar vertebrae have laterally and inclined apophyses that form a narrow angle with the mid-sagittal plane (Ankel-Simons, 2007). This positioning of the lumbar apophyses permits the dorso-ventral sagittal bending of the lumbar vertebrae (flexion and extension of the spine).

The overall shape of the lumbar vertebrae differs in Hominoidea. Their lumbar vertebrae experience an increase of the vertebral diameter relative to vertebral length. In contrast, monkeys and strepsirhines exhibit a greater increase in vertebral length relative to the vertebral diameter (Ankel-Simons, 2007; Gebo, 2014).

The position of the lumbar apophyses prevents lateral rotation of these vertebrae. Moreover, some primate species have caudal bony projections posterior to the apophyses that lock the cranial apophyses of the following vertebra (Gebo, 2014). Cebids have very broad dorsal spines, which reinforce lumbar stiffness by leaving very little space between vertebrae on the dorsal aspect therefore limiting the range of movement (Ankel-Simons, 2007). Other vertebral adaptations are expected in the lumbar spine due to differences in movements and postures (e.g., Shapiro, 2007; Granatosky et al., 2014; Russo and Williams, 2015).

The sacral and caudal regions are highly diverse among the primate order. However, they are not considered in this thesis and thus no details on anatomical or functional descriptions are provided here. The aforementioned descriptions explain the nature of the movements of the spine. However, the movements associated to the vertebral column (i.e. flexion, extension and rotation) are only possible with the aid of the girdles (Aiello and Dean, 2006) and thus, movement should not be considered in one isolated body compartment with no consideration of the rest.

2.2.3 The limbs

All the joints of the limbs considered in this thesis are synovial, highly mobile joints. Primates are tetrapods and thus have two sets of limbs: forelimbs and hindlimbs (Fleagle, 2013). These limbs connect to the axial skeleton by means of girdles (thoracic and pelvic), encompassing the movement of the axial skeleton (for the purposes of this thesis the vertebral column) and the limbs (Aiello and Dean, 2006; Ankel-Simons, 2007).

The primate **forelimb** is divided into four different segments: the thoracic girdle (shoulder), arm, forearm and hand (Norkin and Levangie, 1992; Aiello and Dean, 2006; Fleagle, 2013). The thoracic girdle comprises the clavicle and the scapula, a triangular shaped bone containing the glenoid fossa, which articulates with the humerus, the only bone of the arm, in a highly mobile ball and socket synovial joint (Ankel-Simons, 2007). Crossing this joint are most of the propulsive muscles of the forelimb (Fleagle, 2013). The forearm comprises the radius and the ulna, which articulate with the humerus via a hinge joint (Gebo, 2014). Movements here include flexion and extension of the elbow but there is also pronation and supination of the forearm (Gosling et al., 2008). The latter is achieved through the movement of the radius around the ulna (Fig. 2.5), this movement probably being an adaptation to arboreality and climbing activities that is prevalent in primates (Fleagle, 2013; Gebo, 2014). Distally the radius articulates with the carpal bones. The articular surface of the distal radius is relatively bigger than the distal the ulna, which is never in direct contact with the carpal bones (Fleagle, 2013). The more distal joints of the forelimb (those in the hand) are not included in this thesis and, thus, are not considered further.

Figure 2.5 Representation of an example of pronation vs. supination, with the radius moving over the ulna (after Ankel-Simons, 2007)

The primate **hindlimb**, similarly to the forelimb, is divided into different segments: pelvic girdle, thigh, leg and foot (Norkin and Levangie, 1992; Aiello and Dean, 2006; Fleagle, 2013). The pelvic girdle is composed of the convergence and fusion of three bones (ilium, ischium and pubis), which form the pelvis (Schwartz, 2007; Gebo, 2014). The mammalian pelvis serves many functions and, in contrast to the shoulder girdle, it is not particularly mobile (Fleagle, 2013). Located on the pelvis is the acetabulum, into which the head of the femur articulates, forming the hip joint (Norkin and Levangie, 1992). Similarly to the forelimb, around this joint are the main hindlimb propulsive muscles (Fleagle, 2013). The distal femur articulates with the tibia at the knee joint. This is a modified, complex hinge joint with a strong weight-bearing function and it has a high number of associated structures giving stability to the joint (Gosling et al., 2008; Gebo, 2014). The main movements at this joint are flexion and extension which would make it a uniaxial joint, but it is also able to perform some degree of rotation, making it a biaxial joint (Gebo, 2014). In the tendon of the extensor musculature lies the third bone of the joint: the patella (a sesamoid bone) (Aiello and Dean, 2006; Ankel-Simons, 2007; Fleagle, 2013). Distally, the tibia forms the main articulation with the talus, which conform the ankle joint, where flexion of the foot (dorsiflexion and plantarflexion) is performed (Ankel-Simons, 2007; Gosling et al., 2008; Fleagle, 2013; Gebo, 2014). Inversion and eversion of the foot takes place at more distal joints of the foot, despite being executed by the leg musculature (Gosling et al., 2008).

The joints of the limbs among primates are similar in structure but present certain adaptations in different groups. Most of the adaptations observed in the primate limbs, however, are due to differences in locomotor behaviour and habitat exploitation (e.g., Gebo and Sargis, 1994; Fleagle and McGraw, 1999; Fleagle, 2013; Dunham et al., 2017) (more information on Chapter 3).

2.3 Degenerative joint disease

Changes in the integrity of the cartilage found on the surfaces of joints of vertebrates (Fig. 2.6) often lead to joint disorders, such as DJD (Rogers *et al.*, 1987), defined as a

> *"noninflamatory, chronic, progressive pathological condition characterised by the loss of joint cartilage and subsequent lesions resulting from direct interosseus contact within diarthrodial joints" (Aufderheide and Rodríguez-Martín, 1998: 93).*

DJD is often classified as an idiopathic disorder, as in 80% of the cases reported in humans it is not possible to attribute an apparent cause for its development (Aufderheide and Rodríguez-Martín, 2011). A common characteristic of DJD is new bone formation as a consequence of a lesion affecting the cartilage, exposing the bone surfaces of the joint against each other during movement.

Researchers have used different traits in order to record DJD (e.g., Rogers et al., 1987; Aufderheide and Rodríguez-Martín, 2011). However, three of the most commonly used diagnostic traits are osteophytes, porosity and eburnation. **Osteophytes** are ossifications of fibrocartilage or formations of new bone on the surroundings of the articular surface. Subchondral bone reactions may take place and usually consist of sclerosis of the bone, understood as hardening of the underlying bone. **Porosity** (or osteochondrosis) on the articular surfaces is usually linked to osteoarthritic processes, however its causes may be varied and the exact origin remains unknown (DeRousseau, 1988). **Eburnation** is a more advanced stage and it results from friction between two skeletal elements once the cartilage is too damaged or non-existent to protect the bone surface (Swales and Nystrom, 2015).

Figure 2.6 Representation of the structure of a synovial joint, showing the articular cartilage and the joint capsule (after Rogers et al., 1987)

One of the most common degenerative disorders reported in the archaeological record is **osteoarthritis (OA)**, a pathological disorder that involves all the tissues that form the synovial joints: synovium, bone and joint capsule (Buckwalter and Lane, 1997). In skeletal remains OA entails a change in the natural shape of the articular surface and is characterised by the formation of marginal osteophytes, eburnation, pitting of the joint surfaces and, in severe cases, alterations of the joint contour (Rogers et al., 1987; Knüsel et al., 1997; Jurmain, 2000). However, OA would only be considered present if either eburnation was found or with a combination of osteophytes and porosity simultaneously (Rogers et al., 1987; DeRousseau, 1988). Osteophyte formation and pitting of the articular surface in isolation are not diagnostic traits on their own for OA (Fig.2.7). OA has been considered a pathological expression of DJD, implying that other levels of DJD are expressed before it becomes a pathological condition and thus implying a continuous transition between its non-pathological and its pathological expression (DeRousseau, 1988).

DJD has a wide distribution on the human skeleton but it is particularly prevalent on weight-bearing joints, in which DJD is not only more severe but it also develops earlier in the individual's life (Cook et al., 1983; Hutton, 1987; Rogers et al., 1987; Knüsel et al., 1997; Jurmain, 2000; Aufderheide and Rodríguez-Martín, 2011). The

Figure 2.7 Pictures of examples of OA. Eburnation is visible on the head of a femur (circled on the left picture) and porosity and osteophytes are visible on the sterno-clavicular joint (right) (modified from Rogers et al., 1987)

spine is often a widely affected region (sometimes leading to vertebral fusion or ankylosis due to severe degeneration) and shows different patterns of distribution of DJD (Knüsel et al., 1997; Hukuda et al., 2000; Woo and Pak, 2014; Swales and Nystrom, 2015), although it is typically found in the regions with greater ranges of flexion (Rogers et al., 1987; Aufderheide and Rodríguez-Martín, 2011). Spinal DJD (SDJD) is particularly interesting because of it being a complex system of joints, combining synarthrodial (bodies) and synovial joints (apophyses) both of which are subject to degenerative modifications (Knüsel et al., 1997; Hukuda et al., 2000; Woo and Pak, 2014; Swales and Nystrom, 2015).

Previous research on human DJD has showed that apophyseal changes are likely to be under great effect of genetic control whereas osteophytosis of vertebral bodies is likely to be influenced by ageing processes (Woo and Pak, 2014). However, differences in stress as a result of movement are likely to have some effect on the prevalence and distribution of DJD (Hukuda et al., 2000).

In this project DJD is regarded as a general process, with no intention of diagnosing OA or other specific joint pathologies. Therefore, the indicators for DJD were considered individually (osteophytosis, porosity and eburnation) and treated with the same importance (more information in Chapter 5), focussing on the non-pathological expression of DJD.

2.3.1 DJD in non-human primates

Studies of DJD in non-human primates are scarce (Jurmain, 2000) compared to the number of studies based on humans. However, DJD is a well-established disease among the whole order (DeRousseau, 1985, 1988; Jurmain, 1989; Lovell, 1990; Rothschild and Woods, 1992, 1993; Jurmain, 2000; Nakai, 2001, 2003; Rothschild and Rühli, 2005; Nuckley et al., 2008; Swales and Nystrom, 2015).

The first studies on DJD in non-human primates started as reports on the skeletal health of particular groups of primates: captive rhesus monkeys (*Macaca mulatta*) (De Rousseau, 1985), free-ranging Gombe chimpanzees (*Pan troglodytes*) (Jurmain, 1989) and the Virunga mountain gorillas (*Gorilla beringei beringei*) (Lovell, 1990). In all cases osteophytosis and porosity were reported, but in different proportion and locations. Exceptionally high rates of DJD were present in the captive group of rhesus macaques, developed either at the first stages of adulthood or at advanced age but it did not seem common to develop DJD in middle age years (De Rousseau, 1985). Furthermore, DeRousseau (1985) observed an asynchrony between joints: SDJD appeared much earlier than DJD at the hip. DJD is also highly prevalent among mountain gorillas (Lovell, 1990), especially SDJD, with some cases of lumbar ankylosis (Fig. 2.8) (De Rousseau, 1985).

Comparative studies across taxa have been made on free-ranging apes and monkeys (both Old World and New World) (e.g., Rothschild and Woods, 1992, 1993; Jurmain, 2000; Nakai, 2001, 2003). These studies, however, were rather descriptive and specific causes for the disease were not tested. Instead, these were an attempt to draw parallelisms with the human expression of DJD despite reporting different patterns of prevalence of DJD. Chimpanzees, for example, presented low frequencies of DJD, compared to humans and other African apes. Asian apes had lighter expression of DJD compared to the African apes, with little evidence present in gibbons and extremely low frequencies in orangutans (Rothschild and Woods, 1992; Jurmain, 2000).

Figure 2.8 Image of the fusion of lumbar and sacral vertebrae in an adult female of Gorilla beringei beringei *from a ventral view (after Lovell, 1990)*

There are fewer studies including New World monkeys (Rothschild and Woods, 1993), which report DJD especially on the elbow and knee joints in free-ranging individuals. Captive New World monkeys showed not only higher prevalence of the disease but also different distribution of it, similarly to the results obtained by DeRousseau (1985).

Some general conclusions that can be drawn from these studies are that DJD in non-human primates is less prevalent than seen in humans (Rothschild and Woods, 1992, 1993; Jurmain, 2000) and that SDJD, similarly to humans, seems to be age-related in both captive (De Rousseau, 1985) and wild non-human primates (Lovell, 1990), despite lack of evidence supporting this conclusion in the small sample of chimpanzees studied by Jurmain (1989). It was also observed that captive primates were more affected by DJD than wild ones (DeRousseau, 1985; Rothschild and Woods, 1993). However, the most important conclusion is that there does not seem to be a species-specific aetiology for the disease (Rothschild and Woods, 1992).

Many interpretations and potential causal factors have been considered by different authors, such as phylogeny, ageing, body mass or infections (Cook et al., 1983; Rothschild and Woods, 1992, 1993; Jurmain, 2000). Locomotion, however, was rarely mentioned as a causal factor. The only systematic study that considers locomotion as a potential causal factor for DJD is DeRousseau's work (1988), a comparison of OA between the quadrupedal rhesus monkeys (*Macaca mulatta*) and gibbons

(*Hylobates lar*), a highly proficient brachiator; two species with slightly differing body size. DeRousseau (1988) observed striking differences in OA prevalence, severity and distribution between the two species. While macaques presented severe OA in several joints that varied according to sex and age, gibbons presented much lower prevalence, less severe lesions, no differences according to sex and little correlation between OA and age. This study suggested an important influence of body weight in different locomotor behaviours, also linking OA and biomechanical differences resulting from different locomotor adaptations. The results confirmed the multifactorial nature of DJD development in non-human primates but introduced biomechanical aspects in the study of DJD.

Other studies in which locomotion was mentioned, DJD was always treated as a result of abnormal loading of a joint (e.g., Lovell, 1990; Jurmain, 2000). However, primates do not always experience abnormal loading of joints and, thus, the association between DJD and abnormal loading of a joint is not a sufficiently robust argument. The link between abnormal load and degeneration was questioned by Nuckley and co-workers (2008) who studied spontaneous disc degeneration disease in long-tailed macaques (*Macaca fascicularis*). In the specific case of degenerative disc disease it has been observed that other mammals, in contrast to humans, do not experience spontaneous disc degeneration, whereas at least this species of non-human primate does, regardless the loading pattern.

These studies are the foundation of this thesis, where some of the issues of previous research are addressed with the aim of obtaining clearer information on the nature of DJD in primates. The first problem with previous work was the lack of a standard methodology, which led to recordings of DJD based on presence and absence, losing information on the severity of DJD. Swales and Nystrom (2015) provided evidence that standard methodology used in human recordings is applicable to non-human primates. Moreover, previous studies placed great emphasis on diagnosing the degenerative process and, thus, the focus was on the pathological expression of DJD. This thesis lies far from that aim and no clinical diagnoses are given. Instead, the main interest is to recognise earlier stages of DJD by recording presence and severity of the three main DJD indicators, thus paying attention to the non-pathological stages of DJD. This entails an advantage for comparative purposes, as the definitions of DJD indicators are simple and easy to observe, allowing a more systematic approach and the possibility of testing different potential causal factors.

2.4 Growth, development and ageing: determination of maturity from skeletal evidence

Maturity is a key concept in the biological history of animals. Bones are very reactive in early stages of the development of an individual, as they need to grow (Wintheiser et al., 1977; Dainton and Macho, 1999; Joganic, 2016). However, modifications due to degenerative processes develop once the individual has reached maturity; otherwise changes are likely to be developmental. Developmental stages in mammals have commonly been defined based on the degree of epiphyseal fusion, tooth eruption and gonad maturation (sexual maturity). Therefore, in primates, maturity is attributed at the completion of these three aspects (Shigehara, 1980).

Complete **fusion of epiphyses** in the skeleton indicates the completion of bone growth as evidence of a mature skeleton (Baker et al., 2005; Schaefer et al., 2009; Bolter and Zihlman, 2012), and it distinguishes three fusion stages: unfused, partially fused and fully fused (Wintheiser et al., 1977; Zihlman et al., 2007; Brimacombe et al., 2015). Previous studies have reported age of fusion of the epiphyses in primate species (e.g., Shigehara, 1980; DeRousseau, 1985; Bolter and Zihlman, 2012; Brimacombe et al., 2015), and despite the fact that there is no specific information for all the primate species, it was observed that the sequence of fusion is rather consistent among the order, despite slight variations often linked to differences in sex due to dimorphism (Zihlman et al., 2007; Bolter, 2011; Bolter and Zihlman, 2012).

Growth, however, does not stop with epiphyseal fusion, for body mass increases after epiphyseal fusion is completed (Dainton and Macho, 1999; Humphrey, 1999; Zihlman et al., 2007) and, therefore, skeletal maturity is not an indicator of the end of the growth period. **Dental maturation and eruption** patterns are other consistent indicators of growth and development. For instance, eruption of the first molar is linked with the achievement of 90-95% of brain growth in Old World monkeys (Smith, 1989; Bolter, 2011). Dental maturity is defined by the presence of upper and lower third molar (M3) in full occlusion (Kuykendall, 1996; Balolia, 2015; Brimacombe et al., 2015). Similarly to what happens with epiphyseal fusion, the timing for dental maturity might differ among primates, but the sequence of molar eruption is consistent (Schultz, 1935; Shigehara, 1980).

There is a wealth of information on epiphyseal fusion and dental eruption patterns in primates, as indicators of postembryonic growth (Wintheiser et al., 1977). Furthermore, several researchers assessed how these two processes are encompassed during growth in primates (Tappen and Severson, 1971; Wintheiser et al., 1977; Dainton and Macho, 1999; Zihlman et al., 2007; Bolter, 2011; Balolia, 2015; Brimacombe et al., 2015; Joganic, 2016). These studies point out that there are inter-specific differences in the times of epiphyseal fusion in relation to dental development. However, "there is a basic pattern common to most, if not all anthropoidea" (Wintheiser et al., 1977: 195). Most of these studies also pointed out that dental maturity was achieved earlier in the life of primates than skeletal maturity. Thus, complete epiphyseal fusion concluded after the full eruption of M3 (Zihlman et al., 2007; Bolter and Zihlman, 2012; Balolia, 2015; Brimacombe et al., 2015). Furthermore, Balolia (2015) observed that a significant number of the studied apes (*Gorilla gorilla, Pan troglodytes schweinfurthii* and *Pongo pygmaeus pygmaeus*) showed unfused spheno-occipital sutures at the time of eruption of M3 (especially orangutans, when over 50% of the individuals exhibited the unfused suture), seeing an association between suture fusion and age, which could be fully fused during later years of adulthood. Brimacombe and co-workers (2015) stated that despite the fact that some of the studied chimpanzees (*Pan troglodytes*) showed full fusion at the time of dental maturity, most did not, meaning that even within one species different maturation patterns are to be expected.

The third indicator of maturity is sexual maturity, understood as **maturity of the gonads** (Shigehara, 1980). Sexual maturity can be reached at an early stage of a primate's life. For instance, baboon females often give birth to their first offspring prior to M3 eruption (Phillips-Conroy and Jolly, 1988), providing clear evidence that these females are already sexually mature. Therefore, sexual maturity happens before somatic growth finishes. In fact, male sperm production occurs before growth has come to an end (a pattern applicable to many male primates, including humans) (Zihlman et al., 2007).

It can therefore be established that maturity is a complex biological stage. Moreover, reaching maturity is accomplished at different stages of life in different species, expressing variability in patterns sometimes even within species. However, from skeletal remains, maturity can be determined rather confidently combining information on epiphyseal fusion and dental eruption, despite lacking information on the individual's sexual maturity.

CHAPTER 3: PRIMATES IN CONTEXT

3.1 The Order of primates

3.1.1 What is a primate?

Primates are an order of mammals within the phylum of chordates of the animal kingdom. They occupy a good range of the tropical and semitropical regions of the planet and most of them exhibit a strong association with forests, often living and moving up in the trees (Ankel-Simons, 2007; Nystrom and Ashmore, 2008; Heads, 2010; Fleagle, 2013), with humans being the main exception. The Order as a whole consists of generalist foragers with rather large brains that live in relatively complex social systems (Hartwig, 2011) and exhibit an extraordinary array of locomotor behaviours (Hunt et al., 1996; Ankel-Simons, 2007; Schmidt, 2011; Larson, 2018).

Primates, unlike other groups of mammals, do not share a particular trait that is exclusive to the Order (a keystone feature). For instance, artiodactyls (i.e. even-toed ungulates) are an Order defined by double-pulley astragalus bone (Rose, 1982; Cachel, 2015; Vaughan et al., 2015). Primates, however, lack such a defining single trait. Despite the relatively conservative and generalised anatomy of primates (Napier and Napier, 1967; Schmidt, 2011; Fleagle, 2013; Elton et al., 2016), there is a good amount of variability in their morphology (e.g., Fleagle, 1977, 2013; Fleagle and Simons, 1982; Gebo and Sargis, 1994; Nakatsukasa, 1994; Fleagle and McGraw, 1999; Ankel-Simons, 2007; Bitty and McGraw, 2007). Consequently, in an effort to define primates, researchers often rely on several traits shared by all or almost all primates even if these characteristics are not exclusive of the Order.

Carl von Linné was the first person to give a definition of what a primate is in his book *Systema naturae* and he described primates as those mammals that met at least four characteristics: presence of four incisors, two clavicles, two mammary glands on the chest and at least two extremities that act as grasping hands (Conroy, 1990; Nystrom and Ashmore, 2008). Further definitions took into consideration other factors, such as geographic distribution, habitat, locomotion, sensory organs, dentition, relative brain size or the shape of the primate cranium (Martin, 1990), eventually developing rather detailed lists of traits that would generally allow the separation of primates from other mammals. Some of the traits most commonly considered are the following (Martin, 1990; Cachel, 2015):

- Retention of clavicles and generalised limb anatomy with five digits in each extremity.
- Grasping extremities as a result of their freely mobile and long digits, especially the first digit of hands (pollex) and feet (hallux).
- Flat nails instead of claws, at least for one digit and fleshy pads responsive to touch in every digit.
- Shortened snout, which in some species may have been secondarily elongated as a result of longer postcanine dentition.
- Reduced olfactory bulbs compared to other mammals (lesser reliance on the sense of smell).
- Frontally oriented eye orbits and binocular vision, which has come with retinal and nervous rearrangements allowing stereoscopic vision (greater reliance on the sense of vision).
- Bony separation between the eye orbit and the anterior fibres of the *Temporalis* muscle. The morphology and extent of the bony structure can range from a small bar of bone to a complete bony plate or septum.
- The tympanic bulla of primates (which encloses the middle ear) is formed by a different bone (the petrosal bone) rather than from an independent ossification.
- The occlusal surface of the molars is simple in topography with no intricate crests or enamel folds. Primates only have four incisors and lose one premolar at an early age.
- More elaborate placental tissues.
- Elongated growth periods.
- Large brain relative to body size, especially the neocortex.

3.1.2 Taxonomy of extant primates

Taxonomy is a means of ordering the natural world and its diversity in a set of categories and names that are commonly accepted (Fleagle, 2013). This organisation follows the system proposed by Linné, which consists on a hierarchy of levels grouping categories into larger groups (Groves, 2004). For certain groups of organisms the different common levels are subdivided in order to reflect specific distinctive characteristics. The taxonomic classification should reflect the phylogeny of organisms and the bigger groups, such as orders, families or superfamilies should be monophyletic (of a single evolutionary origin) (Martin, 1990; Vaughan et al., 2015). Thus, even though most biologists agree in the use of the Linnaean system to name organisms, sometimes they disagree in the classification of organisms, as phylogenies are constantly being revised (Groves, 2004; Fleagle, 2013).

The taxonomy used in this thesis distinguishes Strepsirhini and Haplorhini as monophyletic groups (Hartwig, 2011) (Table 3.1). The suborder Strepsirhini includes the lemurs of Madagascar (Cheirogaleidae, Lemuridae, Lepilemuridae, Indriidae and Daubentoniidae), the African Galagidae and the Afro-Asian Lorisidae (Vaughan et al., 2015). They are characterised by the presence of a rhinarium (a moist nose) and large mucous membranes within the nasal cavity (Nystrom and Ashmore, 2008).

The suborder Haplorhini includes the tarsiers and all the monkeys and the apes. These are largely diurnal primates (with the exception of two genera) and rely more on vision than on olfaction. Therefore, contrary to the Strepsirhines, the Haplorhines have dry rhinaria, enclosed eyeballs within bony sockets, larger brains and more complex social systems (Nystrom and Ashmore, 2008). There are three distinct infraorders within the Haplorhines: the Tarsiiformes, Catarrhini (Old World primates) and Platyrrhini (New World primates) (Groves, 2004; Nystrom and Ashmore, 2008; Hartwig, 2011; Vaughan et al., 2015), which are in turn further divided into families and subfamilies, constituting more specific taxa (Table 3.1).

3.1.3 The origin of primates

Primates is a monophyletic Order showing a good degree of variability among both extant and extinct forms, derived from a common ancestor that was likely to have lived during the Palaeocene (Fig. 3.1) (Sussman et al., 2013). From this common ancestor the typical primate characteristics evolved and several hypotheses have been formulated to establish the drivers of change responsible for the acquisition of the typical primate traits.

Plate tectonic movements and the separation of land masses have commonly been used in the past to explain the differentiation of primate groups (Cachel, 2015). Heads (2010) hypothesised that the origin of the major primate groups

Table 3.1 Taxonomy of extant primates to the level of subfamily and to the level of genus only for those taxa included in this thesis (modified from Nystrom and Ashmore, 2008)

ORDER	**SUBORDER**	**INFRAORDER**	**SUPERFAMILY**	**FAMILY**	**SUBFAMILY**	**GENUS**
PRIMATES	Strepsirhini	Lemuriformes	Lemuroidea	Cheirogaleidae		
				Daubentoniidae		
				Indriidae	Indrinae	*Propithecus*
				Lemuridae		
				Lepilemuridae	Lepilemurinae	
			Lorisoidea	Lorisidae	Galaginae	*Euoticus*
						Galago
						Galagoides
						Otolemur
					Perodictinae	*Perodicticus*
					Lorisinae	*Loris*
						Nycticebus
	Haplorhini	Tarsiiformes	Tarsioidea	Tarsiidae		*Tarsius*
		Catarrhini	Cercopithecoidea	Cercopithecidae	Cercopithecinae	*Cercocebus*
						Cercopithecus
						Chlorocebus
						Erythrocebus
						Lophocebus
						Papio
					Colobinae	*Nasalis*
						Procolobus

Table 3.1 (cont.). Taxonomy of extant primates to the level of subfamily and to the level of genus only for those taxa included in this thesis (modified from Nystrom and Ashmore, 2008)

ORDER	**SUBORDER**	**INFRAORDER**	**SUPERFAMILY**	**FAMILY**	**SUBFAMILY**	**GENUS**
PRIMATES	Haplorhini	Catarrhini	Hominoidea	Hylobatidae		*Hylobates*
				Pongidae		*Pongo*
				Hominidae	Gorillinae	*Gorilla*
					Homininae	*Homo*
						Pan
		Platyrrhini	Ceboidea	Atelidae	Atelinae	*Ateles*
						Brachyteles
						Lagothrix
					Pitheciinae	
					Callicebinae	
				Cebidae	Aotinae	
					Cebinae	*Cebus*
						Saimiri
						Sapajus
				Callitrichidae		

took place by tectonic movements and vicariance (i.e. allopatric speciation) from the ancestral form of primates (Euarchonta), which Heads claimed were widespread throughout Pangea. This would solve the long-stood question as to how early primates had arrived to the American continent once this was already separated as a result of the formation of the South Atlantic Ocean (during the Early Cretaceous at 130 mya). However, this hypothesis pushes the origin of Euarchontans back to the Triassic (Fig. 3.1), which is not supported by the current fossil record (Fleagle, 2013; Cachel, 2015).

Figure 3.1 Geological time scale of the Mesozoic and the Cenozoic era, comprising all the ages relevant for the study of the origins of modern primates (modified from the Geological Society of America, 2012)

The first fossil evidence of modern looking primates (Euprimates) is from the Eocene (Fig. 3.1). Their most accepted ancestral forms (Plesiadapiformes), however, appear earlier in the fossil record (in the latest Cretaceous) and information on corrected molecular clock places their origin in the Cretaceous/Tertiary boundary, reaching the Early Palaeocene (Fig. 3.1) (Cachel, 2015). The taxonomy of previous forms of primates is still disputed but three hypotheses on the origin of modern primates are: 1) the arboreal hypothesis, 2) the visual predation hypothesis, and 3) the angiosperm radiation hypothesis.

The **arboreal hypothesis** of primate origins focused on the postcranial primate adaptations. This hypothesis sustains that the main primate characteristics are a result of life in the trees. It emphasises the role of the forelimb as the limb in charge of touch and climbing functions, thus leading to the concept of emancipation of the forelimbs, enabled by the improvement of the hand-eye coordination (Sussman, 1991). Other adaptations, such as prehensile hands and feet, nailed digits or binocular vision are also said to be a consequence to this adaptation to life in the trees (Cachel, 2015). The main limitation is that primates is not the only order of mammals that occupy arboreal environments but these other mammal groups do not share the primate characteristics (Schmitt and Lemelin, 2002; Fleagle, 2013; Sussman et al., 2013; Cachel, 2015). Therefore, there must be more to the origin of the Euprimate morphology than the arboreal occupation.

Cartmill (1974) offered an alternative hypothesis on the origin of primates that complemented the arboreal hypothesis: the **visual predation** hypothesis. This hypothesis emphasises the idea that the frontal convergence of the eyes, the strong grasping extremities and nailed digits are all adaptations from hunting insects in small terminal branches. It was posteriorly stipulated that this first euprimates were nocturnal insect hunters, who benefit from visual accuracy in order to hunt more efficiently in the dark (Cartmill, 1992). However, the primate digestive tract is of an omnivorous nature (Martin, 1990). Moreover, plesiadapiformes do not show any signs of an insectivore diet, but a more herbivorous one (Szalay, 1968). Actually, Cartmill does not consider the plesiadapiformes as early primates, but rather, as a closely related group to primates (Cartmill, 1974; Sussman, 1991; Cachel, 2015), despite the fact that detailed observations of the basicrania of plesiadapiformes (specifically of the genus *Ignacius*) show more similarities with modern looking primates than with any other group of mammals (Bloch and Silcox, 2001), seen as well in the foot and molar dentition (Sussman et al., 2013).

The third hypothesis on the origin of primates is the one presented by Sussman (1991), which states that the diversification of primates was accompanied by the **radiation of angiosperms**. This hypothesis is built upon a potential coevolution of angiosperms and primates as important seed dispersal agents. In fact, Sussman (1991) links the Eocene angiosperm radiation with the diversification of plant-feeding birds, bats and primates, arguing that these animals are important dispersion agents of flowering plants. According to this hypothesis, the availability of fruit resources in the terminal branches of angiosperms led to the adaptations observed in euprimates, which involved becoming well adapted to feeding on a small-branch niche and a greater proportion of plant material intake. One of the limitations of this hypothesis is that angiosperms were already the dominant source of plant life during the Late Cretaceous, whereas primates emerge after the Cretaceous/Tertiary mass extinction (Cachel, 2015).

The fossil evidence predating the third mass extinction points towards high levels of plant diversity and a high number of insect action on the plants, suggesting that insects were the main pollinators and seed dispersers. This is a typical pattern of a healthy tropical forest. After the mass extinction, however, the levels of plant diversity decreased significantly and only one type of insect interaction has been found, showing an abnormal ecosystem function. It was not until the Late Palaeocene that the normal food webs were re-established (Cachel, 2015). The Palaeocene is the time where plesiadapiformes were living and many researchers state that no major changes occurred in the first stages of primate evolution (Sussman, 1991). After the Palaeocene, during the Eocene, angiosperms started growing fruits with big seeds which were likely to have been dispersed by bigger animals and not only by insects (Sussman, 1991). Furthermore, in a re-evaluation of this hypothesis, Sussman and co-workers (2013) state that the frontal convergence of the eyes would be of greater benefit in a daily fruit-eating primate up in the canopy than it would be for a nocturnal insectivore, as Cartmill suggested (1974; 1992). Binocular stereoscopic vision would be particularly advantageous when foraging in dense foliage, similar to an x-ray machine, which would allow the animal to see through the clutter of the dense canopy (Sussman et al., 2013). In fact, for some time stereoscopic vision was considered a keystone feature of primates until it was also discovered in fruit bats (Cachel, 2015), which are not flying primates but shared the retino-tectal system and also allowed them to feed on fruit from the dense canopy (Sussman et al., 2013).

Primate scholars and palaeontologists, thus, have supported different hypotheses on the appearance of the modern primate morphologies. However, what seems to be supported by all of these hypotheses is that the origin of euprimates is of an arboreal nature. Regardless of who were the first primates and what phenomena drove their adaptations and determined their success in their new ecological niche, it seems certain that it happened up in the trees. This is also supported by biomechanical studies, showing a greater reliance on the hindlimb for locomotor purposes and diagonal sequence gait (Wallace and Demes, 2008), which is highly beneficial when moving in complex networks of supports (more information on Chapter 4). As a consequence, the extant non-arboreal primate behaviours are likely to have been adopted secondarily, as well as the morphologies that allow terrestrial exploitations.

3.2 Ecology of primates

3.2.1 Distribution of primates and habitats

Primates are generally found in the tropical, forested habitats of the planet (Nystrom and Ashmore, 2008; Heads, 2010; Fleagle, 2013; Vaughan et al., 2015). More specifically, with the exception of humans, the vast majority of primates are found in the tropical and semitropical parts of Africa, Asia and America, the temperate regions of North Africa and Asia and marginally in Europe (Gibraltar) (Smuts et al., 1987; Nystrom and Ashmore, 2008; Fleagle, 2013; Vaughan et al., 2015). Some species, however, face extreme climates with significant changes in vegetation, like some species of macaques (*Macaca*), which can outlive the cold winters of Japan and Nepal (Fig. 3.2) (Fleagle, 2013).

Extant primates are found in a variety of habitats, ranging from deserts to tropical rainforests (Fig. 3.3). Very few species are able to endure in dry, poorly vegetated environments. Rather, most primates are found in different kinds of forests, which can vary in characteristics, such as rainfall, altitude, topography, type of soil, fauna or type of vegetation (Fleagle, 2013).

Figure 3.2 Distribution of extant and extinct non-human primates. The complete line represents the Equator and the dashed lines the Tropic of Cancer (23^{o} 28′ north) and the Tropic of Capricorn (23^{o} 28′ south) (after Fleagle, 2013)

Different types of forests can be defined depending on the type and distribution of the vegetation. The primary rainforest is characterised by a very tall canopy belt resulting from the competition for light in highly vegetated forests. The tall, dense trees prevent the light from reaching lower levels of the forest, which involves rather open understories composed mainly by vines and trunks (Dudley and DeVries, 1990; Mitani et al., 2000). Within the primary forest, however, there can be occasional tree falls, allowing the light to penetrate into the lower levels and promoting the renewal of the forest. These areas around alterations of the main canopy conform the secondary forests (Manduell et al., 2012). They are characterised by more continuous vegetation as a result of the easier access to light (McGraw, 1998a). The vegetation comprises short trees and vines and the canopy is less distinct from other levels than in the primary forest (Fleagle, 2013). Some forests grow around a river in dry habitats, forming a gallery forest. The African woodland is made of relatively short trees (often deciduous) with areas of bushes and low grasses. With a decreasing density of trees the woodlands conform bushlands, scrub forests and in last instance savannahs (Fleagle, 2013).

Figure 3.3 Representation of the different kinds of habitats occupied by primates (after Fleagle, 2013)

The niches that primates can occupy within one forest are rather diverse as a consequence of the stratification of the forests (Napier, 1976). Some species of primates have specialised in the exploitation of particular strata within a forest (Fig. 3.4), often preferring trees of specific size and specific productivity (Fleagle, 2013). Thus, sympatric species are likely to exploit different niches.

Figure 3.4 . Representation of the different strata of a rainforest (after Napier, 1976)

3.2.2 *Forest architecture and implications for moving primates*

Differences in habitat occupation and in niche exploitations within a forest entail significant differences in terms of food availability, predator pressure, abiotic conditions and the type of supports available for primates to conduct their daily activities, among which is locomotion. Locomotion consists on propelling an animal's body through its environment (Prost, 1965; Martin, 1990; Youlatos, in press) and therefore, the habitat occupied has a direct effect on the strategies adopted by primates to move about.

Arboreal and terrestrial primates, for example, face very different challenges during locomotion. The arboreal canopy consists of a complex network of supports of different size and orientation (Schmitt, 1998; Garber, 2011; van Casteren et al., 2012; Shapiro et al., 2014, 2016; Youlatos, 2018) conforming discontinuous paths that present gaps. Cant (1992) described four main habitat-related challenges that arboreal primates face during locomotion: a need for straightening the discontinuous paths of movement within trees, negotiating with large vertical supports, increasing the speed along irregular paths and crossing gaps between trees. Moreover, in an arboreal environment there is the added difficulty of keeping balance. This is why arboreal primates distribute their weight differently and lower their centre of gravity (flexing and abducting their limbs) (Schmitt, 1994, 1998; Larson et al., 2000). Primates exploiting terrestrial environments, in contrast, deal with more uniform substrates and more direct routes to food resources (Garber, 2011), but with the major disadvantage that on the ground primates are more susceptible to predators (Thorpe and Crompton, 2006, 2009; Fleagle, 2013). All the obstacles that come with the different environments are negotiated in different ways, often leading to the adoption of different locomotor strategies.

Each level of a forest is characterised by a unique combination of supports and provides different potential conditions for the primates in it. Thus, the specialisation of primates in the exploitation of specific strata of a forest has important implications in the type of supports available and their activities, from foraging, to feeding or resting, resulting in differences in locomotor and postural behaviours coupled with the use of certain types and sizes of supports (McGraw, 2017). Generalisations concerning differences in **support composition** and architecture of a forest are sometimes easily attributed. For instance, near the ground, in the shrub layer and the understory of a primary forest there are more discontinuous vertical supports, trunks or lianas (Crompton and Andau, 1986; McGraw, 1998a; Crompton et al., 2010), while the canopy is composed of the leafy part of the trees and, thus, the supports are more continuous and horizontal (McGraw, 1998a; Schmidt, 2011), presenting more gaps and thinner branches in the emerging layers of the canopy (Cant, 1992). Secondary forests reach lower overall heights than primary forests and are characterised by continuous vegetation throughout the different levels as a result of the lower competition for light (Fleagle, 2013). The three-dimensional architecture of an arboreal habitat is determined by the size of the branches, their degree of inclination and their deformability, as well as their density and pattern of distribution (Schmidt, 2011). This restricts what kinds of supports are made available for primates during locomotion, although support choice is not random, as it does not uniquely answer to support availability (McGraw, 1996). For instance, tarsiers usually propel themselves from and land on supports of very similar size, regardless the type or part of the forest they are found in, suggesting that the choice is deliberate and not only dependant on what is available to them (Crompton et al., 2010).

Support use is an important source of variability related to locomotion. Despite the range of variability of locomotor behaviour in primates, it is more likely that habitat and support use will vary before locomotor behaviour (McGraw, 1996). For instance, different species of arboreal primates may not vary much in terms of locomotion but if they occupy different strata of the forest, they are likely to interact with different types of supports despite moving similarly (e.g., Fleagle and Mittermeier, 1980; Gebo and Chapman, 1995a; McGraw, 1998a). In contrast, intra-specific observations have showed that the use of different types of supports by one individual or different individuals of the same species can result in differences in locomotion. For example, orangutans can exhibit very distinct locomotor strategies, moving only on their hindlimbs, on four limbs or in suspension (i.e. hanging) from the branches, and the choice of locomotor mode is closely related to the diameter of the support used as well as the number of supports involved. This way, orangutans move on their hindlimbs when they use multiple supports of small diameter, on the four limbs using single large supports, and below the branches when they use middle-diameter supports (Fig. 3.5) (Thorpe et al., 2007). In fact, the locomotor behaviour in orangutans of Borneo and Sumatra is more varied in forests that present a wide range of supports available, whereas in forests with less diversity in support types orangutans present a more homogeneous locomotor repertoire (Manduell et al., 2011, 2012).

Differences in habitat composition and structure, therefore, can play an important role both in locomotion of primates and in support use. Some primates exhibit inter-population differences in locomotion due to varying ecological factors, like forest composition or distribution of food resources (Mekonnen et al., 2018), as well as presence of terrestrial predators (Thorpe and Crompton, 2006, 2009). Cercopithecines occupying different natural habitats, however, did not differ significantly in terms of locomotion (McGraw, 1996), whereas some other primates have been observed performing different behaviours in distinct habitats (Gebo and Chapman, 1995b; Dagosto and Yamashita, 1998), showing different patterns of locomotor plasticity for different species or different populations.

Figure 3.5 Variability of locomotor strategies of orangutans in relation to support type: assisted bipedalism (A), quadrupedalism (B) and orthograde suspension (C) (modified from Thorpe et al., 2007)

Anthropogenic modifications of the natural habitats of non-human primates usually come with important changes to forest structure, distribution of primate resources and support availability, potentially modifying the behaviour of primates (e.g., Garber and Pruetz, 1995; Gebo and Chapman, 1995a; McGraw, 1998b; Mekonnen et al., 2018). Unfortunately, habitat loss and fragmentation of the primate habitats are the most serious threats to biodiversity and conservation (Haddad et al., 2015; Crooks et al., 2017) and some of the primates suffering this are showing high levels of plasticity, sometimes modifying their behaviour. One example is the arboreal Bale monkey (*Chlorocebus djamdjamensis*). The Bale monkeys that occupy areas of fragmented forests adopt semi-arboreal behaviours interacting a lot more with the ground, as a result of increasing levels of terrestrial foraging compared to the individuals that inhabit the undisturbed bamboo forests, and during arboreal locomotion they switched from medium-sized supports as their preferred type of support to very small or very large ones (Mekonnen et al., 2018).

The adaptability of primates to different or changing habitats has its limitations. Not all primates can exploit any kind of ecological niche. One of the main limiting factors in this respect is **body size**. Weight and positional capabilities enable and constrain the use and exploitation of certain strata of a forest (Cant, 1992). Due to the laws of proportionality, a large arboreal primate must either use very large branches to move on or distribute its weight among several supports at once for it not to fail under its own weight (Fleagle and Mittermeier, 1980). Consequently, it is generally accepted that big primates choose big supports to move on in order to avoid branch failure, whereas smaller primates tend to move on smaller supports. Moreover, large arboreal primates tend to use those strata of the forest with high frequencies of large supports, while smaller primates are more diverse in the use of the canopy as, at least theoretically, they can use a wider range of supports (Gebo and Chapman, 1995a; McGraw, 1998a). However, this generalisation has its limitations, as some primates have adopted different strategies in order to deal with small arboreal supports despite their large size, such as using different supports at once or hanging from the support instead of balancing on top of it (Mittermeier and Fleagle, 1976; Fleagle and Mittermeier, 1980; Youlatos, 2001, 2017). Furthermore, relatively small primates have been observed using larger or stiffer supports in comparison to larger-bodied primates (McGraw, 1996, 1998b, 1998a).

The study of sympatric species of primates has produced valuable information regarding support use in relation to body mass (Fleagle and Mittermeier, 1980; Crompton and Andau, 1986; Gebo and Chapman, 1995a; McGraw, 1996, 1998a; Crompton et al., 2010). In the study of seven sympatric species of monkeys from Surinam, Fleagle and Mittermeier (1980) observed how the larger monkeys generally used boughs (supports of over ten centimetres in diameter) during locomotion, whereas the smallest ones used twigs instead (supports of under two centimetres in diameter) with the main exception of the large-bodied spider monkey (*Ateles paniscus*) that used smaller supports thanks to its suspensory behaviour and the utilisation of several supports simultaneously. A later study done in Kibale National Park in Uganda showed a similar relationship between body mass and diameter of the supports most commonly used in Old World monkeys, so despite the fact that all the primates considered occupied the middle and upper canopy, the smaller species of monkeys used the smaller-diameter branches, whereas the larger species used boughs in higher proportion (Gebo and Chapman, 1995a). These studies support the relationship between body mass and support diameter, considering the particularity of the suspensory primates that can work around the limitation of support diameter and larger body sizes. However, McGraw (1998a) found that among six sympatric species of colobines and guenons, large monkeys did not always use larger supports than smaller monkeys, suggesting that there is certain variability to this rule. This could be due to the fact that variability in body size among the selected species may not be sufficiently large to reflect the relationship between support use and body size reported by Fleagle and Mittermeier (1980) or Gebo and Chapman (1995b). However, it is important to bear in mind that most primates use several types of supports of different diameters despite having preference for certain supports and there can be cases of larger animals using smaller supports than would be expected and vice versa.

The literature on specific primate support utilisation that especially details support diameter is, unfortunately, incomplete. There is an increasing number of studies on support use among primates (e.g., Fleagle and Mittermeier, 1980; Crompton and Andau, 1986; Boinski, 1989; Cannon and Leighton, 1994; Gebo and Chapman, 1995b; McGraw, 1996, 1998a; Youlatos, 2001, 2002; Thorpe and Crompton, 2005; Bitty and McGraw, 2007; Crompton et al., 2010; Blanchard et al., 2015) despite the observational difficulties and the fact that support diameter approximation is not an easy task. However, it is still more common to find information on the stratum of the forest that a primate is found in (e.g., Jones and Sabater Pi, 1968; Gebo and Sargis, 1994; Nakatsukasa, 1994; Off and Gebo, 2005) but because of the stratified nature of forests and the characteristic composition of each of the strata (Fleagle and Mittermeier, 1980; Gebo and Chapman, 1995a, 1995b; McGraw, 1998b; Schmidt, 2011; McGraw, 2017) it is sometimes possible to draw approximations on the most abundant type of support and consider it the most probable support chosen for primate locomotion.

3.2.3 Mechanical properties of tree branches

Differences in the type of support used by a primate during locomotion entail differences in the mechanical challenges the animal must face, depending mainly on the degree of deformability of the support. It has been established that the use of highly deformable supports during locomotion comes with higher energy expenditure (Demes et al., 1995; Channon et al., 2011). However, some primate species seem to actively benefit from the compliance of branches (Thorpe et al., 2007) and, therefore, determining the mechanical properties of branches and, particularly, their degree of compliance can be of great importance in order to understand the way primates use the forest as well as the plasticity of primate locomotion.

An arboreal tropical environment consists of a very complex three-dimensional network of supports of varying morphological and mechanical properties (van Casteren et al., 2013). However, it is not simple to test for deformability of supports *in situ* for primates living in the wild. Instead, experimental work on tree branches mechanical properties has been conducted with the final aim of assessing how a branch would react to the weight of a primate and how a primate can predict branch properties (Ennos and van Casteren, 2010; van Casteren et al., 2012, 2013). Many factors can contribute to the degree of deformability and resistance of a branch. For instance, different species of trees have different density of wood, which conditions the way a branch may fail when subjected to extreme bending (Ennos and van Casteren, 2010; van Casteren et al., 2012). Nevertheless, all branches vary in two mechanical ways that may influence a primate's locomotion: the degree of compliance (i.e. deformability) and oscillatory frequency (van Casteren et al., 2013).

Compliance and oscillatory frequency of a branch can be assessed rather accurately from morphological features. The diameter of the branch is the best indicator of its compliance (Fig. 3.6), explaining up to 60% of the total compliance, a value close to the optimum predictive capability for a tropical forest canopy (van Casteren et al., 2013).

Figure 3.6 Level of compliance along two branches of different diameters, with branch 1 being significantly thicker than branch 2 (after van Casteren, 2013)

The oscillatory frequency within a branch is mainly determined by the distance from the tip of the branch, thus branch diameter and oscillation are negatively correlated, whereas diameter and time of oscillation are positively correlated with branch diameter (long big branches have higher times of oscillation) (van Casteren et al., 2013). Therefore, a primate will perform certain types of locomotor activities at different points of a branch in order to move more effectively, as seen, for example, with different types of leaps performed by gibbons (Channon et al., 2011).

3.3 Locomotor positional behaviour in non-human primates

Positional behaviour comprises two different components: postural and locomotor behaviours (Prost, 1965; Nystrom and Ashmore, 2008; Garber, 2011). While posture is characterised by the movement and positioning of the limbs with no displacement of the body, locomotion or locomotor behaviour consists of a set of movements performed by an animal in order to propel itself through its habitat (Prost, 1965; Martin, 1990). Locomotion is one of the fundamental activities of vertebrates and it is a major aspect of their foraging strategies (Ankel-Simons, 2007; Garber, 2011; Fleagle, 2013; Vaughan et al., 2015).

The study of locomotion is, therefore, central in the study of primates. Firstly, locomotor diversity is characteristic of primates, in comparison with other mammals (Hunt et al., 1996; Schmidt, 2011; Fleagle, 2013; Larson, 2018). Secondly, locomotor behaviour is key to understanding the primate adaptive diversity, as most traits of the postcranial primate body are influenced by locomotion and the interaction with the environment (e.g., Fleagle and Simons, 1982; Martin, 1990; Nakatsukasa, 1994; Fleagle, 2013; Molnar et al., 2017), as a result of the extreme forces that the musculoskeletal system bears during locomotion (Hunt et al., 1996; Garber, 2011). Lastly, nearly all the adaptive radiations of primates involved differences in locomotor behaviours, which would ultimately allow new niche exploitations and the success of the Order (Garber, 2011; Youlatos, 2018).

3.3.1 *Variability of locomotor behaviour among non-human primates*

Positional behaviour is not exclusively species-specific, but it is also activity and context-specific (Garber, 2011). Consequently, primates adopt different locomotor behaviours depending on their immediate environment and on the activity they are performing. As a result of the great diversity in locomotor and postural behaviours of primates the definition of locomotor categories can be difficult and has been extensively discussed (Prost, 1965; Napier, 1967, 1976; Hunt et al., 1996; Ankel-Simons, 2007; Schmidt, 2011; Fleagle, 2013).

Primates maintain great flexibility and adaptability in their locomotor behaviours as a result of their rather generalised morphology, which allows them to perform a broad range of movements (Schmidt, 2011; Elton et al., 2016). Hunt and co-workers (1996) proposed a detailed description of several locomotor and postural modes observed in the wild, serving as a standard list of behaviours. Nevertheless, the grouping of locomotor behaviours into major locomotor categories also provides useful information, especially for the purpose of examining general patterns in morphology (Fleagle, 2013), despite having been considered at times too broad to reflect the variety of movements that primates can perform (Fontaine, 1990; Hunt et al., 1996).

Some of the major classifications of primate locomotion widely used are Napier's (1976) and Fleagle's (2013), who defined quadrupedalism, leaping, suspensory behaviours and bipedalism as the main locomotor categories (Fig. 3.7). These locomotor categories differ in the pattern of use of the limbs in order to travel and access certain forest structures (Fleagle, 2013), a factor that has often been taken into account, even in earlier studies of primate locomotion (Ashton and Oxnard, 1964). In this thesis Fleagle's (2013) classification is used. This does not mean, however, that locomotor diversity within each category should not be considered. Actually, further information on locomotor diversity is particularly useful in comparisons among species within one locomotor category as well as for those species that have a very mixed pattern of behaviours, such as in squirrel monkeys (*Saimiri* sp.), for instance. Squirrel monkeys are efficient arboreal quadrupeds but they also habitually leap in their locomotor activities (Boinski, 1989; Fontaine, 1990).

Quadrupedalism consists on locomotion using four limbs (Shapiro and Young, 2017). It is one of the most performed locomotor modes among terrestrial mammals (Vaughan et al., 2015) and nearly all primates include quadrupedalism in their locomotor repertoire even if it is not their habitual or characteristic mode of locomotion (Hunt et al., 1996; Ankel-Simons, 2007; Nystrom and Ashmore, 2008; Garber, 2011; Schmidt, 2011; Fleagle, 2013; Shapiro and Young, 2017). Quadrupedal gaits can be further classified as lower speed "walks" and higher speed "runs" (Shapiro and Young, 2017), which entail different biomechanical requirements and different footfall patterns (more on Chapter 4). However, a very common differentiation of types of quadrupedalism is based on habitat exploitation.

Arboreal quadrupedalism is characterised by the use of trees during locomotion. Arboreal quadrupeds use supports (mainly branches) of different diameter to move on relying on the four limbs. Terrestrial quadrupedalism, in contrast, consists on locomotion on the ground using the four limbs (Fig.3.7).

Figure 3.7 Representation of Fleagle's main locomotor categories: quadrupedalism (arboreal, terrestrial and knuckle-walking), leaping, suspensory behaviours and bipedalism (after Fleagle, 2013)

Knuckle-walking is a modified type of terrestrial quadrupedalism performed by bonobos, chimpanzees and gorillas. This type of quadrupedalism is characterised by the loading of the dorsum of the middle phalanges of the forelimb during walking (Fig. 3.7) instead of using the palm of the hand as observed in palmigrades or the palmar side of the digits as observed in digitigrades (Fig. 3.8) (Aiello and Dean, 2006; Ankel-Simons, 2007; Nystrom and Ashmore, 2008; Shapiro and Young, 2017). The other non-human great ape, the orangutan, is essentially arboreal. However, when moving quadrupedally on the ground, it can also perform a modified type of quadrupedalism known as **fist-walking**, where the forelimbs make contact with the ground closing their hands into a fist in order to protect their digits, which are especially important for grasping supports during their more habitual arboreal behaviours (Hunt et al., 1996).

Climbing can be considered a type of quadrupedalism (Napier, 1976), where the position of the trunk is orthograde (vertical) and often involves the use of the four limbs (Hunt et al., 1996; Fleagle, 2013; Hanna et al., 2017). This is also referred to as

Figure 3.8 Skeletal representations and pictures of a terrestrial primate (a and b) exhibiting digitigrady (Papio sp.) and an arboreal primate (c and d) exhibiting plantigrady (Saimiri sp.) (after Nystrom and Ashmore, 2008)

quadrumanous climbing and it is observed in ascending or descending movements on supports that are angled at least 45º (Hunt et al., 1996). Climbing is a divers locomotor strategy in terms of limb activation patterns, which makes the lumping of all climbing activities under one locomotor mode somewhat challenging (Schmidt, 2011).

Leaping allows primates to cover gaps in the canopy or to move fast between supports regardless their orientation (Hunt et al., 1996; Nystrom and Ashmore, 2008; Schmidt, 2011; Fleagle, 2013). It is a very efficient quick way of locomotion, which led to its consideration as the main strategy of predator-avoidance in strepsirhine solitary foragers (Crompton and Sellers, 2007). Contrary to hopping, leaping is not a cyclic mode of locomotion but, instead, it is usually a single locomotor event (Schmidt, 2011). A leap is always characterised by a rapid extension of the hindlimbs followed by an aerial phase. There may be trunk rotation during the free flight phase of a leap, positioning the hindlimbs in front of the body to break the impact of the landing (Schmidt, 2011). This is a characteristic of specialised leapers, which tend to both take off and land hindlimbs first (Crompton and Sellers, 2007), despite the fact that forelimb-fist landing is also observed among efficient leapers (Demes et al., 1999, 2005).

Vertical clinging and leaping (VCL) is a specialised form of leaping, originally considered as an independent locomotor category by Napier (1976). VCL is a type of progression often observed between vertical or near-vertical supports to which the primate clings in an orthograde posture before performing a powerful leap through hindlimb extension followed by the landing onto the next support (often also vertical or near-vertical) with rotation of the trunk in mid-air (Fig. 3.9) (Crompton and Andau, 1986; Crompton et al., 2010). This is typical of some strepsirhines and the tarsiers (Crompton and Andau, 1986; Crompton and Sellers, 2007; Gebo, 2011) and, despite seeming rather uniform as a locomotor mode, the way it is performed differs among species. For instance, tarsiers and galagos propel themselves by means of rapid extension of the ankle joint (i.e. plantar flexion), which is particularly effective as a result of the elongated tarsal bones which function as lever arms. Large indriids, on the other hand, perform the leaps by means of a quick, powerful extension of the hip joint and are characterised by elongated thighs (Gebo, 2011; Schmidt, 2011).

Figure 3.9 Illustration tarsiers, specialised vertical clinger and leapers. The individual on the left is on a clinging position and the one on the right is starting the leap by pushing its body away from the vertical support by means of hindlimb extension and has begun the trunk rotation to face the landing support (after Fleagle, 2013)

Animals that perform **suspensory behaviours** position their centre of mass below the point of contact with the support or superstrate (Youlatos, 2017) and at least one of the limbs is loaded in tension instead of compression (Schmidt, 2011). Several points of contact are frequent in these types of behaviours. This allows the animal to distribute its weight among different supports, helping gain balance as well as avoiding the problems of balancing on top of small, slender branches (Fleagle, 2013). These behaviours are prevalent (though not exclusive) in relatively larger-bodied arboreal primates, such as atelines, gibbons and non-human great apes (Youlatos, 2017). The way that suspensory behaviours are performed vary among primates depending on the number of limbs used, pattern of use of such limbs, including the prehensile tail if available (for instance, in New World monkeys) (Hunt et al., 1996; Youlatos, 2017).

Suspensory behaviours can differ significantly depending on the positioning of the trunk, thus performing pronograde or orthograde suspension (Hunt et al., 1996). During pronograde suspensory behaviours the trunk is more or less parallel to the support, consisting on an inverted form of quadrupedalism or **below-branch quadrupedalism** (Fig. 3.10), usually performed with rather extended limbs (Granatosky et al., 2016). During orthograde suspension the position of the trunk is vertical and either the forelimbs or the hindlimbs are in contact with the support, although other limbs can also be engaged, including prehensile tails (Youlatos, 2017). **Brachiation** consists of a hand over hand way of locomotion accompanied by arm swing and it is characterised by the forelimbs bearing at least half of the total weight of the individual and a high degree of trunk rotation reaching sometimes 180^{o} (Hunt et al., 1996). Brachiation can be fast (ricochetal) or slow (Bertram, 2004), entailing different biomechanical characteristics (Chapter 4).

Figure 3.10 Representation of below-branch quadrupedalism in a monkey assisted by the prehensile tail (after Hunt et al., 1996)

Bipedalism consists on progression along a support using only the hindlimbs and freeing the forelimbs (Fleagle, 2013). Bipedalism is characteristic of humans but can also be performed by several species of non-human primates (e.g., Hewes, 1964; Jenkins, 1972; Fleagle, 1976, 2013; Aiello and Dean, 2006; S.K.S. Thorpe et al., 2007; Duarte et al., 2012). Facultative bipedalism can be observed while carrying objects or food items (Hewes, 1964; Susman, 1984; Duarte et al., 2012) but also to negotiate with certain supports. For instance, when gibbons and siamangs move arboreally on large boughs they tend to walk bipedally with their forelimbs extended above their heads to provide balance (Fleagle, 1976). Another interesting case is seen in the biggest arboreal primate: the orangutan. Orangutans can move bipedally similarly to the way humans do, with rather extended hip and knee joints. This strategy allows them to move on top of highly flexible branches, by means of hand-assisted bipedalism (Thorpe et al., 2007). In contrast, non-human African great apes walk bipedally on the ground, but they do so adopting the very characteristic bent-hip, bent-knee gait (e.g., Jenkins, 1972; Larson and Stern, 1987; Aiello and Dean, 2006; Schmidt, 2011; O'Neill et al., 2015).

Finer classification of locomotor modes have taken into account different factors, such as the type of support, differentiating between substrate (a structure on which the animal balances itself) and superstrate (a structure from which the animal suspends itself), the orientation of the supports (vertical, subvertical, horizontal, subhorizontal or angled), hand and foot contact and orientation, weight distribution and tail grips in the case of New World monkeys (Hunt et al., 1996). As observed, the positioning of the trunk can also be critical in defining some locomotor modes and it can have further consequences on other compartments of the body, especially concerning loading patterns. In practice, primates in the wild can perform a number of "hybrid" positions or locomoor modes, making the study of primate locomotor behaviour extremely diverse and exciting.

3.3.2 Morphology and locomotor behaviour

Locomotor behaviour is influenced by a series of factors such as diet, body mass, musculo-skeletal morphology, predation risk, habitat architecture and spatiotemporal distribution of resources (e.g., McGraw, 1996; Youlatos, 2001; Ankel-Simons, 2007; Schmidt, 2011). In a comprehensive way, locomotion can be considered a "response of morphology (e.g., physiology, anatomy) to the architectural challenges of the environment (substrate availability, size, inclination, texture, etc.)" (Youlatos, in press). This entails that the morphological traits of an animal provide the capacities for specific locomotor behaviours that can be used to overcome the challenges presented by the habitat (Cant, 1992) that have already been discussed in this chapter. Youlatos (2001) studied thirteen species of platyrrhines in two different forests assessing the interactions between intrinsic (morphology-related) and extrinsic (environment-related) factors that could condition locomotor behaviour finding that specific combinations of the extrinsic factors characterise the adaptive niche of groups of species. For instance, the occupation of mainly primary, mature forest, the use of the canopy and frugivory clustered together defining the Atelinae and its particular suspensory behaviour, whereas the use of the understory, insectivory and leaping, with a further use of liana forest and vertical support use was characteristic of the smaller Callitrichinae (Youlatos, 2001). These results show that the habitual adoption of certain locomotor behaviours is not something isolated and characteristic of a primate species as a defining trait *per se*, but rather it is the result of a combination of factors, some of which come from the environment and some other factors concerning the ability of a primate to perform certain behaviours as a result of its anatomy.

Locomotor behaviour, therefore, is highly influenced by morphological features, from body mass to specific adaptations for particular strategies, as well as limb and tail length (Bitty and McGraw, 2007; Garber, 2011; Fleagle, 2013). **Body size** is a limiting factor for most aspects of the life of a mammal (Cachel, 2015) and it also shapes primate locomotor behaviour (e.g., Cant, 1992; Schmidt, 2011; Youlatos, 2017). Smaller primates tend to leap more than larger ones, whereas the latter often have higher proportion of climbing in their locomotor repertoire (Fleagle and Mittermeier, 1980). Both strategies are often associated with particular strata of the canopy, with leaping happening in lower strata and on small supports and climbing at greater heights and on larger supports (Fleagle and Mittermeier, 1980; Gebo and Chapman, 1995a; Bitty and McGraw, 2007). For instance, gibbons can travel in higher levels of the canopy than orangutans, as they are able to leap across major gaps between terminal branches typical of the emerging layers of a forest (Cant, 1992). As a matter of fact, small primates encounter big gaps (relative to their body size) that can only be crossed by leaping. Large primates, on the contrary, are often able to overcome the gaps of the canopy by bridging or by suspending themselves from the terminal branches (Fig. 3.11). However, there is variability in terms of locomotor behaviour and body mass. For example, there is no clear correlation between body mass and the amount of climbing among guenons, and similarly, leaping has not been observed more often in guenons of smaller body size

(McGraw, 2004). Further, Gebo and Chapman (1995a) found that the smaller of the five species of guenons and colobines climbed more and leaped less than the larger ones, challenging the general assumption that large primates leap less.

The ability to leap is greatly determined by the capacity of the hindlimbs to generate enough power to propel the animal's body (Schmidt, 2011). The power required to propel a large animal in a big leap is, in general terms, too big to be efficient, unless power amplification strategies or morphologies are present (Aerts, 1998; Vereecke and Channon, 2013). Postcranial anatomy, therefore, is paramount to the performance of certain locomotor behaviours, which are enabled or constrained by specific **functional adaptations**. Consequently, despite the fact that the primate skeleton is rather generalised (Ankel-Simons, 2007; Schmidt, 2011; Gebo, 2014; Elton et al., 2016), the major differences in postcranial skeletal shape are related to locomotion (Fleagle, 2013).

Figure 3.11 Difference between leaping (above) and bridging (bellow) on terminal branches for gap-crossing (after Fleagle, 2013)

Due to the arboreal origin of primates most of the characteristic traits of the primate body are either adaptations to life in the canopy or retention of primitive traits that were preserved for being advantageous in such environments (Martin, 1990; Ankel-Simons, 2007). Consequently, most adaptations have been studied considering how the original primarily arboreal body plan might have been modified in order to adapt to new environments or different strata of the forest (Elton et al., 2016). Differences in canopy level exploitation in *Presbytis* sp. (Fleagle, 1977) and arboreal *vs.* terrestrial behaviours in *Macaca* sp. (Rodman, 1979) result in anatomical differences concerning limb proportions, muscle lever arms and range of joint mobility. Moreover, differences in habitat use are also reflected in muscle fibre architecture, suggesting that semi-terrestriality is a distinct locomotor category in anatomical and physiological terms (Anapol and Barry, 1996; Anapol and Gray, 2003). In general terms arboreal quadrupeds have longer digits, enhancing the grasping capabilities, longer tails to help them keep the balance and generally, less stable limb joints, which allows them to perform greater ranges of movement, compared to terrestrial quadrupeds (Fleagle, 1976, 2013; Nakatsukasa, 1994; Shapiro and Young, 2017). For example, the increase of mobility at the glenohumeral joint is determined by a more globular head, narrow and confined humeral tuberosities, increased humeral torsion, more distal muscle insertion of the rotator cuff muscles (compromising muscle power as a result of smaller lever arms) or greater inter-tuberosity angles (e.g., Fleagle and Simons, 1982; Larson and Stern, 1989; Nakatsukasa, 1994; Dunham et al., 2017).

A very interesting example of morphological features related to locomotor behaviour is the case of the cercopithecines. The ecological origin of Old World monkeys has been extensively discussed, as they represent a lineage where arboreal-terrestrial transitions seem to have been common in their evolutionary history with one main transition to the terrestrial habitat (Gebo and Sargis, 1994; Tosi et al., 2004; Sargis et al., 2008; Elton et al., 2016). Phylogenetic factors are of minimal importance in the morphology of congeneric species (Fleagle, 1977) and therefore, a good number of functional differences observed in limb morphology are likely to be due to differences in positional behaviours and habitat use (Nakatsukasa, 1994), especially at the level of the **limbs** (e.g., Fleagle, 1977; Rodman, 1979; Fleagle and Simons, 1982; Fleagle and Meldrum, 1988; Meldrum, 1991; Gebo and Sargis, 1994; Nakatsukasa, 1994; Fleagle and McGraw, 1999; Anapol et al., 2005; Elton et al., 2016; Dunham et al., 2017), as they are the main propulsive compartments of the primate body (Badoux et al., 1974; Molnar et al., 2017).

Several studies have been undertaken contrasting the morphology of the mangabey and guenon limbs (Gebo and Sargis, 1994; Nakatsukasa, 1994; Anapol et al., 2005; Sargis et al., 2008; Elton et al., 2016; Dunham et al., 2017) aiming to establish the ancestral condition of guenons and mangabeys, spotting morphological differences reflecting habitat use. Guenons and mangabeys are a good proxy for the study of ecomorphological adaptations, as they represent a good range of types of habitat exploitation in a relatively close group of species, despite their polyphyletic origin (Fleagle and McGraw, 1999; Tosi et al., 2004).

The majority of species of the guenon group exploit the arboreal levels of the forest. Some of the main exceptions are, for example, the patas monkey (*Erythrocebus patas*), a terrestrial quadruped, or vervets (*Chlorocebus aethiops*), a semi-arboreal species of the guenon group (McGraw, 2004). Comparisons among species of the guenon group pointed out specific adaptations of the terrestrial patas monkeys typical of cursors (fast runners), such as lengthened limbs (especially the distal elements), reduction of joint sizes, narrow scapulae and different curvature of the humerus (Gebo and Sargis, 1994; Nakatsukasa, 1994). In contrast, Gebo and Sargis (1994) state that the morphology of the vervet is closer to the other arboreal guenons than it is to the terrestrial patas, despite showing some adaptations to terrestriality, like reduced joint size (restricting mobility of the limbs to the parasagittal plane) or a narrow and tall talar head, which restricts the range of inversion and eversion promoting movements of plantar- and dorsiflexion at the ankle (Gebo and Sargis, 1994). *C. aethiops* is, thus, a “mosaic” primate. Despite the terrestrial component of its behaviour, it is not one of the largest primates among the guenon group. However, it retains a great ability to climb but it moves with adducted and extended limbs, the typical limb positioning of terrestrial quadrupeds (Nakatsukasa, 1994). Compared to other arboreal guenons, it has a rather short (and thus less flexible) trunk and larger distal segments of the limbs, adaptations characteristic of terrestrial cursors, but it has a longer tail than other arboreal primates, which can be interpreted as a compensation for reduced balance in arboreal quadrupedalism resulting from the stiffer back and longer limbs (Anapol et al., 2005).

Comparisons between guenons and mangabeys provided further nuance to the ecomorphological adaptations of cercopithecines. Among mangabeys, the most arboreal species (*Lophocebus albigena*) shows much more mobile joints and gracile bones than the semi-arboreal mangabeys (*Cercocebus* sp.). However, comparing the semi-arboreal mangabeys with the vervets and other semi-arboreal guenons, the mangabeys show stronger adaptations for terrestriality than the semi-arboreal guenon species (Nakatsukasa, 1994). It is important to bear in mind that there is not a typical overall morphology of a terrestrial, arboreal and semi-arboreal cercopithecine, as no (or very few) osteological features are shared by all the species of the same locomotor adaptation (Gebo and Sargis, 1994; Sargis et al., 2008). Thus, despite the differences, all cercopithecines exhibit the Cercopithecinae morphotype, characterised by a certain degree of restriction of joint movement for economical parasagittal movements, compared to the Colobinae, the Cebidae and the Hominoidea (Nakatsukasa, 1994).

The morphology of the ancestral guenon is, thus, still discussed. Some authors argue that the most likely basal guenon was an arboreal or perhaps a semi-arboreal form from which there was a radiation to the terrestrial habitat followed by a slow acquisition of the terrestrial adaptations (e.g., Tosi et al., 2004; Sargis et al., 2008; Elton et al., 2016). Other authors argue that the original guenon was a terrestrial quadruped from which some species returned to an arboreal mode of life with great success. This is supported by the typical terrestrial quadrupedal pattern with adducted and extended limbs in contrast with the arboreal mode, characterised by abducted and flexed limbs (e.g., Fleagle and Meldrum, 1988; Meldrum, 1991; Nakatsukasa, 1994; Fleagle and McGraw, 1999)

Studies on the **spine** are less abundant, maybe due to its complexity or maybe because of its dual function as a weight-bearing, stabilising compartment as well as a propulsive one (Badoux et al., 1974). However, differences in motion of the spine coupled with differences in locomotor habits are reflected in certain morphological features. The degree of movement of the spine is partially determined by the length of its different functional regions (Fleagle, 2013). In fact, the number of vertebrae of each vertebral region varies among primates (McCollum et al., 2009; Williams, 2011) (Table 3.2) and sometimes even within one same species (Whitehead et al., 2005), having consequences in the range of movement. For instance, extant hominoids (especially great apes) have shorter lumbar and longer sacral regions compared to other primates (Fig. 3.12) (Williams, 2011), reducing the range of movement at the lumbar region and bringing close together the ribs with the iliac blades (Aiello and Dean, 2006). This provides these primates with much stiffer lower backs and thus experiencing a decrease in sagittal bending at this region but potentially reducing the compressive stress the intervertebral discs bear that would come with a more orthograde position (Thompson and Almécija, 2017).

Table 3.2 Average number of vertebrae of different families of primates, excluding sacral and caudal vertebrae (modified from Ankel-Simons, 2007)

Family	Cervical	Thoracic (# of ribs)	Lumbar
Lemuriforms	7	13	7
Lorisidae	7	16	7
Galagidae	7	13	6
Tarsiiformes	7	13	6
Callithrichidae	7	13	7
Cebidae	7	14	5
Cercopithecidae	7	12	7
Hylobatidae	7	13	5
Pongidae	7	13	6
Hominidae	7	12	5

Figure 3.12 Comparison of the length of the spine among primates, evidencing the short lumbar spine of apes (after Thompson and Almécija, 2017)

Comparative studies between the patas monkey (*E. patas*) and vervet monkey (*C. aethiops*) reveal functional differences that are again associated to different modes of quadrupedal locomotion and habitat exploitation (Hurov, 1987; Zihlman and Underwood, 2013). At the level of the spine, most primates, as many other tetrapods, perform sagittal bending over lateral bending with the exception of some strepsirhines, especially those of the genera *Loris* and *Nycticebus*, which are characterised by the lateral bending of the lumbar spine during locomotion (Shapiro et al., 2001). In other primate species the degree of sagittal bending varies depending on the locomotor needs of each species (Hurov, 1987; Zihlman and Underwood, 2013). For instance, *E. patas* has a much lower degree of spine sagittal bending than C. *aethiops* (Fig. 3.13). As already seen, the patas monkey is well adapted to terrestrial behaviours, and as a result of the long limbs and trunk it can perform long strides during fast quadrupedalism. Furthermore, contrary to what has been observed in guenons, that move using semiplantigrady strides, patas monkeys exhibit hindfoot digitigrady, also increasing the length of the stride (Meldrum, 1991). Vervets have shorter limbs and trunks, so during fast quadrupedal locomotion they increase the levels of spine sagittal bending, thus increasing the effective stride length (Hurov, 1987). This is anatomically supported by thicker intervertebral discs, which permit a greater degree of intervertebral flexion and is also a sign of arboreal behaviour, fitting perfectly with the ambivalent character of the vervet locomotion (Hurov, 1987).

Figure 3.13 Representation of the sagittal bending of the spine in vervets and patas monkeys estimated by measuring the difference in length of the trunk at different moments of the stride during fast quadrupedal progression (after Hurov, 1987)

It is important to bear in mind that despite the differences in morphology there is one great advantage for comparative anatomists, which is that the primate body always follows a general plan. Actually, "only when the past adaptations cannot cope with new stresses, significant modifications will be developed" (Nakatsukasa, 1994: 40). Therefore, the need to assess the amount of stress the primate body bears is critical in order to understand their anatomical design. Mechanical stress can potentially have a dramatic effect on the postcrania of primates, even challenging their morphological integrity and, thus, biomechanical studies of movement need to be considered in a thorough study of primate locomotion.

CHAPTER 4: BIOMECHANICS OF PRIMATE LOCOMOTION

4.1 Principles of biomechanics applied to primatology

Biomechanics is a discipline used to study forces and accelerations that produce or are produced by the movements observed on living organisms. Living organisms are subject to the same physical laws that apply to inanimate bodies. Similarly to what happens with mechanics there are two divisions: biodynamics (the set of forces and torques that produce acceleration, therefore, responsible for movement) and biostatics (the set of forces and torques acting on a system without experiencing any acceleration). Despite both being important in understanding the musculoskeletal system of vertebrates in this work special focus is placed on the forces and torques experienced by primates during locomotion.

Primates can perform very versatile sets of movements and adopt exceptionally different postures. Nevertheless, the mechanical principles applicable to primate locomotion fall under the three basic laws of motion, or Newton laws:

- First Newton's law (the law of inertia): in normal conditions a body stays in a state of rest or uniform motion unless forces act to change such state.
- Second Newton's law (the definition of force): a change of speed over time (acceleration) of a moving object is directly proportional to the force acting upon said object. Therefore, force (F) equals the mass (m) of the object times the acceleration (a) of its movement.

$$F = m * a$$

Equation 4.1

- Third Newton's law (the law of reciprocity): for every action there is a reaction; for every force there is a reaction force of equal magnitude and opposite direction.

These laws are based on broad principles that can explain in general terms the system of forces acting upon the vertebrate skeleton. For instance, if a monkey leaps from a branch, according to the first of Newton's laws, its body would continue in constant speed and trajectory if it was not for the acceleration of gravity and the friction with the air that act in different directions than the original trajectory of the monkey (Badoux et al., 1974). Similarly, the acceleration of the propulsive momentum of the leap of this monkey will be proportional to the force applied (Newton's second law).

The third of Newton's laws, the law of reciprocity, is probably the most important one in this work as it states that for each force (action) a new force is generated of equal magnitude and in opposite direction (a reaction force). This entails that when a primate generates a force against a support there always is a reaction force of equal magnitude that "rebounds" on the animal. These reaction forces shape the functional aspects of the structural system of an animal.

The skeletons of mammals that exploit terrestrial habitats must face one common challenge: being able to bear stresses that result from supporting their bodies and moving under the action of gravity (Biewener, 1990). Therefore, forces are crucial in order to understand the musculoskeletal system of mammals and their adaptations. Whereas intrinsic forces (those coming from the individual under the effect of gravity) are important to determine theoretical morphologies, substrate reaction forces are particularly important in determining ecological adaptations (Franz et al., 2005).

Most mammal skeletons maintain a safety factor (ratio between the failure stress and the actual or functional stress born by an element) that prevents them from failure. The mechanism by which this factor is obtained, however, varies depending on the size of the animal (Biewener, 1990). As seen previously, many skeletal structures in the primate body are determined and designed based upon biomechanical principles (Chapter 2). Any skeletal structure must be able to bear the forces that act upon it without failure (conceived as breakage or any modification that entails the non-functionality of the structure).

Size and shape are, therefore, functionally linked in order to withstand forces and torques and so avoiding failure. Scaling differences in the increase of volume (body size) with respect to surface entail a decrease in the capacity of bone, muscle and tendon to support or generate forces (e.g., an increase of 10 times in diameter of a terrestrial mammal would entail a mass or volume increase of 1000 times but only of 100 times of the surface of the limbs that host the supporting musculoskeletal system, Fig. 4.1) (Martin, 2007; Kardong, 2015). As a result, a change in body design would be necessary in order to mechanically maintain differences in body size among mammals saving the scaling differences.

Diameter = length = L

Surface =L^2

Volume (i.e. mass) = L^3

Figure 4.1 Scaling conflict of allometric differences in size in mammals. Left: scalar differences among size variables. Right: Theoretical size and shape of a proportionally scaled bone from Galileo Galilei (after Martin, 2007)

Changes in bone shape in different mammals allow bigger animals to bear greater forces in. However, in terrestrial mammals ranging from 0.1 to 300 Kg these skeletal changes are less drastic than would be necessary to withstand differences in forces of different sized mammals (Biewener, 1990). Moreover, in skeletal terms, mammals are geometrically similar (isometric) and, therefore, peak stress on the supporting limbs is predicted to increase with size. Consequently, different strategies have been adopted for peak forces on the skeleton to decrease and avoid structural failure.

Primates exhibit rather divers body sizes among the Order, ranging between 60g and approximately 160 Kg (Smith and Jungers, 1997) but they preserve similar musculoskeletal patterns. Therefore, the question as to whether these differences in body size entail significantly different biomechanical requirements remains open. Moreover, as previously stated, primates perform an extraordinary array of locomotor behaviours, which also entails a great variability of mechanical input. As a result, similarly to other mammals, primates have acquired a set of adaptations, both morphological (e.g., Hurov, 1987; Gebo and Sargis, 1994; Zihlman and Underwood, 2013) and behavioural (e.g., Reynolds, 1985a, 1985b, Schmitt, 1994, 1999) in order to deal with the different biomechanical demands during locomotion.

4.2 Particularities of the quadrupedal gait in primates

Quadrupedalism is the most common type of locomotion among primates. Despite the fact that primates have developed different locomotor adaptations nearly all primates include quadrupedalism as part of their locomotor behaviour (Shapiro and Young, 2017). Furthermore, it is likely to represent the antecedent mode of locomotion to other more specialised non-quadrupedal strategies (Byron et al., 2017). Primate quadrupedalism shows some kinetic and kinematic differences with non-primate mammals' quadrupedal locomotion (e.g., Ishida et al., 1990; Demes et al., 1994; Larson, 1998; Schmitt, 1998, 1999; Larson et al., 2000; Larson and Stern, 2009). Some commonly listed particularities of primate quadrupedal gait are (Larson, 1998; Larson et al., 2000; Larney and Larson, 2004; Schmitt, 2006):

- Diagonal footfall sequence.
- Greater reliance on the hindlimb for propulsion and support.
- Use of longer strides at lower frequencies, as a result of greater angular joint excursion and relatively long limb bones.
- Near absence of a running trot.
- Different muscle engagement patterns during a stride.

Gait is the term used to describe the step cycle and the stride is its primary unit of analysis (Aiello and Dean, 2006). Each **stride** is defined as

> *"[…] a single, complete cycle of limb movement and is comprised of a propulsive phase, during which the foot is in contact with the substrate, and a swing phase, during which the foot is free of the substrate"* (Goslow et al., 1989: 289).

The main interest of this research lies on the propulsive or contact phase of the stride cycle, when the animal's limbs are in direct contact with the support. This is a dynamic phase and is composed of the touchdown, stance and liftoff phases. Therefore, the key moments of a stride used to assess forces during locomotion are touchdown, mid-stance or mid-support, liftoff and mid-swing (Fig. 4.2) (Larson and Stern, 1987).

Early observations noted that the primate footfall pattern differs to that of other mammalian quadrupeds (Demes et al., 1994). Primates use a **diagonal sequence** footfall pattern, which entails that diagonal or contralateral limbs (right forelimb and let hindlimb or left forelimb and right hindlimb) make contact with the support simultaneously, contrary to the pattern observed in non-primate mammals, where ipsilateral limbs make contact with the support simultaneously during quadrupedal walking (Fig.4.3). The diagonal sequence pattern provides stability, especially for those species that move and forage on fine terminal branches (Schmitt, 2006).

Figure 4.2 Different moments of the contact phase of a stride. From left to right: touchdown (TD), mid-stance (MS) and liftoff (LO) for the forelimb (above) and the hindlimb (below) of an arboreal quadruped (after Larney and Larson, 2004)

Angular **joint excursion** is greater in primates (and in some arboreal marsupials) than in non-primate mammals (Fig. 4.3 and 4.4), exhibiting highly protracted limbs (i.e. flexed at the hip or the shoulder or cranial displacement of the limb) at the moment of touchdown, with lorisids being the extreme case of humeral protraction (Larson, 1998; Larson et al., 2000, 2001; Larson and Stern, 2009). Greater angular joint excursion is achieved despite exhibiting a lesser degree of limb retraction (extension at the shoulder joint or caudal displacement of the limb) compared to other mammals (Larson et al., 2000).

Figure 4.3 Representation of different degrees of forelimb protraction and of a lateral footfall typical of terrestrial non-primate mammals (left), where the ipsilateral limbs (forelimb and hindlimb of the same side) make contact with the support simultaneously vs. diagonal footfall, typical of primates (right), where the contralateral limbs (for instance the right forelimb and left hindlimb) make contact with the support simultaneously (after Granatosky et al., 2016)

Greater joint mobility is, in part, facilitated by the longer muscle fascicles in primates limb musculature (Thorpe et al., 1999) and the decrease in osteological stabilisation of joints and reduced robusticity of limb bones, especially in arboreal species (Schmitt, 1998). This results in primates performing **longer strides**. As previously seen, another contributing factor to the elongation of the stride is the higher degree of sagittal bending of the spine typical of most mammalian species, in contrast to the lateral bending, typical of the non-mammalian vertebrates (Hurov, 1987; Shapiro et al., 2001; Zihlman and Underwood, 2013). Greater stride lengths enable primates to move at higher speeds despite exhibiting **lower frequency of strides** during quadrupedal walking (Larson et al., 2000). In an arboreal environment, reducing the frequency of strides translates in reducing the amount of repetitive impact on a branch, leading to a reduction of branch sway. Therefore, a reduction of stride frequency facilitated by a longer stride length, is highly beneficial for primates, which can perform a more stable above-branch quadrupedal locomotion (Larney and Larson, 2004).

Figure 4.4 Representation of forelimb joint excursions in quadrupedal mammals, including some non-human primates, where the two segments represent the humerus and the ulna and the point of contact with the ground is the wrist (after Larson, 1998)

Walking is a basic type of gait in which each foot is in contact with the support at least half of the time of a step (Larson et al., 2001). As many other terrestrial vertebrates, primates can also move at higher speeds. However, they **rarely perform a running trot** (a high frequency and high stiffness gait). Instead, primates perform an intermediate-speed run with no fully aerial phase. This ensures that there is always a point of contact with the support, providing stability and avoiding big oscillations of the centre of mass (Schmitt, 2006). Therefore, primates generally advance from a walk to a gallop (Larson, 1998) and, as a consequence, Schmitt (2006) described the primate walk as an amble gait with no mid-speed running. The absence of a running trot among non-human primate locomotor behaviour is regarded as a strategy to avoid high peak stresses on the limbs (Larson, 1998).

Increased mobility of joints can only be obtained at the expenses of joint stability and the extraordinary level of mobility of the primate forelimb would not be possible if this limb was subjected to high locomotive forces (e.g., Larson, 1998; Schmitt, 1998; Larson and Stern, 2009). Therefore, primates have **greater reliance on the hindlimb** in comparison to the forelimb. Some of the first observations reported that terrestrial mammals support on average 55-60% of their body weight on their forelimbs, whereas primates only support 30-45% (Reynolds, 1985a, 1985b). Further studies have shown that these proportions vary among taxa, even showing inverse patterns in the case of the slow loris (Ishida et al., 1990; Schmitt, 1994, 1998; Schmitt and Lemelin, 2004; Hanna et al., 2017).

This uneven limb reliance is, in part, possible due to different **musculature recruitment patterns** (Reynolds, 1985b; Larson and Stern, 1987, 1989; Larson et al., 2000; Larson and Stern, 2009). Vertebrate muscle activation patterns have remained rather unaltered throughout evolution (e.g., Goslow et al., 1989; Diogo and Wood, 2013; Molnar et al., 2017), as evidenced by the conservative neuromuscular activation routes in different species of vertebrates. Homologous muscles exhibit the same patterns of motor regulation and the original neural control has persisted in derived groups despite presenting differences in morphology (Goslow et al., 1989; Okada, 1978 in Larson, 1998; Molnar et al., 2017).

The evolution of the primate forelimb is conservative and consistent with the phylogeny of the Order in terms of number of musculoskeletal elements (all primate taxa have five different groups of musculature acting as anatomical units depending on organisation and function). However, the way the forelimb's musculature is arranged is independent to phylogeny, but a result of adaptation to behavioural needs or locomotor requirements of each taxon (Molnar et al., 2017), with most of the organisational groupings among primates answering to a locomotor behaviour proxy. As a result, the proximal modules of the limb are less variable within primates in comparison to other vertebrates, and it is the more distal segments that exhibit substantial variation (Diogo and Wood, 2013).

Most variability in musculature relies on different engagement patterns during locomotion, concerning mainly the moment of muscle activation during the step cycle, especially for the forelimb, as seen in the chimpanzee's shoulder musculature compared to the lizard's (Larson and Stern, 1987; Goslow et al., 1989). Differences on muscle recruitment were seen, for example, in comparisons between non-primate taxa and the chimpanzee's forelimbs, which in the case of the chimpanzee are subject to different levels of abduction and adduction as a result of overstride (i.e. placing the hindlimb ahead of the forelimb) (Larson and Stern, 1987). In the case of squirrel monkeys, which walk with highly abducted limbs, some flexor muscles might be recruited in order to act as adductors (Schmitt, 1994). Furthermore, muscle activation can happen with the aim of stabilising a joint, especially in those species with adaptations to suspensory and climbing activities that show high degrees of joint mobility at the girdles at the expense of skeletal stabilisation and not with pure locomotive purposes (Larson and Stern, 1987). Comparisons were made using terrestrial and semi-terrestrial species of primates that present laterally placed scapulae and joint morphology closer to that of an opossum or a cat and still the musculature recruitment pattern was closer to that of a chimpanzee than to the non-primate taxa (Larson and Stern, 1989). These results support the idea of a particular pattern of muscle recruitment in primates compared to other terrestrial quadrupedal mammals.

These particularities of the quadrupedal gait of primates seem to reflect a set of strategies adopted in order to facilitate locomotion on an arboreal niche where primates deal with small branches, supporting the idea of the arboreal origin of primates among terrestrial mammals (Chapter 3).

4.3 Limb mechanics during quadrupedal locomotion

Differences in gait characteristics entail different mechanical requirements, in particular for the weight-bearing regions of its body. During locomotion a set of forces is produced and received by the animal, some allow for its movement and some act on the animal's body as a result of movement, a principle based on the third Newton's law or law of reciprocity (e.g., Biewener, 1990; Schmitt, 2003a;

Schmidt, 2005a). In primate walking the basic system of forces of the resultant reaction force during the support phase of a stride includes three different components (Fig. 4.5), often expressed as a percentage of the individual's body weight (Schmitt and Hanna, 2004):

1) Vertical peak forces that enable the exchange of potential and kinetic energy and produce a reaction force from the support of equal magnitude and opposite direction, called the support reaction forces (SRF).

2) Propulsive and breaking forces (also referred to as fore-aft forces), which are the components of the system acting on a cranio-caudal direction, therefore, going in or against the direction of movement and result in changes of acceleration of the body (Abdelhadi et al., 2012).

3) Medio-lateral forces, side-to-side forces that are a result of the direction of the limb at the moment of contact (Schmitt, 1998, 2003a; Schmidt, 2005a; Abdelhadi et al., 2012).

Figure 4.5 Representation of the skeleton of a baboon walking on the ground. The baboon applies to the support a vertical force, a propulsive-breaking force (fore-aft) and a medio-lateral force that produce a combined reaction force acting in the opposite direction and consisting of the vectorial sum of the other forces (after Schmitt, 2003a)

The substrate reaction resultant (SRR) is the vectorial sum of the three components mentioned above (Schmitt, 2003a). This force always takes the opposite direction of the resultant vector.

The action of these forces during a step is continuous and of a fluctuant nature. Therefore, in different moments of a stride's support phase (touchdown, mid-stance and liftoff), forces will vary in magnitude and direction. For instance, right after touchdown a braking force takes place, followed by a vertical peak force around the moment of mid-stance. Then there is a transition from a braking to a propulsive force (fore-aft forces) before the propulsive peak, followed by the moment of liftoff, concluding the step cycle (Schmitt, 1998). The magnitude and direction of the resulting forces vary among and within primate species (Fig. 4.6).

Figure 4.6. Comparison of the magnitude of forces between a baboon (left) and a vervet (right) during the different moments of the contact phase of a stride: touchdown (TD), braking force (BRAKE), mid-stance (MSP), vertical peak force (VERT), braking/propulsive transition (B/P), propulsive force (PROP) and liftoff (LO). The dashed lines represent the adjusted mean values during locomotion on small supports and the solid lines during terrestrial locomotion (after Schmitt, 1998)

Figure 4.6 reveals how the magnitudes of the forces described are not equal and vary at different moments of the step cycle. In general terms the vertical peak forces (SRF) are the greatest in magnitude. Braking and propulsive forces are consistently lower in all primate species, despite the unique situation of standing leaps and jumps, where the propulsive peak force can be up to a half of the vertical peak force, depending on the need to gain horizontal momentum from a zero horizontal velocity (Demes et al., 2005). Fore-aft forces seem to be influenced by the position of the centre of mass relative to the limb point of contact with the support (Granatosky et al., 2017). Medio-lateral forces are often ignored in biomechanical studies (Franz et al., 2005), with the exception of the study done by Schmitt (2003). Schmitt (2003) observed that morphological features on the joints, as well as limb alignment with the resultant force, often accompany greater medio-lateral forces in order to help withstand such forces. Considering this, SRF is the main force considered in the remaining of this thesis.

4.3.1 Limb positioning in primates and loading of joints

The recording of the positions of joints at different phases of the stride is a key part in the analysis of locomotion. By doing this, it is possible to calculate moment arms, correlate forces and movements and assess joint movement, velocities and accelerations (Thorpe, 1997). For instance, a flexed limb posture results in higher joint and bone stresses if the substrate reaction forces are of equal magnitude in a comparison with a more extended limb position. This is because in a more flexed position there is an increase of the moment arm, a measure of the amount of load that a joint must bear (Fig. 4.7) (e.g., Biewener, 1990; Schmitt, 1998).

Figure 4.7 Representation of the skeletons of an arboreal (a) and a terrestrial primate (b) walking on an arboreal vs. a terrestrial support. Differences in the degree of flexion of the limbs are noticeable as well as the dimensions of the vertical, fore-aft and medio-lateral forces (depicted as the white headed arrows), leading to a difference in magnitude of the SRF (black headed arrow). As a result of the limb positioning and the degree of flexion there are noticeable differences regarding the magnitude of the moment of force on the elbow joint of both species (dotted line). Thus, moments of force of arboreal quadrupedal primates tend to be greater than moments of force of terrestrial quadrupedal primates (after Schmitt, 1999).

Moment arms or moments of force represent the amount of load born by a joint and it is quantified as the perpendicular distance between the centre of joint and the resulting vertical reaction force (Biewener, 1990; Thorpe, 1997; Schmitt, 1998) (Fig. 4.7). Thus, the joints of the flexed limb shown in figure 4.7 would bear a greater load, as the distance between the joint and the reaction force is also greater. An increase of the moment arm of the reaction force (moment of force) is coupled with a decrease in the mechanical advantage of the muscles that hold the position, generating higher force requirements and stress for the muscles to maintain the posture (Thorpe, 1997; Schmitt, 1998). Mechanical advantage is often regarded as greater muscle moment arms, allowing for greater joint movements (Biewener, 1990; Thorpe et al., 1999; Leardini and O'Connor, 2002; Payne et al., 2006; Michilsens et al., 2010). Therefore, the **effective mechanical advantage** (EMA) of a joint is understood as the ratio between the agonist muscle's moment arm (r) and the moment arm of the substrate reaction force or moment of force (R) (Equation 4.2; Fig. 4.8) (Biewener, 1990) and this is the reason for which greater substrate reaction force moment arms (R) entail greater load, as it directly reduces the EMA.

$$EMA = \frac{r}{R}$$

Equation 4.2

Figure 4.8 . Graphic representation of the substrate reaction resultant force (Fg), the muscle moment arm (r) and the moment of force (R) on the limb of a squirrel monkey (modified from Biewener 1990)

In contrast, following Biewener's definition of EMA, greater muscle moment arms would increase the overall value of the EMA reducing the load on the joint. A muscle's moment arm is "the measure of the ability of a muscle to produce joint torque in order to generate rotation and/or to resist external forces" (Leardini and O'Connor, 2002: 220) and it graphically represented as the perpendicular distance between the line of force of a muscle and the centre of rotation of a joint (Thorpe, 1997) (Fig.4.9).

Figure 4.9 Graphic representation of a moment arm of gastrocnemius (flexor of the knee). The moment arm is the perpendicular distance between the line of action of the muscle and the centre of rotation (CR) of the knee joint (after Thorpe, 1997)

A comparative study between humans and chimpanzees showed that in order to effectively withstand equal maximum SRF, chimpanzees would need muscles capable of exerting larger moments at the joints during bipedal locomotion (Thorpe, 1997; Thorpe et al., 1999). Chimpanzee muscles' exert smaller moment arms at the hindlimb joints due to slightly different muscle attachment sites but also due to the smaller physiological cross section area (PCSA) of their muscles, thus performing forces of lesser magnitude, which diminishes the magnitude of the moment arm.

Differences in musculature PCSAs, attachment sites of muscles and range of movement of joints, therefore, play an important role in determining muscle's moment arms acting on a joint. Unfortunately, information on PCSA, detailed anatomy and quantification of muscle moment arms for limb joints is rare and despite there being studies on detailed dissections (e.g., Swindler and Wood, 1982; Diogo and Wood, 2013) as well as moment arm assessment in different species of primates (e.g., Thorpe, 1997; Thorpe et al., 1999; Payne et al., 2006; Michilsens et al., 2010; Goh et al., 2017), the information available is too fragmentary. Consequently, musculature moment arms and its role in reducing mechanical load will not be included in this thesis.

Moments of force are mainly determined by the direction and magnitude of the peak reaction force from the support and the positioning of the limb during locomotion and, therefore, they are easier to assess and have been further studied. For instance, larger mammals generally locomote with more extended limbs, so that the limb joints are more closely aligned with the resultant substrate reaction forces. This involves greater EMA that counteracts the greater magnitude of the reaction forces due to their bigger body size, especially during running or high speed gaits (Biewener, 1990). Compared to other mammals, primates walk with generally more extended limbs in nearly every stage of the step cycle (Larney and Larson, 2004), which results in a reduction of the joint moment arms, ultimately, increasing the EMA.

The degree of limb extension among primates, however, varies considerably within the Order. In general terms the limbs of terrestrially adapted primates move in a more extended position on the parasagittal planes, whereas arboreal primates exhibit a more abducted and flexed position of the limbs in contrast to terrestrial primates (Larson, 1998), with some exceptions. As previously seen, Old World cercopithecines are basically adapted to terrestrial quadrupedalism. However, some of these cercopithecines inhabit arboreal environments (e.g., guenons) and these arboreal monkeys, contrary to what is seen in other tree-dwelling primates (both strepsirrhines and platyrrhines), still exhibit a rather extended and adducted position of the limbs (Larney and Larson, 2004; Schmidt, 2005a, 2005b). These differences in limb positioning and the degree of flexion result in different biomechanical requirements and, here, an interesting paradox arises. Primates are predominantly arboreal mammals and a more crouched position is expected, despite some exceptions. Therefore, if the magnitude of the reaction force was equal to that observed during terrestrial (and more extended) locomotion they would experience much greater absolute substrate moment arms. Schmitt (1998) proposed two alternative mechanisms to explain this: 1) that there is more to the crouched position during arboreal locomotion than has been observed and described, or 2) a change in the magnitude of substrate reaction forces in arboreal *vs.* terrestrial environments that accompanies the differences in postures, reducing the absolute load.

Differences in the amount of flexion are not only observed between species or locomotor behaviours. There are noticeable differences between forelimb and hindlimb in almost all primate species (e.g., Schmitt, 1994; Larney and Larson, 2004), entailing differences, not only on the amount of load for homologous joints of the two sets of limbs, but also in modulating the substrate reaction forces.

4.3.2 Substrate reaction forces (SRF) on limbs and variability among taxa

Kinetic studies of primarily arboreal primate species have shown that primates experience a unique distribution of substrate reaction forces, supporting greater forces with their hindlimbs, corresponding with the characteristic shift of weight towards the hindlimb (section 4.2). The rationale for this shift of support is the use the hindlimb as the main supportive organ, releasing the forelimb from weight-bearing stresses, giving it a more versatile function (Schmitt, 1998; Patel et al., 2015; Granatosky et al., 2016a). A study on gait mechanics of the woolly opossum showed that this is the only studied non-primate mammal that has identical gait mechanics to the general primate. They show a diagonal sequence gait, protracted arms at touchdown and lower peak reactive forces for the forelimb than the hindlimb, questioning whether this type of gait mechanics is an adaptation to the small-branch niche occupation instead of being a unique primate characteristic (Schmitt and Lemelin, 2002). Despite this being the most common pattern of distribution of SRF among primates (e.g., Demes et al., 1994; Schmitt, 1998, 1999, 2006; Schmitt and Lemelin, 2002; Schmitt and Hanna, 2004; Hanna et al., 2006, 2017; Granatosky et al., 2017), the degree of differentiation between forelimb and hindlimb regarding the intensity of SRF can vary.

The first exception to the general rule of primate gait mechanics are some **catarrhine monkeys**, who tend to show no significant differences between forelimb and hindlimb when walking on the ground (Schmitt, 2003b; Schmitt and Hanna, 2004). Furthermore, *Papio anubis* and *Erythrocebus patas*, two terrestrially adapted primates, reveal an inverted pattern, with greater SRF born by the forelimb. Thus, Old World monkeys seem to be closer to other non-primate mammals (Schmitt and Hanna, 2004).

The slender **loris** (*Loris tardigradus*) and the slow loris (*Nycticebus coucang*) show reverse patterns of limb force bearing: forelimb peak SRFs are higher than those for the hindlimb, despite exhibiting slightly longer contact times with the support (Ishida et al., 1990; Schmitt and Lemelin, 2004). The peak SRFs for *L. tardigradus* were overall higher than those of *N. coucang*, probably due to the lower speed of *N. coucang* (more information regarding the role of speed is presented in section 4.3.4). Current biomechanical models cannot explain these different patterns and further research needs to be done, but it seems that these lorisids do not actively reduce SRF on their forelimbs and it might be because of the lack of functional differentiation between limbs (Schmitt and Lemelin, 2004). Strepsirhines are highly variable in locomotor strategies. For instance, lemurids have different functional limb length compared to other primates. They walk with their trunks inclined forward and downwards, which might entail differences in the system of forces acting on these limbs (Franz et al., 2005). Other strepsirhines, on the other hand, are highly efficient jumpers and have functionally different limbs.

Jumping and leaping among strepsirhines, however, can be rather variable. Jumping in lemurs is often performed with a run up and run out and, whereas the intensity of peak SRF is similar to that observed during quadrupedal walking, their distribution is variable. During the takeoff phase of the jump the hindlimb always supports higher peak SRF, whereas at the moment of landing, the more heavily stressed limbs are the first limbs making contact with the support. For instance, in a comparison between *Lemur catta* and *Eulemur fulvus* both species carry higher SRF on their hindlimbs during takeoff but at the moment of landing *L. catta* almost exclusively lands hindlimbs-first, loading these limbs a lot more than the forelimbs, whereas the opposite happens in *E. fulvus*, which almost exclusively lands forelimb-first, increasing the load of SRF for these limbs (Demes et al., 2005). Stronger SRF in the forelimb is a rare observation among primates. Moreover, the magnitude of the landing forces for the forelimb in *E. fulvus* is never greater than the peak forces for their hindlimbs at the moment of takeoff, whereas the landing SRF born by the hindlimb of *L. catta* is always greater in magnitude than the takeoff SRF, meaning that there is still a need for minimising forelimb peak SRF.

Primates performing standing leaps are subject to much greater SRF as well as propulsive forces. This is characteristic of specialised **vertical clingers and leapers**

(VCL), which perform leaps with no run up phase and almost exclusively relying on the power produced by the hindlimb. In these types of jumps the propulsive forces significantly increase in magnitude, reaching up to half of the vertical force, depending on the need to gain momentum from 0 horizontal velocity (Demes et al., 2005). VCLs, in contrast to quadrupeds, have higher degree of femoral bending (less rigidity) and higher extensor muscle mass as adaptations to deal with higher impact (Demes et al., 1999, 2005). Considering the mechanical stress of this locomotor strategy, it is likely that these primates benefit from a power amplifier that releases previously stored energy (Aerts, 1998). During quadrupedal walking VCLs follow the same pattern as other habitual quadrupeds, despite the mechanical differences experienced during jumps (Granatosky et al. 2016b).

Some primates have the ability of switching from above- to **below-branch quadrupedal locomotion**, where the forelimb becomes the main weight-bearing and propulsive limb (Granatosky et al., 2016a). In the study conducted by Granatosky and co-workers (2016a) the biomechanical patterns observed were reversed for most aspects during below-branch locomotion, such as the greater force by the forelimb. They assess that many of the anatomical features of slow-moving primates that commonly adopt below-branch quadrupedal locomotion are similar to those of arm-swinging primates. Therefore, in a way, below-branch quadrupedalism can be regarded as a potential antecedent for brachiation.

Fluid **brachiation** reminds the oscillations of a pendulum and allows for the constant interchange of gravitational potential energy and kinetic energy (Bertram et al., 1999; Bertram, 2004; Byron et al., 2017). Two distinct types of brachiation gaits are observed from a mechanical point of view and both are characterised by the single involvement of the forelimbs during locomotion. At slower speeds, brachiators adopt a continuous contact gait, where the individual seems to simply swing under the support and resembles a simple-pendulum model. At higher speeds, however, brachiators perform a ricochetal gait, with a contact phase followed by an aerial one, thus, combining a pendulum-like motion with a parabolic flight stage (Fig. 4.10).

Regulation of speed is a critical aspect for brachiators, who move in a complex network of supports. One strategy of regulating speed is to modify the distribution of their mass around the swing pivot (Bertram and Chang, 2001). However, these changes in mass distribution do not account for higher speeds, which are often adopted through ricochetal brachiation, where the forward speed increases, as it compensates for the deceleration observed during the second half of the contact phase (Bertram, 2004), also decreasing the energetic cost of it (Michilsens et al., 2011).

Figure 4.10 . Graphic representation of the trajectory of ricochetal brachiation, consisting of two phases: one pendulum-like contact phase and one ballistic, parabolic-like aerial phase, with detail on the transition from the parabolic trajectory of the ballistic phase to the circular arc of the swing phase (modified from Bertram et al., 1999)

SRFs on the forelimb are only produced during the contact phase of both brachiation gaits. The system of SRF is not too different to that observed during above-support motion but with the peculiarity that, in this case, the forelimb is the only limb involved. Peak vertical forces are high, they reach the peak value at mid-support of the swing phase and they are the reaction of the force produced during rotational motion. The fore-aft forces are lower and have a propulsive nature in the first half of the swing and a breaking nature in the second half. The medio-lateral forces are very low and often ignored (Byron et al., 2017). The vertical force, however, is greater in ricochetal brachiation, presenting negative correlation with the contact time of the hand and the support (Bertram and Chang, 2001).

4.3.3 Models of reduction of forelimb reaction forces

Primates, not only perform a shift of their weight towards the hindlimb, but, in general terms, they also bear stronger peak reaction forces on this limb compared to their forelimbs, contrary to what has been observed in other terrestrial quadrupedal mammalian species. The shift towards the hindlimb liberates the forelimb from a weight-bearing function and allows it to function as a manipulation structure, or a steering element during fast arboreal locomotion, where quick changes of direction are necessary (Schmitt, 1999). This shift is not produced by a change in position of the centre of gravity in the primate body (Reynolds, 1985a), but instead, it is a result of other mechanisms.

Two main models have been suggested to achieve the shift in weight bearing and the reduction of magnitude of SRF acting on the forelimb:

1. Reynold's model of hindlimb retractors (1985a, 1985b).
2. Schmitt's model of the compliant primate gait (1999)

The first model was based on the action of **hindlimb retractors** as a means of reducing peak reaction forces on the forelimb (Reynolds, 1985a, 1985b). The first observations by Reynolds (1985b) pointed out that, in a standing quadruped, greater weight support by the hindlimb could be achieved through higher protraction of the hindlimb and/or the forelimb. However, the levels of protraction observed were never enough to explain for the total amount of weight born by the hindlimb (Larson and Stern, 2009). Therefore, this would support Reynold's suggestion that the shift is generated by muscular effort. A limb is considered a strut if its musculature is not engaged and a set of forces, including reaction forces, act on this limb when in contact with the support. However, when the musculature is engaged, the limb acts as a lever and this modifies the horizontal and vertical forces acting on the limb, as depicted in figure 4.11. The engagement of retractor musculature reduces the magnitude of horizontal and vertical forces on the forelimb and shifts the trunk towards the hindlimb, whereas the action of protractor musculature increases these forces (Reynolds, 1985b). The role of the extensors is particularly effective as a weight shifter when the hindlimb is protracted.

Reynolds (1985a) argued that the importance of the action of hindlimb retractors is based on the need to reduce the stress on the forelimbs, especially in those species that present more dorsally located scapulae, as they present more highly mobile joints and shear stress is greater at these joints. This was confirmed by Demes and co-workers (1994) who conducted a force plate study seeing that those species with dorsally located scapulae presented the highest disparity between forelimb and hindlimb force incidence.

Figure 4.11 Example of the modifications of the system of forces with the limbs acting as struts (no musculature engaged) or as levers (with musculature engaged) (modified from Reynolds, 1985b)

The second model of force reduction for the forelimb is based on the **compliant primate gait** (Schmitt, 1999). This study proved that there is an overall reduction of the peak reaction forces, both for the forelimb and the hindlimb, when a compliant gait is used. A compliant gait is characterised by: a) an increased step length, b) prolonged contact time with the support, and c) substantial limb yield, defined as the change in angle during a step (flexion from touchdown to mid-stance and re-extension from mid-stance to liftoff) (Schmitt, 1994, 1998, 1999; Larney and Larson, 2004). Different degrees of forelimb/hindlimb peak reaction forces can, therefore, be explained by longer contact time with the support and the higher degree of forelimb yield typical of primates (section 4.3.1), with the exception of the cercopithecines that show greater hindlimb yield, a common pattern of terrestrial quadrupeds (Larney and Larson, 2004).

These two models of reduction of forelimb peak vertical reaction forces are valid and both have been repeatedly corroborated in experimental studies. These models are thus compatible and it is likely that they complement each other in the reduction of forelimb SRF.

4.3.4 *Other factors modulating the effect of forces: body size and speed.*

The magnitude of the SRF is adjusted by the two aforementioned mechanisms but the intensity of these forces is also determined by other factors. Body size, for instance, is a limiting factor for locomotion and musculoskeletal design and SRF are highly influenced by it, playing an important role within mammals in determining the speed of movement. Furthermore, body size and speed account for a good number of positional strategies observed for the limbs of primates.

SRF is a reaction force and the main contributor to the action force is the animal's body weight. The heavier an animal is the bigger the action force against the support is and so is the reaction force. However, large animals have strategies to deal with these big forces. As mentioned before, large mammals run with more extended limbs, aligning the joints with the reaction force, decreasing the moment arms and increasing the EMA (Biewener, 1990).

Differences in dimensions, however, do not always apply to the animal as a whole. Cercopithecine monkeys are a good example, as body mass and limb proportions do not scale proportionally; they have longer limbs relative to their overall dimensions compared to other mammals. A comparison of SRF among different species of cercopithecine species showed that animals of similar body sizes with longer limb segments exhibit more extended limbs during locomotion and, thus reduce the moment arms (Polk, 2002). Therefore, bigger primates adopt strategies to deal with greater reaction forces (i.e. limb extension) but those primates with bigger relative limb proportions perform similar strategies to neutralise the effect of apparently greater moment arms.

Dynamic properties of locomotion in mammals such as speed are also dependent on body mass. In general terms, mammals with body sizes greater than 5 Kg use straight-legged or cursorial type of running, whereas animals under the 1 Kg threshold tend to use a bent-legged position or non-cursorial (Stein and Casinos, 1997). The speed of movement of a primate using a specific gait is of critical importance in some postural traits but also in the modulation of SRF.

Speed is negatively correlated with maximum arm protraction-retraction, maximum elbow flexion and height of the shoulder, and shows a positive correlation with SRF (Schmitt, 1998). Therefore, an increase in speed is coupled with an increase in the SRF and a decrease in the duty factor (Reynolds, 1985a; Thorpe et al., 1999), defined as the "duration for which a limb is in contact with the support" during a stride (Polk, 2002: 3399).

Hanna and co-workers (2006) compared two different speeds in primate gaits (walking and gallop) and tested whether there were different patterns of limb differentiation in force bearing. Galloping is a higher speed gait and it has periods of single limb contact with the support and a fully aerial phase, contrary to what is seen during walking where at least two limbs are in contact with the support (Fig 4.12). Their results suggest that the pattern of force distribution during walking and galloping is similar for most primate species. However, the degree of differentiation of the forelimb is reduced during galloping, thus showing an increasing trend for the intensity of SRF for the forelimb despite it not being statistically significant. Furthermore, some primate species present an inverted pattern of forelimb-hindlimb force bearing when galloping, like the capuchin monkeys and the common marmoset (Hanna et al., 2006).

Figure 4.12 Graphic representation of a walking gait (A), with the individual always presenting at least two limbs in contact with the support, and galloping (B), showing a fully aerial phase and moments of one limb in contact with the support (after Hanna et al., 2006)

4.4 Variability of substrate reaction forces according to differences of support

Experimental mechanical studies have shown that the reaction forces acting on primates significantly change according to the type of support utilised. On arboreal supports primates experience lower overall SRF than on the ground for both limbs. Quadrupedal primates moving on arboreal supports preserve the typical primate force distribution pattern, experiencing higher peak forces on the hindlimb than on the forelimb and all forces on both sets of limbs are reduced, maybe as a result of increasing limb yield from a more crouched position adopted by primates moving on arboreal supports (Schmitt, 1994; Franz et al., 2005) or an increased contact time of the limb with the support in arboreal locomotion (Schmitt, 1999). Despite a decrease of forces in both sets of limbs, the reduction of forces is in all cases more extreme in the case of the forelimb (Schmitt and Hanna, 2004), coupled with a closer alignment of the forelimb with the resulting force in a coronal plane (Schmitt, 2003a). Therefore, forces acting on the forelimb, in comparison to the hindlimb, are more dependent on the type of support used and particularly of the diameter of the support. Schmitt (2003b) observed that kinetics and kinematics of the walking gaits of Old World monkeys on large poles did not significantly differ from the values observed on the ground, whereas these values do vary among smaller diameter poles. He reported that as support diameter decreases, the five studied species increased the degree of flexion, whereas not all of them protracted their limbs to a higher degree. There is a definite trend, however, in reduction of vertical peak forces with decreasing support diameter.

Terrestrial cercopithecines are the most obvious example of this reduction. During terrestrial locomotion their force distribution between forelimbs and hindlimbs is almost equal if not shifted towards a greater bearing character of the forelimb. During simulated arboreal locomotion, however, this pattern is reversed and their hindlimbs become the main force-bearing element (Schmitt and Hanna, 2004).

Smaller arboreal supports entail greater compliance, essentially connecting the diameter of a support with its degree of stiffness (Thorpe et al., 2009; van Casteren et al., 2012, 2013) (Chapter 3). The use of compliant branches during locomotion generally comes with an increase of the energetic cost during locomotion (Alexander, 1991). For instance, takeoff during a leap requires a greater generation of energy from a compliant support than from a stiff one. This is observed in leaping lemurs as well as in gibbons (Demes et al., 1999; Channon et al., 2011). Primates, however, have developed specific strategies in order to deal with the higher energetic cost of using compliant supports. Gibbons, for instance, can perform slower orthograde leaps with greater hip excursion in order to neutralise the deformability of the support or they can perform faster pronograde leaps applying the vertical peak force earlier in the leap, where the branch is effectively stiffer, decreasing the amount of energy loss (Channon et al., 2011).

The studies aforementioned are mainly experimental using poles in order to simulate arboreal supports. However, there are cases in natural environments where the use of compliant supports has been observed to be highly beneficial. Despite there not being specific evidence from experimental studies pointing towards compliant supports as energy storage structures, orangutan females and juveniles have been observed to use the energy from compliant branches in gap crossing, a more efficient strategy than climbing down and crossing on the ground to climb up the next tree (Thorpe et al., 2007, 2009). Furthermore, a compliant support damps the impact at landing from a leap or a jump. Fleagle (1978) reported that the leaf monkey (*Presbytis* sp.) leaps from bigger supports and lands on thinner ones thus avoiding energy loss and minimizing the impact (in Demes et al., 1999).

4.5 The primate spine during locomotion

Studies of the mechanics of the primate spine are scarce in comparison with those focussing on limbs. Most research on the spine concerns the degree and plane of movement of the vertebral column, while no work has been done regarding the system of action-reaction forces.

The primate spine's role in locomotion is undeniable but, contrary to what may be observed with the limbs, the spine exhibits a high degree of morphological variability that corresponds to variability in locomotor and postural behaviour (e.g., Johnson and Shapiro, 1998; Shapiro and Simons, 2002). One particularity of the spine in order to accommodate different postural and locomotor behaviours is the degree of rigidity of the spine (Granatosky et al., 2014). This is determined by differences in number of vertebrae of each of the vertebral regions (e.g., Johnson and Shapiro, 1998; McCollum et al., 2009; Russo and Williams, 2015; Thompson and

Almécija, 2017) and differences in the morphology of the lumbar vertebrae (Shapiro, 1995; Johnson and Shapiro, 1998; Shapiro and Simons, 2002; Shapiro, 2007; Granatosky et al., 2014). The morphological differences respond to different degrees of loads on the spine under the action of gravity, such as bending loads, torsion, compressive or tensile stresses depending on positional and locomotor behaviour (Johnson and Shapiro, 1998; Hanna et al., 2017). Such differences, however, allow the set of movements performed at the level of the spine described in Chapter 3.

One particularity of spinal movements in primates is the degree of sagittal bending, as mentioned in Chapter 3. Terrestrial non-mammalian vertebrates bend the spine in the coronal plane, whereas mammals (including primates) generally perform sagittal bending of the spine, accompanied by soft tissue adaptations, such as differences in musculature or in the thickness of intervertebral discs (Hurov, 1987; Zihlman and Underwood, 2013). It is important to bear in mind, though, that some strepsirhines exhibit spinal lateral bending (Shapiro et al., 2001), which is coupled with morphological traits of their lumbar spine as well as kinetic differences on their limbs.

CHAPTER 5: MATERIALS AND METHODS

5.1 Materials

5.1.1 Selection of species and material

The materials used consist of postcranial skeletal remains of different species of non-human primates. All available weight-bearing joints (Table 5.1) were assessed for DJD in 35 primate taxa at the level of genus, species or subspecies. The taxa were selected in order to have a good representation of a wide range of locomotor adaptations (Table 5.2), as well as the fact that these species exploit different habitats and use a diverse repertoire of supports when moving, allowing the accurate testing of specific hypotheses.

Table 5.1 List of weight-bearing joints considered and skeletal elements recorded for each individual

Compartment	Joint	Elements
Spine	Apophyseal	Cranial apophyses
		Caudal apophyses
	Vertebral	Cranial body
		Caudal body
Forelimb	Shoulder	Glenoid fossa
		Proximal humerus
	Elbow	Distal humerus
		Proximal radius and ulna
	Wrist	Distal radius
		Distal ulna
Hindlimb	Hip	Acetabulum
		Proximal femur (head)
	Knee	Distal femur
		Proximal tibia
	Ankle	Distal tibia
		Proximal talus

Table 5.2 List of studied taxa (at a generic, specific or subspecific level) classified according to the locomotor strategy performed with sample size (N) and museum of provenance of the materials (AMNH=American museum of natural history; FM=Field museum; MfN=Museum für Naturkunde; MNHN=Muséum National d'Histoire Naturelle; PCM=Powell-Cotton Museum; RMCA=Royal Museum of Central Africa; SI=Smithsonian Institute)

Locomotor adaptation	Locomotor strategy	Species	N	Provenance
Vertical clingers and leapers and slow arboreal quadrupeds	Slow-moving	*Loris sp.*	10	FM, MfN, MNHN, SI
		Nycticebus sp.	16	FM, MfN, MNHN
		Perodicticus potto	19	FM, MfN, PCM, SI
	Fast-moving	*Galago alleni*	7	PCM, SI
		Propithecus sp.	31	MNHN
		Tarsius sp.	17	FM, MfN, MNHN, SI
Leapers	Slow-moving	*Otolemur crassicaudatus*	15	FM, MfN, MNHN, SI
	Fast-moving	*Euoticus elegantulus*	50	PCM
		Galagoides demidoff	51	PCM
		Saimiri sp.	48	AMNH, FM, SI
Quadrupeds	Arboreal	*Cebus albifrons*	50	AMNH, FM
		Cercopithecus ascanius	21	MfN, RMCA
		Cercopithecus cephus	25	MfN, PCM
		Cercopithecus nictitans	4	MfN, RMCA
		Cercopithecus pogonias	24	MfN, PCM, RMCA
		Lophocebus albigena	30	MfN, PCM, RMCA
		*Nasalis larvatus**	11	FM, MfN, SI
		Procolobus badius	25	PCM
		Sapajus apella	53	AMNH, FM

* High percentage of swimming in their locomotor behaviour.

Table 5.2 (cont.). *List of studied taxa (at a generic, specific or subspecific level) classified according to the locomotor strategy performed with sample size (N) and museum of provenance of the materials (AMNH=American Museum of Natural History; FM=Field Museum; MfN=Museum für Naturkunde; MNHN=Muséum National d'Histoire Naturelle; PCM=Powell-Cotton Museum; RMCA=Royal Museum of Central Africa; SI=Smithsonian Institute).*

Locomotor adaptation	Locomotor strategy	Species	N	Provenance
Quadrupeds	Semi-arboreal	*Cercocebus agilis*	6	PCM, RMCA
		Cercocebus torquatus	11	PCM
		Chlorocebus aethiops	20	MfN, RMCA
		Lemur catta	5	AMNH, SI
	Terrestrial	*Erythrocebus patas*	5	RMCA
		Papio anubis	20	FM, MfN, PCM, RMCA, SI
Knuckle-walkers	Terrestrial	*Gorilla beringei*	20	RMCA
		Gorilla gorilla	29	PCM
		Pan troglodytes schweinfurthii	25	RMCA
		Pan troglodytes troglodytes	16	PCM, RMCA
	Arboreal	*Pan paniscus*	19	RMCA
Suspensory	Fast-moving	*Ateles sp.*	30	AMNH, FM, MNHN, SI
		Hylobates sp.	38	FM, SI
	Slow-moving	*Brachyteles arachnoides*	5	MfN
		Lagothrix sp.	20	AMNH, FM, MfN, SI
		Pongo sp.	21	SI

The taxa selected for this study represent diverse taxonomic and phylogenetic relationships, comprising New World and Old World primates, with representatives of both strepsirhines and haplorhines. Even though phylogeny was not used as a proxy for DJD in this thesis, the taxonomic diversity represented entails morphological variability among the species considered. One example is the variation in the number of vertebrae. As previously seen, the number of vertebrae varies among primates between and within species (Whitehead et al., 2005; McCollum et al., 2009; Williams, 2011; Thompson and Almécija, 2017). To overcome this the spine was divided into functional groups of joints instead of independent pairs, which were in turn divided into five different sections, regardless the number of vertebrae in each: cervical, upper thoracic, middle thoracic, lower thoracic and lumbar spine. This approach resulted in a substantial reduction of the number of variables, making the data analyses more manageable (section 5.6).

For each taxon wherever possible only adult individuals were used although on occasions sub-adult individuals close to adulthood were included (section 5.5). The majority were of known sex, although occasionally individuals of unknown sex were included to increase the sample size. The selection of adults and in a few cases sub-adults close to maturity was done in order to avoid possible confusion with developmental processes (Wintheiser et al., 1977; DeRousseau, 1988; Dainton and Macho, 1999; Joganic, 2016), which lie outside the research interest of this project.

Non-human primates have relatively high prevalence of traumatic events visible on the skeleton. The most common type of trauma observed is fractures and those individuals presenting evidence of such trauma were excluded. The main reason to exclude these individuals was to avoid DJD produced as a result of such trauma instead of DJD as a natural process (Jurmain, 1989). Furthermore, trauma (and injury in general) is known to entail modifications in the locomotor behaviour of the individuals affected (Munn, 2006), which would make the testing of one of the main hypothesis impossible. Aside from trauma other pathologies of probable infectious origin were observed. Even though these are not discussed here, some of these pathologies were considered relevant when the integrity of the joint was at stake, which would, in turn, put habitual locomotor behaviours in jeopardy. Therefore, the cases where joints appeared to be compromised as a result of pathological process led to their exclusion from the study (see Appendix 1 for further information on prevalence and distribution of trauma).

5.1.2 *Provenance of the material and equipment used*

The materials used for data collection comprised non-articulated postcranial skeleton and the corresponding mandibular dentition, belonging to museum osteological collections. All the individuals were skeletonised wild specimens housed in the following museums: the Muséum National d'Histoire Naturelle of Paris (France), the Royal Museum of Central Africa of Tervuren (Belgium), the Powell-Cotton Museum of Kent (United Kingdom), the Museum für Naturkunde of Berlin (Germany), the American Museum of Natural History of New York City, the Field Museum of Chicago and the National Museum of Natural History, Smithsonian Institution of Washington D.C. (United States of America) (Table 5.2).

Electronic callipers were used to take measurements of some epiphyses of long bones for body mass estimation purposes (section 5.4). In addition to recording severity of DJD, photographs were taken of the majority of skeletal elements showing DJD with a Nikon D80 digital SLR camera with a fixed 40mm macro lens, using a camera stand. Observations of the articular surfaces were made directly or, when necessary, with the help of magnifying lenses or a stereomicroscope.

5.2 Recording of DJD

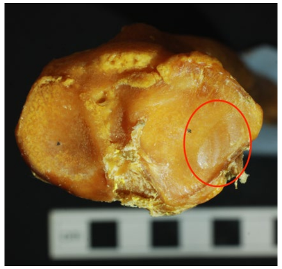
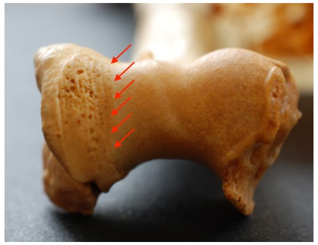
The recordings of DJD were based on macroscopic osteological observation of the articular surfaces of weight-bearing joints of the postcranial skeleton. The aim of this study was not to attribute particular disorders (e.g., osteoarthritis, calcium pyrophosphate deposition disease or erosive arthritis) to specific individuals or species, but to report the presence of any type of osteological degenerative process taking place in the weight-bearing joints of non-human primates. Therefore, in this thesis special attention was given to the non-pathological expression of DJD, which usually precedes the pathological processes or comes in combination with this pathological expression. Hence, osteophytosis, porosity and eburnation on the joint surface were observed and recorded.

The expression of the three indicators of DJD was quantified by means of discrete categories expressing the severity of the process, scaling from 0 to 3 (where

0=absent; 1=mild; 2=moderate and 3=severe) (Table 5.3). Osteophytosis is expressed as new bone formation at the edges of the articular surface, making the perimeter of the joint rough and irregular. Porosity is present as pitting on the bone surface, but rather than affecting the edges of the articulation it is usually found on the articular surface itself, similarly to eburnation, which appears as a polished area of shiny bone. Eburnation is produced as a result of friction between bones of the joint once the cartilage has been eroded away. The severity stage was always assessed based on the dimension of the edge of new bone or the pits present on the surface of the bone in relation to the total size of the bone, which can be very variable among species. Concerning eburnation, severity is assessed based on the degree of deformation of the joint and level of smoothness of the affected area. This methodology is based on the protocol used to record DJD in human remains recovered from the archaeological record (e.g., Hukuda *et al.*, 2000), which was proved informative and transferable to the study of DJD in non-human primates (Swales and Nystrom, 2015).

The applicability of the methodology was tested during a preliminary study at the *Museu de Zoologia* of Barcelona (Spain). However, these data were not used in the final analyses, as the individuals of this collection come from the Barcelona zoo. This preliminary study served two purposes: 1) to test the described methodology and pinpoint potential challenges during the actual data collection, and 2) to allow the researcher to become familiar with high levels of expression of DJD in order to be able to critically assess the range of degeneration observed in the wild individuals used in this study. Extreme condition was likely to be encountered in this collection, due to the fact these specimens come from captive environments and thus are likely to have severe expression of DJD (DeRousseau, 1985; Uno, 1997; O'Regan and Kitchener, 2005).

Table 5.3 Definition of the different stages of expression of osteophytosis, porosity and eburnation for the articular surfaces of the weight-bearing joints observed for the assessment of DJD

Process	**Stage 1**		**Stage 2**		**Stage 3**	
Osteophytosis	Bony protrusion on the margin of the joint, nearly perpendicular to the articular surface. It forms a prominence but without height.		Bony protrusion forms a lip (2x stage 1) on the margin of articular surface. No invasion of the adjacent articular space.		Irregular lipping on the edges of the articular surface (2x stage 2). Bony protrusion invades the adjacent articular space, sometimes leading to fusion.	
Porosity	Evidence of coarse joint surface resulting from light pitting (very small diameter pori).		Greater diameter pori (2x stage 1), often accompanied by smaller pori (similar to stage 1).		Great diameter pori (2x stage 2) that contribute to the loss of the natural shape of the joint surface.	
Eburnation	Shiny area with no apparent shape change of the articular surface. Better observed with an extra source of light, showing refraction.		Shiny area with evidence of shape change of the articular surface (present as a concavity). No need for an extra source of light and no evidence of friction lines.		Shiny area with evidence of shape change of the articular surface; irregular concavity with friction lines (grooves) present in both elements of the joint.	

An intra-observer error study was carried out in order to evaluate the accuracy of the methodology. Thus, data on DJD were collected twice, in two independent events separated by eleven months, for a set of individuals from different species (Table 5.4). The materials used come from the Royal Museum of Central Africa in Tervuren (Belgium). In the comparison of the two sets of data obtained most individual articular surfaces were assessed accordingly to the first recordings, but some articular surfaces were given a different score for eburnation, osteophytosis or porosity, depending on each particular case. The differences in recording were never of more than one severity stage. This is likely to have happened in those cases where the expression of DJD is between two categories, making it difficult to assess its degree of severity with accuracy. Unfortunately, this is a problem difficult to control when using categorical scoring of continuous traits, as the development of DJD is a continuous process forced into discrete categories. Therefore, accuracy is not guaranteed and some precision will be lost.

Table 5.4 List of species and number of individuals recorded for the intra-observer error study

Species	**N**
Cercocebus agilis	4
Cercopithecus ascanius	19
Cercopithecus nictitans	1
Cercopithecus pogonias	1
Erythrocebus patas	2
Lophocebus albigena	12
Papio anubis	8

The differences in recordings for the articular surfaces in the two collection processes were significantly minimised once the indices of prevalence for joints or groups of joints (in the case of the spine) were calculated (section 5.6). Therefore, differences in the overall value of DJD for the joint or region were not statistically significant. Since the body of data consisted of indices calculated from categorical data (i.e. non-normally distributed), a Wilcoxon signed rank test was used. This test is used to observe differences in paired variables of non-parametric nature, which usually translate in the assessment of change over time for a particular variable (or different observations of the same variable in different moments) (Hammer and Harper, 2006).

The results of the Wilcoxon signed rank test showed that across the data set no significant differences were found between the two observations (p>0.05 in all cases). Therefore, despite some differences in the recording in individual articular surfaces, these do not affect the overall distribution of DJD for the recorded individuals. Therefore, the same degree of DJD was observed in the two separate occasions for the selected sub-sample.

An inter-observer error study could not be conducted due to the fact that none of the collections were housed in our department and the main researcher alone did all the visits and data collection, as the materials could not leave their home collections. However, the preparation of the researcher, as well as the results from the intra-observer error study and the fact this methodology has already been applied in previous research with non-human primates (Swales and Nystrom, 2015) provide enough evidence to consider the methodology described applicable, reliable and informative.

5.3 Determination of different locomotor strategies: speed, support use and support compliance

Two different locomotor strategies were considered in this study as potential sources of intensity modulators of the SRF acting on joints, possibly affecting DJD development. One of these strategies was the difference in **locomotor speed**. Primates can move at different speeds depending on the activity performed. However, some taxa perform typically fast locomotion (e.g., *Hylobates* sp. or *Tarsier* sp.) while others perform slow, deliberate locomotion (e.g., *Pongo* sp. or *Nycticebus* sp.) (e.g., Bertram and Chang, 2001; Schmitt and Lemelin, 2004; Crompton and Sellers, 2007). Such differences were considered in the taxa selection process based on reports of their habitual locomotor behaviour (Table 5.2) and treated as potential drivers of DJD variability.

The second locomotor strategy considered a potential modulator of DJD concerned the way in which primates interact with their habitats (Table 5.2) and, consequently, how they **use the available supports**. Primates behave differently when interacting with supports of different compliance levels and the use of supports of different dimensions modulates the intensity of the forces acting on the joints (Chapters 3 and 4). Therefore, information of the most commonly used types of supports was drawn from the literature for some of the studied taxa and different supports were classified into categories that reflected their level of compliance. In the case arboreal supports the degree of deformability was attributed considering their diameter. The ground was considered the stiffest of the supports with no compliance.

The quadrupeds were selected as the sample of study of the effect of different support use in DJD development. The quadruped sub-sample exhibits great variability of habitat and support use, which has been well studied and reported. Fleagle and Mittermeier (1980), in their study of sympatric monkeys in Surinam reported the differences in support use and classified the types of support considering their diameter, thus obtaining three categories: **boughs (>10 cm), branches (>2 cm; <10 cm) and twigs (<2 cm)**. Other authors have since used this classification (e.g., Gebo and Chapman, 1995a, 1995b; McGraw, 1996, 1998a, 1998b), which became the standard way of classifying supports when studying quadrupeds. In the present study, determining the degree of compliance of supports was simple when the diameter of the supports used had been reported in published sources. Therefore, in the case of the quadruped sample six different compliance categories were considered depending on the type of supports used, ranging from the ground to twigs, using a finer consideration of branches, that were divided into small (>2 cm; <5 cm) and large (>5 cm; <10 cm) branches (Table 5.5).

This approach assumes that the individuals recorded in this study behaved similarly to those observed in the published studies, regardless the specific location of the forest where they lived and assuming they were interacting with similar supports. One potential limitation is that the specific location of the individuals recorded was not always available and even if it was there was no way of knowing the characteristics of the forest at the moment when the animal lived there. As previously seen, modified forests can differ significantly to undisturbed forests and primates living in fragmented forests can exhibit different behaviours and interact with different supports, as their environment is also different. Unfortunately, this is a factor that could be not controlled for in the present research and, therefore, all the individuals were treated as inhabitants of an undisturbed forest of similar characteristics of those reported in the literature.

Table 5.5 Classification of support compliance for the quadruped sample. There are 6 different categories ranging from 1 (stiffest) to 6 (most deformable), where 1 = ground; 2 = ground and boughs; 3 = boughs; 4 = boughs and big branches; 5 = small branches; 6 = twigs and small branches

Species	**Support compliance**	**Preferred habitat in canopy**	**Type of support preferred**	**References**
Cebus albifrons	6	Understory and main canopy	Branches and twigs	Youlatos, 1999
Cercocebus sp.	2	Main canopy. High terrestrial component	Ground and boughs	Nakatsukasa, 1994
Cercopithecus ascanius	5	Main canopy (middle layers), generally in tree crowns	Small branches (<5cm)	Gebo and Sargis, 1994; Gebo and Chapman, 1995a
Cercopithecus cephus	4	Main canopy of rainforest	Boughs and branches (> than *C.ascanius* but < than *C.nictitans*)	Gebo and Chapman, 1995a; McGraw, 1996; McGraw 2004
Cercopithecus nictitans	4	Main canopy of rainforest	Boughs and big branches, less use of twigs than other guenons	Bitty and McGraw, 2007
Cercopithecus pogonias	4	Main canopy of rainforest	Boughs and branches (> than *C.ascanius* but < than *C.nictitans*)	Gebo and Chapman, 1995a; McGraw, 1996; McGraw 2004
Chlorocebus aethiops	2	Main canopy. High terrestrial component	Ground and boughs	Gebo and Sargis, 1994
Erythrocebus patas	1	Open woodland	Ground	McGraw, 2004
Lophocebus albigena	3	Main canopy (middle layers)	Boughs	Gebo and Chapman, 1995a
Papio anubis	1	Open woodland	Ground	Rose, 1977
Procolobus badius	3	Main canopy (middle layers, sometimes lower)	Boughs	Gebo and Chapman, 1995b; McGraw, 1996
Sapajus apella	6	Canopy. Not great specialisation for habitat use	Branches and twigs	Fleagle and Mittermeier, 1980; Sussman, 2003

5.4 Estimation of body size and mechanical stress on joints

5.4.1 Body size estimation

Body mass is often treated as a synonym of body size in primates (Ruff et al., 1997), and greater body mass implies greater stress on joints due to the force of weight (mass of an individual under the effect of gravity). However, rarely is information on body mass of an individual recorded in skeletal collections held in museums and, therefore, approximations on individual body mass were extracted from the skeletal materials provided as object of study.

The best way of estimating body mass in fossil skeletal remains is to use those traits that have a functional relationship to it (Ruff, 1987, 1988; Aiello and Wood, 1994; Kappelman, 1996; Ruff et al., 1997). Therefore, traits such as diaphyseal breadth and joint breadth of the lower limb long bones have been widely used (Steudel, 1981; Ruff, 1987, 1988, Ruff et al., 1993, 1997). However, diaphyseal breadths are potentially problematic to use across species of primates as body mass estimators, for they strongly respond to different degrees of mechanical loading (Ruff et al., 1997). Thus, different locomotor strategies may imply great differences on diaphyseal breadth and therefore, these cannot be considered as a direct effect of body mass exclusively. In contrast, joints are less environmentally sensitive (Ruff, 1988; Trinkaus et al., 1994; Lieberman et al., 2001; Burgess et al., 2017), making them potentially good indicators for body mass estimates.

There are some studies on body mass estimations of non-human primates, although not as numerous as those for anatomically modern humans and hominins (Steudel, 1981; Ruff, 1987, 1988; Cuozzo, 2001). Ruff (1988) examined the general relationships between body mass and hindlimb articular surface dimensions in hominoidea and *Macaca fascicularis*. Distal femur (and consequently proximal tibia) scale allometrically with body mass but at the same time, it is highly dependent on the degree of varus (bow leggedness) at the knee. Measurements of the proximal femur (Fig. 5.1) provided the best estimates with more robust correlations, being affected to a lesser degree by varus and range of movement.

The degree of varus is likely to vary significantly across species of non-human primates and, therefore, measurements of the proximal femur are the best suited ones in order to estimate body mass in this study, as it has also been applied to fossil materials (Ruff et al., 1997). Different lengths of the femoral head were taken: supero-inferior length (SI), antero-posterior length (AP) and the depth of the head (Fig. 5.1), and calculations of femoral head volume and surface were done, following the formulae of a partial sphere proposed by Ruff (1988):

$$Femoral\ head\ surface = 1.57 * \ depth * \ (SI\ length + AP\ length)$$

Equation 5.1

$$Femoral\ head\ volume = 0.0654 * \ (SI\ length + AP\ length)^3$$

Equation 5.2

Figure 5.1 Measurements of the proximal femur: superoinferior length (SI), anteroposterior length (AP) and depth (after Ruff, 1988)

Ruff (1988), however, only included a small number of species and the question remains open, as to whether these relationships and calculations are applicable across the Primate order. Other observations in gibbons (Jungers, 1988) and some leaping strepsirhines (Runestad Connour et al., 2000) suggest that the relationship body mass-femoral head dimensions is consistent among primates. However, in a recent study on hominoids Burgess and co-workers (2017) observed subtle scaling differences for joint size and body mass. For this reason, further testing was done with the sample of this thesis.

Information on body mass was available only for a few of the individuals sampled in this thesis (N=41), therefore the best available source of information is published average body masses for the relevant species (Smith and Jungers, 1997). Calculations of femoral head surface and volume were made from the measurements taken of all the individuals recorded of known sex, as described by Ruff (1988) (Equations 5.1 and 5.2). Only individuals of known sex were used, as body mass differences due to sexual dimorphism can be considerable in certain species (Smith and Jungers, 1997; Smith and Cheverud, 2002; Plavcan, 2003). Average values for femoral head volume and surface were obtained for each of the taxa for males and females separately and they were plotted against the average values of the corresponding body mass values from Smith and Jungers (1997) (Fig. 5.2), showing strong correlations between the average values of femoral dimensions and the average body mass of each taxon (R^2 = 0.986 in the case of femoral head surface and 0.987 for the volume). Differences in sex or species do not seem to account for different patterns (distance from the graphic representation of the correlation function), as they always fall close to the tendency line in the depicted model (Fig. 5.2). Despite the small sample size for some of the species, the model is robust, showing an undeniable correlation between the two variables across the sample. The raw data were transformed using Log10 transformations in order to reduce the effect of scale across the sample and so that the distribution of cases would be more easily observed.

These results corroborate the conclusions given by Ruff (1988), supporting the correlation between femoral head measurements and body mass across primates and not only for apes and Old World monkeys. Therefore, volume and surface of the femoral head can be confidently used as indicators of body mass across species. Consequently, regression equations were extracted from 41 individuals of 11 different species of known body mass with a present proximal femur (Table 5.6) and, in turn, these equations were used to estimate body mass for those individuals with a proximal femur of unknown body mass at the moment of death.

Calculations of femoral head surface and volume were taken for the 41 individuals and plotted against their real mass (Fig. 5.3). Again, Log10 transformations were carried out in order to reduce differences in scale as well as to facilitate their graphic representation. The model obtained produced high R^2 values, showing a strong correlation between body mass and both femoral head surface and volume (R^2 = 0.988 and 0.989 respectively) (Fig. 5.3). Therefore, body mass can be predicted from the equation of the correlation functions from femoral head surface (Equation 5.3) femoral head volume (Equation 5.4).

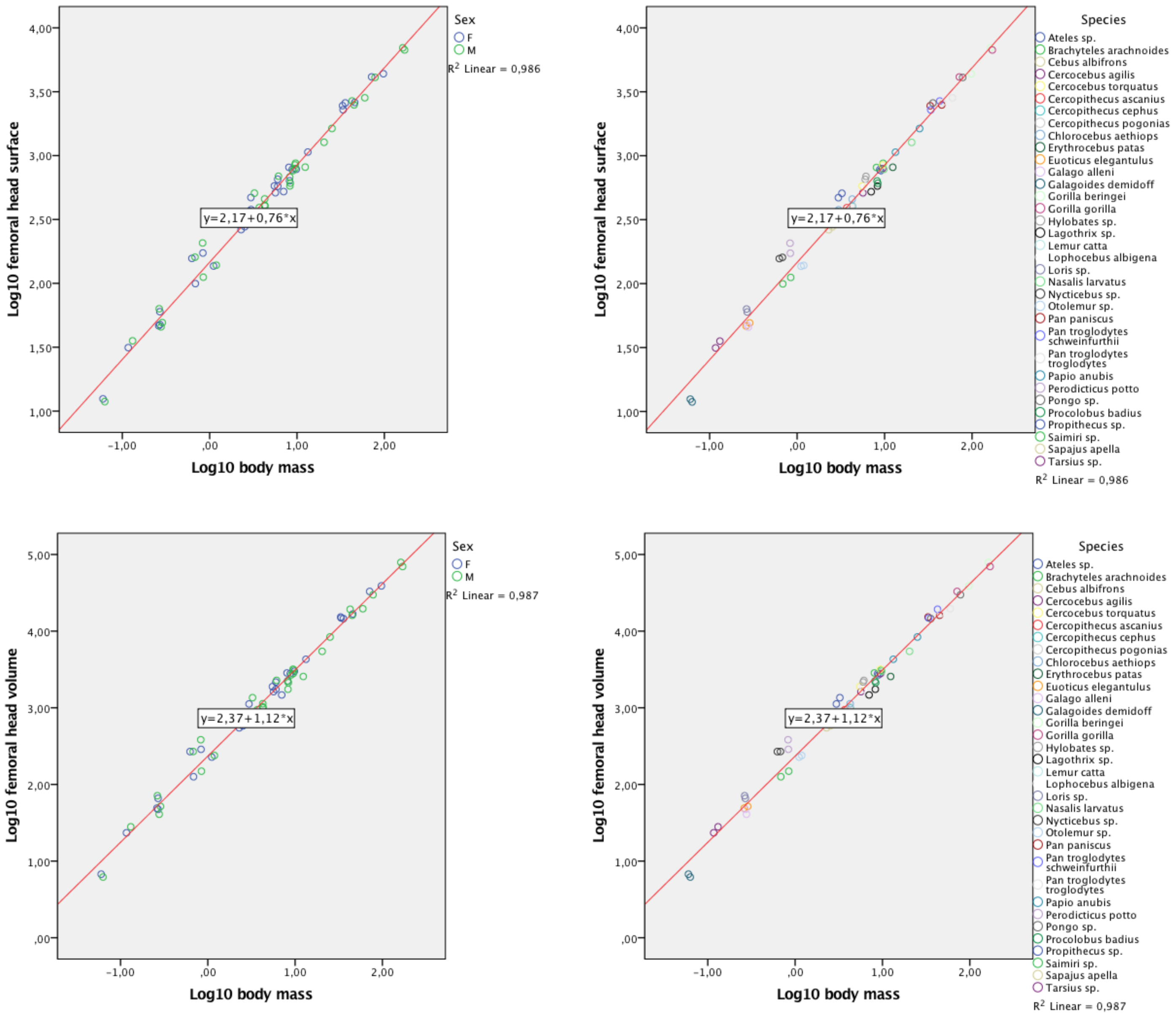


Figure 5.2 Log-transformed plot of published average body mass values vs. average femoral head surface (top graphs) and body mass vs. average femoral head volume (bottom graphs), with discrimination for sex (left graphs) and species (right graphs)

Table 5.6 Number of individuals of known body mass at the time of death classified by species and sex (total=41)

Species	Sex	N
Cercocebus agilis	M	1
Gorilla gorilla	M	1
Gorilla beringei	F	1
Hylobates agilis	M	1
Nasalis larvatus	M	1
	F	1
Otolemur crassicaudatus	F	1
Papio anubis	F	1
Perodicticus potto	M	2
	F	3
Pongo abelii	M	2
	F	7
Pongo pygmaeus	M	4
	F	8
Saimiri sciureus	M	2
	F	5

The predicted body mass for the 41 individuals with recorded weights was the average value of body mass calculated from the regression equations from femoral head surface and femoral head volume calculations. The accuracy of the predictions was tested with a paired t-test using the real body mass and the predicted value, giving no significant differences (p=0.929) and a high Pearson's correlation factor between both values (r=0.972; p=0.000).

These results support the use of femoral head surface and volume as body mass predictors, as 1) there is a strong correlation between published average values of body mass and femoral head dimensions, and 2) the regression equations extracted from the collected data produce robust results for approximations of body mass from femoral head dimensions. As a result, body mass was inferred for all the individuals that had a proximal femur present by means of the equations here presented.

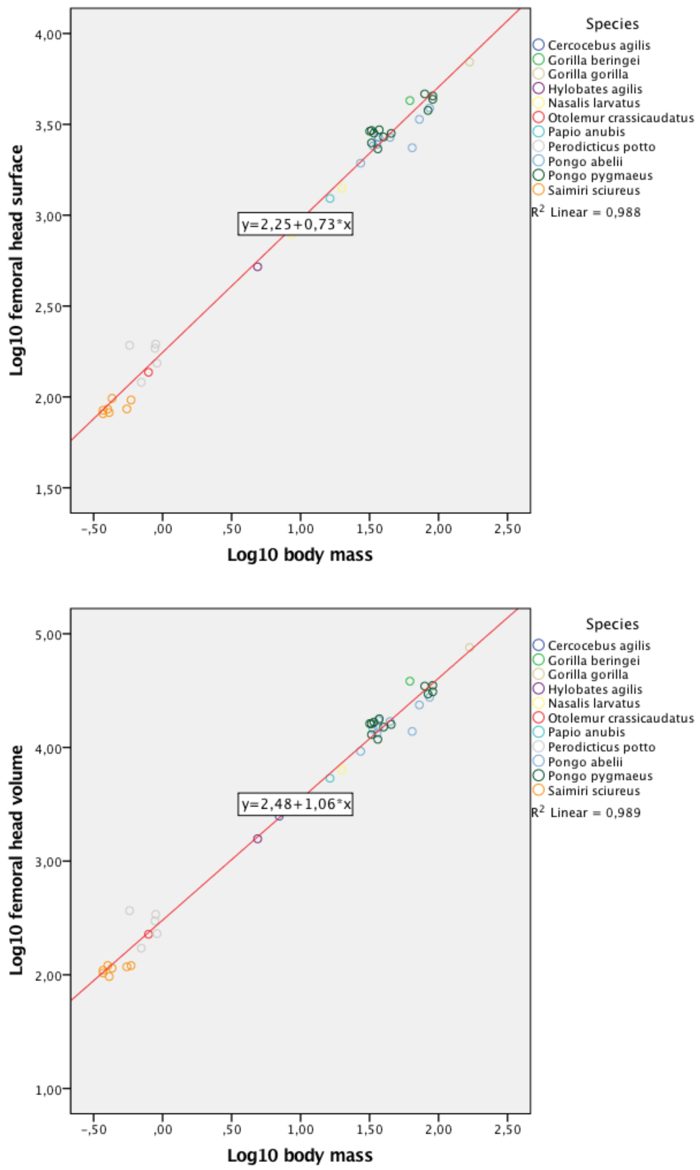


Figure 5.3 Log-transformed plot of known body mass vs. femoral head surface (left) and femoral head volume (right), with discrimination for species

$$y = 2.25 + 0.73x;\ \boldsymbol{x} = \frac{\boldsymbol{(y - 2.25)}}{\boldsymbol{0.73}}$$

$$\boldsymbol{Body\ mass = 10^{x}}$$

Equation 5.3

$$y = 2.48 + 1.06x;\ \boldsymbol{x} = \frac{\boldsymbol{(y - 2,48)}}{\boldsymbol{1.06}}$$

$$\boldsymbol{Body\ mass = \ 10^{x}}$$

Equation 5.4

5.4.2 *Evaluation of mechanical stress on joints*

Weight or **gravitational loading** (W) is a force (a vector) and, following the second of Newton's laws, it results from the body mass of the individual (m) under the action of gravity (G) (Houssaye et al., 2016) (Equation 5.5). In this respect body mass (as an indicator of body size) is directly proportional to weight, with gravity as an immutable constant. However, when it comes to DJD and joints, the critical point is the dimension of the surface upon which the force acts. Therefore, the real cause of stress is the force per unit of area experienced on a particular joint. In physical terms, this is referred to as **pressure** (P) and it is defined as the amount of force (W) applied to a specific area (Aj) (Equation 5.6).

$$W = m * G$$

Equation 5.5

$$P = \frac{W}{Aj}$$

Equation 5.6

The amount of pressure (in Pascals, Pa) was calculated, understood as a coefficient between weight and the surface of a joint. Measuring the area of all weight-bearing joints was too time consuming and inaccurate considering the resources available, so only measurements for the proximal tibia and the glenoid fossa were taken and their area was inferred by applying basic geometric formulae (Equation 5.7; Fig. 5.4 and Equation 5.8; Fig. 5.5). These joints were selected for their weight-bearing character but also because their shape is easily projected as a two-dimensional shape (Fig. 5.4 and 5.5). The elbow joint was initially considered for the forelimb, as the homologous joint of the knee, but it was observed during the pilot study that its convex and highly complex morphology made the 2D projection too simplistic (Fig. 5.6), leading to an inaccurate estimation of its area, hence, making it a worse candidate for the assessment of pressure.

$$A = b * h$$

Equation 5.7

$$A = \pi * a * b$$

Equation 5.8

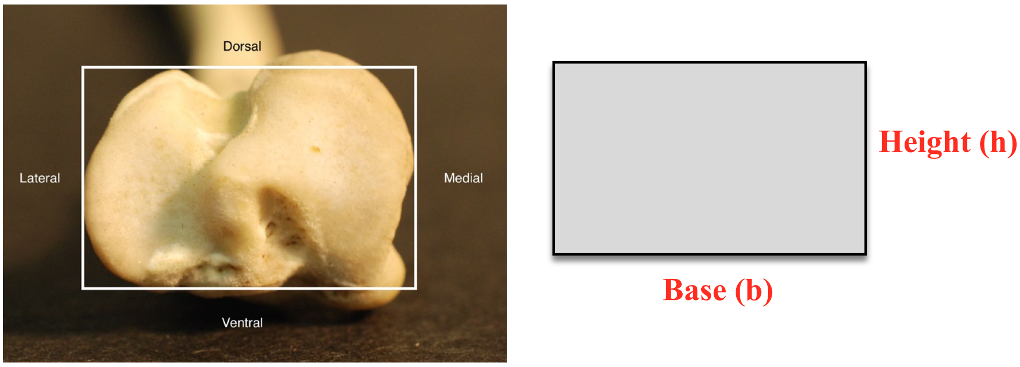


Figure 5.4 . Image of a proximal tibia (left) and approximation of the joint area (right) (photo by Baiges-Sotos)

Figure 5.5 Image of a glenoid fossa (left) and approximation of the joint area (right) (photo by Baiges-Sotos)

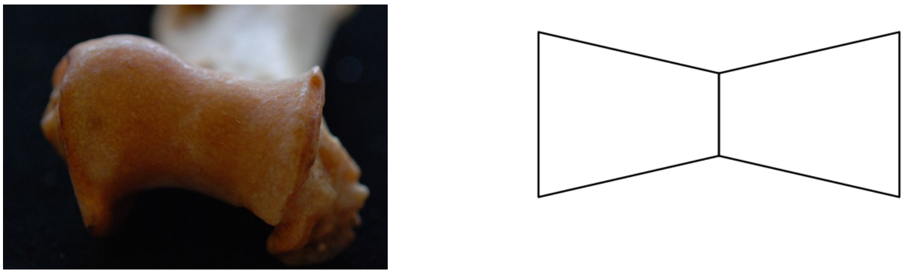


Figure 5.6 Image of a distal humerus with part of its articular surface visible and its 2D projection (photo by Baiges-Sotos)

A loading model was proposed in order to calculate the amount of pressure (in Pa) at the shoulder and knee, reflecting different limb loading patterns that different primates exhibit as a result of their locomotor behaviour and their habitat use (chapter 4). Such models concern only the limbs, as the joints assessed for pressure were the shoulder and the knee, but also because the spine is a highly complex system of joints with a dual function, thus complicating the potential interpretation of the results. As previously seen most primates perform a hindlimb-driven way of locomotion (chapter 4) with greater reliance on the hindlimb (in a variable manner among primates). Main exceptions were the slow loris that exhibits an inverted limb loading pattern (chapter 4) and the suspensory primates that generally load their forelimbs to a greater extent experiencing tensile stress instead of compressive stress. Moreover, Hunt and co-workers (1996) argued that distribution of weight of a primate could be assessed by studying its positional behaviour by looking, for instance, at the position of the torso *vs.* hands and feet in relation to the support. However, this kind of information is not always available for all primate species. Consequently, an approximate theoretical scenario was considered for pressure calculations and testing, with adapted loading percentages according to locomotor adaptation (Table 5.2). This depicted a very generalist but synthetic scenario and would only consist of an approximation of the different percentage of weight loading for the forelimb and the hindlimb (Table 5.7). The different percentages of loading for forelimb and hindlimb were: 20%-80% for most hindlimb-reliant species, 30%-70% for arboreal and semi-arboreal quadrupeds, 40-60% for terrestrial quadrupeds and knuckle-walkers, and 80%-20% for suspensory primates, which are mainly reliant on their forelimbs.

Table 5.7 Summary of the loading model used for pressure calculations, showing the amount of weight (in percentage) born at the forelimb and the hindlimb according to locomotor adaptation

Group	Weight at the forelimb (%)	Weight at the hindlimb (%)
Leapers and vertical clingers and leapers	20	80
Arboreal and semi-arboreal quadrupeds	30	70
Terrestrial quadrupeds and knuckle-walkers	40	60
Suspensory	80	20

Calculations of proportional pressure were made for the shoulder and knee joints across the taxa considering all these different models of loading, and were later contrasted with prevalence and severity of DJD at these joints.

5.5 Assessment of age

5.5.1 Assessment of maturity and sample selection

The specimens analysed in this study were either adults or sub-adults close to reaching skeletal maturity. Therefore, the individuals selected were those with M3 fully erupted and epiphyses fully fused. In those cases when the sample size was too small, individuals with M3 erupted and partially fused epiphyses were included, as they were most likely mature individuals pending some growth. Only occasionally individuals with only M2 erupted were considered if they showed epiphyses fully fused or close to fusion (N=11).

5.5.2 Determination of relative age categories

Age was not specified in the osteological collections and in these cases it is not possible to obtain the precise chronological age but estimates are possible through a combination of evidence and methodologies (Wintheiser et al., 1977; Galbany et al., 2011; Swales and Nystrom, 2015). The precise age of each individual is of moderate importance for this study. Instead, the relative age of each individual among the sample of its own taxon was of greater value, so the comparison between relatively young and relatively old individuals could be done.

All the individuals were classified into five progressive categories of relative age (youngest, second youngest, middle, second oldest and oldest) based on the degree of enamel wear of the molars, which is strongly correlated with age. Digital pictures of the occlusal surface of the mandibular molars were taken with a Nikon D80 digital SLR camera with a fixed 40mm macro lens. The mandibles where lying horizontally with the occlusal surface of the teeth facing the camera lens. If any of the mandibular molars were not present information was taken from the available ones.

Tooth wear depends on: 1) thickness of the enamel and 2) foods consumed, and it was assessed by an approximation and comparison of the area of dentine exposed in relation to the total occlusal area of each molar among individuals (Fig. 5.7) (Phillips-Conroy et al., 2000; Galbany et al., 2011, 2014, 2016; Glowacka et al., 2016).

Enamel thickness varies among primates, which has further implications in the shape and function of a tooth (e.g., Dumont, 1995; Shellis et al., 1998; Vogel et al., 2008; McGraw et al., 2012), as well as in the pattern of wear of each tooth (Shellis et al., 1998). Enamel thickness seems to be dependant mainly on ecological factors (i.e. the properties of the preferred food sources) (Dumont, 1995; Smith et al., 2005, 2012; Lucas et al., 2008; McGraw et al., 2012, 2014; Pampush et al., 2013), phylogenetic factors (Pampush et al., 2013), especially in comparisons at higher taxonomical levels (e.g., superfamily or even suborder), but also on every species life history, particularly lifespan. Generally the primates with thicker enamelled are those that have longer lifespans and consume hard foods (Pampush et al., 2013).

Teeth are an essential component of the foraging apparatus and their morphology is highly dependent on the types of food obtained during foraging activities (Galbany et al., 2011, 2014). As a consequence, differences in tooth wear patterns are partially determined by the kinds of food consumed, both at a macroscopic scale (i.e. macrowear) (e.g., Dennis et al., 2004; Galbany et al., 2011, 2014, 2016; Cuozzo et al., 2014) and a microscopic one (i.e. microwear) (e.g., Nystrom et al., 2004; Scott et al., 2012). Despite the differences in pattern, tooth wear is strongly correlated with age (Dennis et al., 2004; King et al., 2005; Cuozzo and Sauther, 2006; Galbany et al., 2011, 2014, 2016), but interestingly differences in tooth topography are observed as tooth wear takes place in order to maintain the functions of the teeth and, thus, different patterns are observed depending on the processing requirements of the foods consumed (Dennis et al., 2004; Glowacka et al., 2016).

The great variability concerning enamel thickness and wear patterns among primates entails potential problems for broad comparisons across species if the amount of wear is not quantified and scaled for tooth size. Therefore, due to the superficial evaluation of dental wear done in this study, comparisons between taxa were always avoided. As a result, the attribution of relative age was always done comparing individuals of the same taxon, never attempting to attribute an actual age, but giving each individual a relative stage within the sample considered. This means that had the sample been different the age category attributed could potentially change depending on the rest of individuals of the sample. Another potential limitation of this methodology is that ecological differences between populations of the same taxon were not considered. It is not always possible to know the provenance of each of the individuals sampled, however, differences that would radically change the wear pattern of a particular individual within a taxon were unlikely.

Figure 5.7 Examples of different wear stages of mandibular teeth in Cercopithecus cephus. These represent 4 of the 5 categories of relative age, from top to bottom: second youngest (PCM_M578), middle (PCM_M367), second oldest (PCM_M23) and oldest (PCM_M426). The youngest category is characterised by pristine enamel with no signs of pitting or dentine exposure (photos by Baiges-Sotos)

5.6 Data treatment and statistical analyses

The data collected were analysed using the statistical package SPSS (v.24). These are categorical data and, thus, the scope of non-parametric tests was considered for the main body of the analyses.

5.6.1 Raw data and transformations

The data from DJD recordings were categorical, whereas the linear measurements of the epiphyses of long bones consist on continuous variables. For each articular surface data on the severity stage of the three DJD indicators were collected. Considering the great amount of weight-bearing joints assessed and all the articular surfaces within each joint, the amount of variables was far too great to consider them individually.

The number of variables was reduced by grouping the articular surfaces into different anatomical functional compartments. As a result, different indices were obtained for each of the joints of the limbs and for each functional compartment of the spine (cervical, upper, middle and lower thoracic and lumbar) (Table 5.1). Two main types of indices were calculated. These two types of indices were used in separate analyses or partial samples depending on the particular questions asked and the nature of the collected data. Thus, prevalence and severity indices were calculated. **Prevalence indices (PI)** (Equation 5.9) reflected the proportion of skeletal elements within a joint that were affected by osteophytosis, porosity or eburnation, regardless the severity of their expression. Therefore, only presence and absence was considered here.

$$\mathrm{PI} = \frac{\Sigma\, affected\ surfaces}{total\ number\ of\ surfaces\ of\ joint\ or\ group\ of\ joints} * 100$$

Equation 5.9

These indices were used in the first stages of the analyses, mainly in a descriptive way, in order to get a general idea of the distribution of DJD across the sample. However informative, further indices were calculated in order to incorporate information on the degree of expression of the different indicators of DJD. **Severity indices (SI)** (Equation 5.10) were calculated following the same reasoning as in the PI, considering the same joints or groups of joints. In this case, however, instead of presence or absence, the level of severity was used (from 0 to 3) as well as weighing factors for each recording of DJD. The weighing factors ranged from 1 to 1.2 in order to give to each of the severity stages different values without expanding their range too much (Table 5.8). From the weighed values, the SI was calculated. By weighing each of the recordings of DJD a greater level of nuance was kept, as each value of a SI could only reflect a certain combination of values, losing less information with the variable-grouping process. Moreover, by doing this the number of potential resulting values for the SI was increased, bringing the variables closer to linear treatments allowing the use of analyses such as linear models or correlations, despite still having to use the non-parametric versions.

Table 5.8 Table of equivalences of the weighing factors

Severity stage	Weighing factor	Weighed severity stage
1	1	1
2	1.1	2.2
3	1.2	3.6

$$\mathrm{SI} = \frac{\Sigma\ weighed\ severity\ of\ affected\ surfaces}{total\ number\ of\ surfaces\ of\ joint\ or\ group\ of\ joints} * 100$$

Equation 5.10

The datasets obtained from the calculations of these indices were used for the major part of the analyses. In some cases, the combined values of DJD were used (Equation 5.11) as an overall indicator of degeneration for a particular joint.

$$Combined\ DJD = Osteophytes + Porosity + Eburnation$$

Equation 5.11

5.6.2 Univariate and exploratory statistics

General **descriptive statistics** (mean, median, mode and standard deviation) were the starting point of the data treatment. These tests were performed for the overall sample as well as for sub-samples and were sometimes accompanied by graphic representations, such as scatterplots, boxplots or histograms of the data in order to have a more visual source of information. These tests provided a very general idea of what should be expected concerning distribution of DJD among the taxa considered.

Exploratory data analyses were done using both PI and SI by means of **significance tests**. Mann-Whitney U and Kruskal-Wallis tests with pairwise comparisons and Bonferroni post-hoc corrections (to reduce the probability of type I error) were run to test for general differences and to detect patterns in different contexts. These were often performed on sub-samples of the general list of taxa and the main difference consisted on grouping criteria used for each comparison. This way, significant differences in DJD distribution and severity were observed among primates concerning locomotor adaptation or different strategies, among other variables. In some cases, when the variable considered was of a continuous nature or had enough categories (e.g., degree of support compliance) **correlation tests** were run. With these tests it was possible to see how closely related the considered variable was to DJD and in what direction (directly or inversely related to DJD). Again, considering the nature of the data the non-parametric versions of the correlation tests were explored, and due to the monotonic distribution of DJD, Spearman's (ρ) correlation tests was chosen as the most appropriate one.

All these tests were exploratory and treated one variable at a time against DJD.As a result, information was obtained as to whether or not these variables explain some differences on DJD development. These analyses were used to observe emerging patterns in the data that led to the following stage of this research, where all the variables were considered together for some groups of primates.

5.6.3 Multivariate statistics: generalised linear models (GLM)

Multivariate analyses were run in order to analyse the degree of contribution to DJD of each of the independent variable in a multivariate scenario as well as to search for potential interactions between the different potential causal factors of DJD. In these analyses linear models were explored where severity of DJD was treated as the dependent variable and the rest of variables were pooled in as either covariates (for the continuous variables) or factors (for the categorical variables).

Generalised linear models (GLM) are a family of regression-type models that can deal with categorical data as well as with continuous variables (Agresti, 1990). The plasticity of these models rely on the fact that the mean of the response variable (i.e. DJD) can be transformed in a non-linear manner and, therefore, does not call for normality of the data (Greenacre, 2010). It is this transformed mean that reflects the variability of the data that is, in turn, modelled as a linear function of the predictors (i.e. causal factors). Different types of GLMs can be conceived depending on the nature of the data, especially of the response variable (Table 5.9) (Agresti, 1990; Darlington, 1990).

The choice of model was among those where the response variable is non-normally distributed. Multiple logistic regression, for example, is used in those cases when the response variable is binomial (following a Bernoulli distribution) and two or

Table 5.9 Types of generalised linear models, where the random component corresponds to the type of distribution of the response variable and the systematic component to a vector that relates the explanatory variables (modified from Agresti, 1990)

Random component	Systematic component	Model
Normal	Continuous	Simple regression
Normal	Categorical	Analysis of variance
Normal	Mixed	Analysis of covariance
Bernoulli	Mixed	Logistic regression
Poisson	Mixed	Loglinear
Multinomial	Mixed	Multinomial response

more continuous variables as your independent ones (McDonald, 2009). Log-linear models, on the other hand, are strongly related to logistic regression analysis, but they are built on the base of the chi-square (χ^2) test of association, as they deal with data that follow a Poisson distribution (generally counts) (Darlington, 1990). Chi-square is based on two-way contingency tables of categorical variables and on the comparison between expected and observed frequencies with the initial supposition (H_0) that the two variables are independent to each other and with interchangeable categories and, thus, with no set order among them (Shennan, 1997).

The response variable of the present study was initially of an ordinal nature (with severity stages ranging from 0 and 3) and thus, could fall within the range of possibilities of multiple logistic regressions. However, as a result of the transformation of the raw data into severity indices the new data have an ordinal sense and direction but the original categories were not present anymore. The number of new "categories" increased significantly and the data now were more scale-like than of an ordinal aspect. Therefore, the response variable was treated as a scale variable and because of the tight exponential distribution of the data considered in this particular part of the analyses (Fig. 5.8), the main set of models run were those with the generalised algorithm assuming a Gamma distribution of the data with an inverse link function. One of the main limitations of this model is that it cannot deal with 0s as a result of the inverse link function. Therefore, all the data were transformed for two purposes. To begin with the response variable was transformed by summing 2 to all the cases. The reason for this transformation is double: firstly, this way the information of the healthy individuals could be included in the model as a result of getting rid of the 0 values and, secondly, by adding 2 instead of 1 it became possible to perform Log10 transformations on the data in order to reduce the range of distribution of the data so that it would be manageable for the programme.

Post-hoc tests were run on the estimated marginal means of the linear predictor (that take into account the effects of other variables of the model). Paired comparisons using the repeated contrast criterion were run (as the variables analysed were categorical and ordinal), leading to the distinction of different homogenous subsets within each variable. The test used was Fisher's Least Significant Difference (LSD) and these tests were accompanied by clustered boxplots to see the effect of different categorical variables on the data distribution.

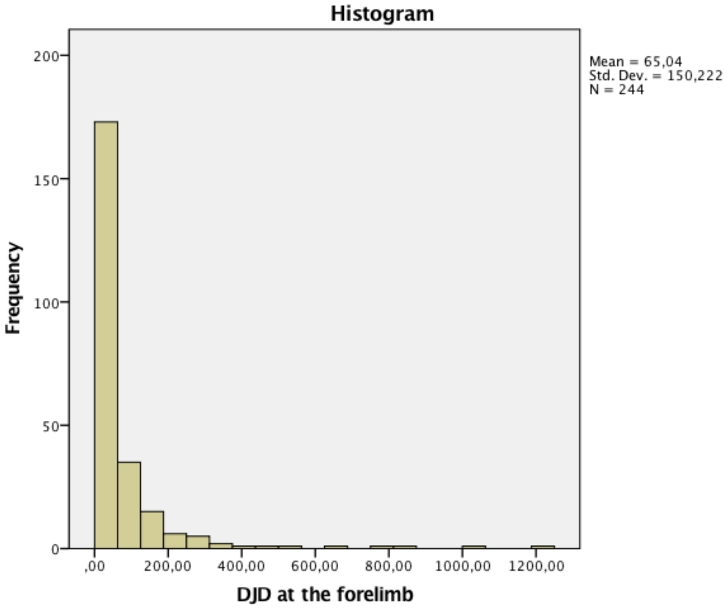


Figure 5.8 Example of the tight exponential distribution of the data for DJD at the forelimb for the monkey sub-sample

CHAPTER 6: DISTRIBUTION OF DJD ACROSS THE PRIMATE SKELETON

Previous research on DJD in non-human primates suggested that DJD was present across the order, but varied in prevalence and severity not only within the primate skeleton, but also among species and groups of primates (e.g., DeRousseau, 1985, 1988; Jurmain, 1989, 2000; Lovell, 1990; Rothschild and Woods, 1992, 1993; Rothschild and Rühli, 2005).

This chapter presents general descriptive results on the data collected of DJD following the methodology explained in chapter 5. Different levels of DJD expression and distribution were analysed based on the calculations of the severity indices (Equation 5.10, chapter 5). The first section of this chapter deals with DJD expression across the whole sample, producing a generalised pattern of expression representing all the individuals for which data were available (N=797). General differences between the human and the non-human patterns of expression of DJD were established and discussed.

The main aim of this study was to see if DJD development varied according to locomotor behaviour. The taxa selected for the study represented a broad range of locomotor behaviours, in an attempt to reflect the locomotor variability of the order. Patterns of DJD expression were obtained for different sub-samples reflecting different locomotor adaptations in order to detect deviations from the general primate pattern and to see if such deviations could be a result of locomotor behaviour or if other factors could be in place concerning DJD.

One characteristic of primate locomotion is that, contrary to other quadrupedal mammals, primates greatly rely on their hindlimbs for locomotor purposes, generally bearing more weight on the hindlimb than on the forelimb (Reynolds, 1985a, 1985b; Demes et al., 1994; Larson, 1998; Schmitt, 1998). In an attempt to explore if greater reliance for locomotion entailed faster joint degeneration, limb ratios of DJD expression were obtained. This was done for primates as a whole as well as for the sub-samples of primates with different locomotor adaptations, as the proportions of weight reliance between forelimb and hindlimb could vary according to locomotor behaviour.

6.1 DJD distribution across primates: generalised primate pattern of expression

The results contained in this section were obtained in order to find a general primate pattern of DJD distribution, evaluating what the most commonly affected joints were in the primate skeleton and the severity with which DJD was expressed. This pattern was obtained by calculating the means and medians of the DJD expression for the whole sample (N=797).

6.1.1 Severity and distribution of DJD across primates

Mean values of DJD expression were overall very low and in all cases the medians were zero (Tables 6.1 and 6.2). The overall distribution of DJD was strongly positively skewed for all DJD indicators at all the joints studied (example in Fig. 6.1). Consequently, mean values would be associated to high standard deviations, making the averages only partially informative.

Average DJD severity values of the limbs showed that the most affected joints were the elbow and the knee joints (Table 6.1). Of the two, the elbow exhibited the highest average values of osteophytes (elbow=17.11; knee=13.52) and porosity (elbow=8.75; knee=8.51), even though elbow porosity was closely followed by porosity at the knee. The knee joint was the most severely affected by eburnation, exhibiting greater values than all the other joints, including the elbow (elbow=1.43; knee=2.48).

Table 6.1 General descriptive results showing means and medians for the whole sample at the level of the limbs. The highest values are shaded

Joint	**Whole sample**							
	Eburnation		**Osteophytosis**		**Porosity**		**Combined**	
	Mean	**Median**	**Mean**	**Median**	**Mean**	**Median**	**Mean**	**Median**
Shoulder	0.31	0	8.58	0	6.36	0	15.26	0
Elbow	1.4	0	17.11	0	8.75	0	27.29	0
Wrist	0.45	0	6.58	0	4.32	0	11.34	0
Hip	0.19	0	6.15	0	3.90	0	10.20	0
Knee	2.48	0	13.52	0	8.51	0	24.40	0
Ankle	1.00	0	9.90	0	6.41	0	17.19	0

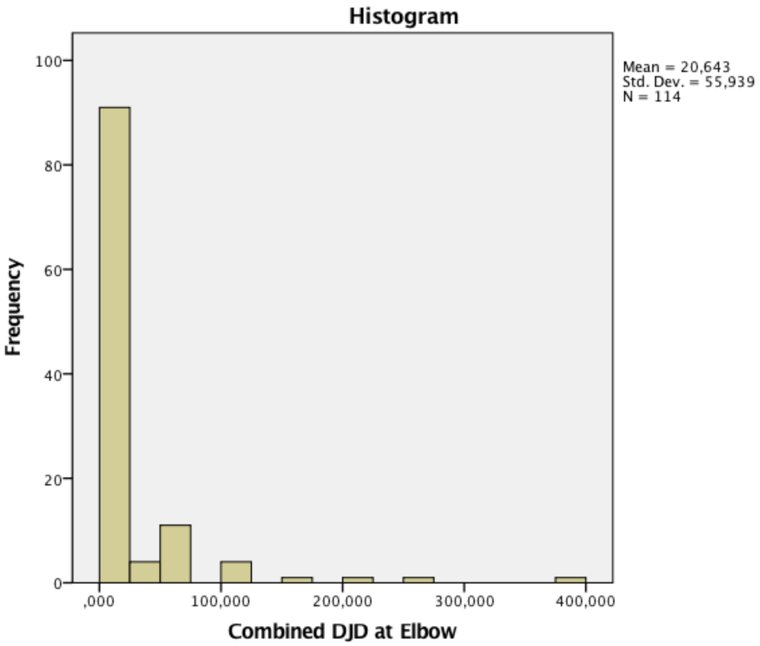


Figure 6.1Frequencies of the combined values of DJD (osteophytosis + porosity + eburnation) at the elbow joint in the knuckle-walkers sub-sample, presented as an example of the distribution of DJD to view the level of skewedness of DJD expression, observed throughout the sample. The greatest number of cases were of a healthy joint (0), whereas the rest of scores were progressively less frequent as severity increased suggesting an overall healthy population

The highest values of spinal DJD (SDJD) were found in the thoracic and lumbar regions, and the vertebral bodies exhibited higher average severity values than the apophyseal joints (Table 6.2). The most affected bodies were in the thoracic region, with the highest values pertaining to the lower thoracic spine for all the indicators of DJD, except for eburnation, which presented slightly higher severity values at the middle thoracic region (osteophytosis middle thoracic bodies=6.82; lower thoracic bodies=7.66; porosity at the middle thoracic bodies=5.09; lower thoracic bodies=7.04; eburnation at middle thoracic bodies=0.28; lower thoracic bodies=0.22). The apophyses were affected by DJD throughout the spine, exhibiting a less defined pattern (Table 6.2). The highest values of osteophytosis, porosity and eburnation were found at different parts of the spine (lumbar apophyses, middle thoracic apophyses and cervical apophyses, respectively). However, the combined values of DJD were the highest at the lumbar region (combined DJD for cervical apophyses=2.44; upper thoracic apophyses=4.28; middle thoracic apophyses=5.67; lower thoracic apophyses=7.73; lumbar apophyses=10.01).

Table 6.2 General descriptive results showing means and medians for the whole sample at the level of the spine. The highest values of the vertebral bodies and for the apophyseal joints are shaded

Joint	**Whole sample (spine)**							
	Eburnation		**Osteophytosis**		**Porosity**		**Combined**	
	Mean	**Median**	**Mean**	**Median**	**Mean**	**Median**	**Mean**	**Median**
Cervical bodies	0.10	0	3.09	0	3.34	0	6.53	0
Upper thoracic bodies	0.00	0	3.00	0	2.29	0	5.29	0
Middle thoracic bodies	0.28	0	6.84	0	5.09	0	11.95	0
Lower thoracic bodies	0.22	0	7.66	0	7.04	0	14.72	0
Lumbar bodies	0.09	0	6.94	0	6.51	0	13.55	0
Cervical apophyses	0.13	0	1.60	0	0.67	0	2.44	0
Upper thoracic apophyses	0.00	0	1.40	0	2.88	0	4.28	0
Middle thoracic apophyses	0.05	0	1.77	0	3.85	0	5.67	0
Lower thoracic apophyses	0.10	0	4.42	0	3.21	0	7.73	0
Lumbar apophyses	0.04	0	7.64	0	3.43	0	10.01	0

6.1.2 Discussion of the general distribution of DJD in non-human primates

The distribution of the data was skewed (example in Fig. 6.1); noticeable by all median values equalling zero (Tables 6.1 and 6.2), but it was still possible to assess the directionality and the relative intensity of the different processes of DJD. The positive skewedness observed entailed a great frequency of cases with no evidence of DJD, i.e. reflecting healthy joints.

The different indicators of DJD were expressed to different degrees as well as at different joints. Osteophytosis generally had the highest levels of expression, making it the most prevalent indicator of DJD, although it often was closely followed and in some cases exceeded by porosity. It was likely that osteophytosis was expressed as the first evidence of DJD in its early stages. However, osteophytosis and porosity were often expressed simultaneously and in fewer cases they could be accompanied by eburnation. Eburnation was infrequently observed and it consistently exhibited the lowest average values of the three (Tables 6.1 and 6.2).

Eburnation has been defined in previous research as the latest stage of degeneration of a joint (DeRousseau, 1988). It develops once the cartilage is completely eroded, leading to direct contact between the bony elements of a joint, generally compromising its normal function, becoming pathological (e.g., Rogers et al., 1987; DeRousseau, 1988; Aufderheide and Rodríguez-Martín, 2011). Consequently, the low levels of expression of eburnation reinforced the rather healthy pattern of joints observed across the sample.

The decreasing averages of expression from osteophytosis, to porosity and finally eburnation confirmed the continuous nature of DJD expression. Despite the overall preponderance of healthy joints observed in the study sample, the greater expression of osteophytosis and porosity in contrast with eburnation suggested a notable expression of non-pathological DJD (i.e. DJD expressions prior to the development of eburnation). The combined values obtained for DJD at a joint were often a reflection of the indicator that showed the highest average values and not necessarily of the joints showing greatest amounts of eburnation and thus of the most severe stages of joint degeneration. These values could be used as a synthetic measure of DJD expression for a joint, which placed emphasis on the non-pathological expressions of DJD, but would not provide information on the stage of degeneration (pathological *vs.* non-pathological).

The spine and the limbs are compartments that differ in terms of structure, function and number of joints, making the values obtained not directly comparable. Therefore, the treatment of the results was done separately for limbs and spine.

The pattern of affected joints in the limbs of non-human primates differed considerably from that observed in humans. In accordance with previous studies of DJD in non-human primates (e.g., DeRousseau, 1985; Jurmain, 1989; Lovell, 1990; Rothschild and Woods, 1992), DJD was found to be less prevalent in the present non-human sample than that reported for humans (e.g., Weiss and Jurmain, 2007; Waldron, 2008; Aufderheide and Rodríguez-Martín, 2011). Even though specific comparisons with humans could not be made due to differences in the methodology employed (mainly pathological DJD has been recorded in humans), general comparisons on prevalence patterns could be approached.

In humans, the knee is the most commonly affected joint closely followed by the hip, with the shoulder joint also showing high prevalence values (Rogers et al., 1987; Waldron, 2008; Aufderheide and Rodríguez-Martín, 2011). In contrast, the hip was not particularly affected by DJD across the present non-human primate sample (combined DJD=10.2) and the most affected joints were the elbow (combined DJD=27.94) and knee (combined DJD=24.4) followed by the shoulder joint (combined DJD=15.26). These different patterns could be explained by locomotor differentiation, relating mechanical stress derived from locomotion and DJD development.

The bipedal gait typical of humans is performed with extended hindlimbs (or lower limb), entailing that neither the knee nor the hip joint experience great distances with the SRF in the sagittal plane (Fig. 6.2). This strategy is commonly adopted by large quadrupedal mammals in order to reduce the moment arms and, ultimately, the load on weight-bearing joints (Biewener, 1990), and could potentially reduce the amount of DJD at the knee, compared to non-human primates.

Figure 6.2 Representation of the SRF during human bipedalism at different moments of the stride, showing the little displacement of the hip, knee and ankle joints from the reaction force (after Vaughan, 2003)

All the joints of the human lower limb have an important weight-bearing role, as they support the total amount of weight of the individual, which is accompanied by specialised adaptations, like the ones observed at the knee joint, mainly designed for weight-bearing purposes. The hip joint is in charge of supporting weight but its main function is to allow a wide range of movement for the lower limb. During normal bipedal walking both the hip and knee joints (specifically the tibio-femoral portion) support similar joint forces that range from approximately 2 to 6 times the body weight at different moments of the walking cycle (Fig. 6.3) (Palastanga et al., 1998). If DJD were a direct reflection of the forces supported, the knee and hip joints in humans would be expected to develop similar levels of DJD. As already mentioned, the hip and knee joints in humans are relatively closely aligned with the SRF during bipedal locomotion, but the hip is slightly more distant to the SRF than the knee joint in the coronal plane. Differently to what is observed in chimpanzees, as an example of non-human primate, humans walk with an adducted femur, placing their feet directly under their centre of gravity, which allows them to perform a more efficient bipedal gait (Jenkins, 1972; Vaughan, 2003). This positioning of the femur in humans entails that the mechanical and the anatomical axes of the lower limb in humans do not coincide (Fig.6.3). The fact that the hip joints are further apart than the ankle joints (Palastanga et al., 1998) is the main reason for the slight displacement of the hip from the SRF that could ultimately involve greater DJD development.

Figure 6.3 Representation of the anatomical and mechanical axes of the human femur and tibia (left) and diagrams of the forces about the hip joint (above) and the knee joint (below) during a stride (right) (modified from Palastanga et al., 1998)

The knee joint experiences intense stress during bipedal locomotion in humans. The force of weight can cross the joint as a result of the adducted femoral angulation during locomotion (Jenkins, 1972; Vaughan, 2003). However, the accompanying structures in charge of great stress reduction, such as the patella or the menisci, may be the main reason why the tibio-femoral portion of the knee joint ultimately bears similar forces to the hip joint. This, together with the fact that the hip joint is generally further away from the SRF and, therefore, supports greater amounts of load as a result of the moment arms could lead to the similar levels of DJD for both of the joints.

The knee of non-human primates, despite not being as heavily affected by weight as in the case of human bipedalism, is generally involved in heavier weight bearing than the elbow joint (Reynolds, 1985a, 1985b; Demes et al., 1994; Larson, 1998; Schmitt, 1998; Larson and Stern, 2009). Therefore, DJD would be expected to be higher at the knee than at the elbow, as greater forces would be coupled with greater loads. However, the average values of osteophytosis and porosity were higher at the elbow joint with only the average of eburnation being higher at the knee (osteophytosis elbow=17.11; osteophytosis knee=13.52; porosity elbow=8.75; porosity knee=8.51; eburnation elbow=1.43; eburnation knee=2.48).

The menisci and patellar tendon as well as the surrounding ligaments and musculature present at the knee joint are likely to protect the bony elements of the joint, keeping its structure despite the great levels of stress. The elbow joint lacks some of these stress reduction structures. Here the surrounding musculature can only absorb part of the impact coming from locomotion, which could potentially make the elbow more susceptible to mechanical stress and, ultimately to joint degeneration. The fact that eburnation was more prevalent at the knee than at the elbow could answer to the differences in structure of the joints. The menisci would prevent accelerated early development of DJD (i.e. osteophytosis and porosity) resulting from stress. However, once the menisci and the joint cartilage wear the joint would degenerate quickly, expressing higher levels of severe DJD (i.e. eburnation). The levels of eburnation were noticeably lower at the elbow joint (1.43, against 2.48 of the knee), suggesting that degeneration at the elbow joint was likely to happen in a more progressive manner, reaching lower overall severity stages of the disease than the knee joint (osteophytosis and prosity *vs.* eburnation).

The patterns of SDJD development for the present sample showed lower levels of prevalence and severity than those expressed for humans (e.g., Trinkaus, 1985; Hutton, 1987; Knüsel et al., 1997; Hukuda et al., 2000; Waldron, 2008; Woo and Pak, 2014), as previously reported in other studies of non-human primates (Jurmain, 1989, 2000; Lovell, 1990). In the present sample, SDJD showed differences of expression between the two functional types of joints found at the spine (bodies and apophyses), suggesting that different types of stress associated to function could entail differences in the development of DJD. The more immobile vertebral bodies are mainly in charge of weight support, the effect of which would vary according to the posture adopted during locomotion (different levels of orthogrady), although they are also subject to stresses derived from spinal movements. In contrast, the mobile apophyseal joints were more susceptible to stress derived from the movements they perform, experiencing less weight-bearing related stress than the vertebral bodies.

The thoraco-lumbar portion of the spine exhibited the highest levels of DJD expression among the study sample, suggesting that the rather orthograde posture adopted by primates during locomotion is reflected on more severe DJD resulting from pressure at the vertebral bodies in the more caudal half of the spine (Table 6.2). In fact, the highest levels of expression were found at the thoracic region (middle thoracic eburnation=0.275; lower thoracic osteophytosis=7.66; lower thoracic porosity=7.04), reflecting the more pronograde postures adopted by some taxa. However, the high prevalence of DJD at the caudal half of the spine, especially at the thoracic region, could result from morphological differences found here, where some vertebrae can be morphologically thoracic but functionally lumbar (Ankel-Simons, 2007; Gebo, 2014). This differentiation could potentially make these vertebrae less efficient than lumbar vertebrae to deal with stress, resulting in greater DJD development.

The varied expression of DJD at the apophyseal joints could be a result of the great variability of spinal movements associated with different locomotor behaviour. Different locomotor bouts may require different types of movements and this could have a direct effect on DJD development at these joints. Further analyses with smaller groups of more consistent locomotor behaviours were required in order to clarify the potential connection between DJD and locomotor behaviour.

6.2 Differing patterns of DJD distribution according to locomotor adaptation

The previous section presented average expressions of DJD at the different weight-bearing joints (or groups of joints), providing a general pattern of DJD expression using all the taxa studied. This section deals with patterns of distribution of DJD of the five different groups of primates defined in chapter 5 according to locomotor adaptation (Table 5.2), where means and medians were calculated: vertical clingers and leapers (VCL) and slow arboreal quadrupeds (N=100), leapers (N=164), quadrupeds (N=310), knuckle-walkers (N=109) and suspensory primates (N=114). Deviations from the general pattern will be discussed and the potential drivers of variability considered.

6.2.1 Severity and distribution of DJD in primates of different locomotor adaptations

The average values of DJD expression were overall low and the medians equalled zero with only one exception (osteophytosis at the elbow of the knuckle-walkers) (Table 6.3). The average values varied across sub-samples, sometimes showing different levels of DJD expression, deviating from the general pattern previously described. The combined values reflected the most commonly prevalent indicator of DJD, so the main focus was placed on the individual indicators of DJD.

VCL and slow arboreal quadrupeds showed no signs of eburnation. The averages obtained for osteophytosis and porosity were overall lower than those obtained for the other locomotor groups, with the exception of the leapers (Table 6.3). The limb joint that showed the highest average for osteophytosis was the ankle joint (osteophytosis ankle=5.00), whereas the highest values for porosity were at the knee (porosity knee=6.10). The most affected regions of the spine were the lower thoracic and the lumbar areas. Osteophytosis was more severely expressed at the lower thoracic spine, both for bodies (osteophytosis lower thoracic bodies=1.47) and apophyses (osteophytosis lower thoracic apophyses=1.88). There were no signs of porosity at the apophyseal joints but it was present on the vertebral bodies, reaching the highest values at the lumbar region (porosity lumbar bodies=4.07).

The **leapers** showed some similarities with the VCL and slow arboreal quadrupeds (Table 6.3). The overall values were low and there was very little evidence of eburnation; it was found only at two joints of the limbs (eburnation shoulder=0.61; eburnation knee=1.00). The highest values of osteophytosis were found at the elbow joint (osteophytosis elbow=6.06) but the greatest evidence of both porosity and eburnation was found at the hindlimb. The ankle joint showed the highest signs of porosity, which was the highest value of all the signs of DJD observed at the limbs of this group (porosity ankle=8.99). The most affected regions of the spine were the lumbar and the upper thoracic portions. The lumbar spine showed the highest values of osteophytosis, both at the bodies and apophyses (osteophytosis lumbar bodies=2.02; osteophytosis lumbar apophyses=1.03). The upper thoracic region, showed the highest signs of porosity at the bodies (porosity upper thoracic bodies=2.18). Here there were no signs of porosity at the apophyseal joints.

The **quadrupeds** exhibited different patterns of expression of DJD, compared to the previous two groups. The overall values of DJD were higher and there was evidence of all DJD indicators in all the body compartments (Table 6.3). The most severely affected joint at the forelimbs was the elbow joint, which exhibited the highest levels of eburnation and osteophytosis (eburnation elbow=2.58; osteophytosis elbow=19.63). The knee joint was the most severely affected joint of the hindlimb, exhibiting the highest levels of porosity recorded for the limbs (porosity knee=7.1). The shoulder joint of the quadrupeds was the only case of all the joints and groups considered that exhibited the highest combined values of the limbs despite not showing the highest values of independent DJD indicators (combined DJD shoulder=27.05; elbow=16.00; wrist=9.52; Hip=22.48; knee=17.74; ankle=5.54). SDJD expression at the vertebral bodies mainly affected the cervical and middle thoracic regions. Eburnation and porosity were the highest at the cervical bodies (eburnation cervical bodies=0.16; porosity cervical bodies=1.49), while osteophytosis reached the highest values at the middle thoracic region (osteophytosis middle thoracic bodies=7.6). SDJD expression at the apophyseal joints was more severe in the caudal half of the spine. The highest levels of eburnation were found at the lower thoracic region (eburnation lower thoracic apophyses=0.12), osteophytosis was highest at the lumbar region (osteophytosis lumbar apophyses=4.11) and porosity was highest at the middle thoracic region (porosity middle thoracic apophyses=2.11).

The **knuckle-walkers** showed the overall greatest values of DJD among the sample (Table 6.3). The mean values were much higher than in all the other locomotor groups and had the only median that did not equal zero, which was found at their elbow for osteophytosis. There were signs of eburnation, osteophytosis and porosity in all the body compartments. At the limbs, the knee showed the highest values of eburnation (eburnation knee=4.78) and osteophytosis, although the elbow joint showed similar levels for osteophytosis (osteophytosis elbow=42.63; osteophytosis knee=43.03). The elbow showed the highest values of porosity (porosity elbow=43.43). SDJD was generally more prevalent in the more caudal portions of the spine. At the level of the vertebral bodies the greatest expressions of eburnation and osteophytosis were found at the lumbar region (eburnation lumbar bodies=0.253; osteophytosis lumbar bodies=22.42) and porosity was highest at the lower thoracic region (porosity lower thoracic bodies=29.25). Concerning the apophyses, while eburnation was highest at the cervical spine (eburnation cervical apophyses=0.38), the lumbar region exhibited the highest values of osteophytosis and porosity (osteophytosis lumbar apophyses=24.6; porosity lumbar apophyses=14.15).

Suspensory primates showed lower values of DJD than the knuckle-walkers but similar to those obtained for the quadrupeds. There were signs of the three DJD indicators in all the body compartments (Table 6.3). At the limbs, the knee joint showed the highest values of eburnation (eburnation knee=4.74), while the highest averages for osteophytosis and porosity were found at the elbow joint (osteophytosis elbow=13.28; porosity elbow=6.49), although the knee joint had very similar expression of osteophytosis (osteophytosis knee=13.16). SDJD was mainly found at the thoracic region, also affecting the lumbar and cervical regions. The lumbar bodies showed the highest levels of eburnation (eburnation lumbar bodies=0.26), but the highest severities of osteophytosis and porosity were found at the middle thoracic bodies (osteophytosis middle thoracic bodies=7.84; porosity middle thoracic bodies=6.59). The distribution of DJD at the apophyses was more spread, showing the highest levels of eburnation at the cervical spine (eburnation cervical apophyses=0.26), of osteophytosis at the lumbar spine (osteophytosis lumbar apophyses=3.44) and of porosity at the middle thoracic spine (porosity middle thoracic apophyses=7.27).

Table 6.3 General descriptive results (means and medians) for all the sub-samples according to main locomotor adaptation for all the main weight-bearing joints (the highest mean values of each compartment are shaded)

	VCL + slow arboreal quadrupeds								**Leapers**							
	Eburnation		Osteophytes		Porosity		Combined		Eburnation		Osteophytes		Porosity		Combined	
	Mean	Med	Mean	Med	Mean	Med	Mean	Med	Mean	Med	Mean	Med	Mean	Med	Mean	Med
Cervical bodies	0.00	0	0.00	0	0.18	0	0.18	0	0.00	0	0.28	0	2.11	0	2.39	0
Upper th. bodies	0.00	0	0.00	0	1.22	0	1.22	0	0.00	0	1.27	0	2.18	0	3.45	0
Middle th. bodies	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.59	0	1.27	0	1.85	0
Lower th. bodies	0.00	0	1.47	0	2.12	0	3.59	0	0.00	0	1.31	0	0.00	0	1.31	0
Lumbar bodies	0.00	0	1.05	0	4.07	0	5.12	0	0.00	0	2.02	0	0.53	0	2.54	0
Cervical apoph	0.00	0	1.25	0	0.00	0	1.35	0	0.00	0	0.19	0	0.00	0	0.19	0
Upper th. apoph	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.70	0	0.00	0	0.70	0
Middle th. apoph	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.88	0	0.00	0	0.88	0
Lower th. apoph	0.00	0	1.88	0	0.00	0	1.88	0	0.00	0	0.43	0	0.00	0	0.53	0
Lumbar apoph	0.00	0	1.26	0	0.00	0	1.26	0	0.00	0	1.03	0	0.00	0	1.03	0
Shoulder	0.00	0	1.50	0	1.50	0	3.00	0	0.61	0	2.87	0	0.00	0	3.48	0
Elbow	0.00	0	4.00	0	0.00	0	4.00	0	0.00	0	6.06	0	0.00	0	6.06	0
Wrist	0.00	0	1.00	0	0.00	0	1.00	0	0.00	0	0.67	0	0.31	0	0.98	0
Hip	0.00	0	1.60	0	2.00	0	3.60	0	0.00	0	0.62	0	0.00	0	0.61	0
Knee	0.00	0	1.00	0	6.10	0	7.10	0	1.00	0	2.56	0	4.16	0	7.56	0
Ankle	0.00	0	5.00	0	2.50	0	3.00	0	0.00	0	0.00	0	8.99	0	8.72	0

Table 6.3 (cont.). General descriptive results (means and medians) for all the sub-samples according to main locomotor adaptation for all the main weight-bearing joints (the highest mean values of each compartment are shaded).

	Quadrupeds								Knuckle-walkers							
	Eburnation		Osteophytes		Porosity		Combined		Eburnation		Osteophytes		Porosity		Combined	
	Mean	Med	Mean	Med	Mean	Med	Mean	Med	Mean	Med	Mean	Med	Mean	Med	Mean	Med
Cervical bodies	0.16	0	3.90	0	1.49	0	5.54	0	0.00	0	5.38	0	9.96	0	15.34	0
Upper th. bodies	0.00	0	2.29	0	0.18	0	2.46	0	0.00	0	6.00	0	6.84	0	12.83	0
Middle th. bodies	0.00	0	7.60	0	0.88	0	8.49	0	0.13	0	11.61	0	17.86	0	29.59	0
Lower th. bodies	0.00	0	6.71	0	1.05	0	7.76	0	0.10	0	17.98	0	29.25	0	47.33	0
Lumbar bodies	0.03	0	2.89	0	0.44	0	3.36	0	0.25	0	22.42	0	27.42	0	50.10	0
Cervical apoph	0.06	0	0.67	0	0.06	0	1.52	0	0.38	0	5.12	0	2.99	0	8.49	0
Upper th. apoph	0.00	0	0.79	0	0.72	0	3.35	0	0.00	0	3.29	0	9.24	0	12.53	0
Middle th. apoph	0.05	0	1.18	0	2.11	0	4.93	0	0.13	0	4.49	0	10.10	0	14.72	0
Lower th. apoph	0.12	0	3.62	0	1.19	0	4.36	0	0.20	0	11.02	0	10.00	0	21.22	0
Lumbar apoph	0.03	0	4.11	0	0.22	0	18.03	0	0.13	0	24.60	0	14.15	0	33.81	0
Shoulder	0.16	0	10.97	0	6.90	0	27.05	0	0.46	0	21.74	0	23.21	0	45.41	0
Elbow	2.58	0	19.63	0	4.84	0	16.00	0	2.20	0	42.63	33.33	43.43	0	88.26	66.67
Wrist	1.16	0	8.70	0	6.13	0	9.52	0	0.00	0	17.06	0	12.75	0	29.82	0
Hip	0.48	0	6.97	0	2.07	0	22.48	0	0.00	0	17.34	0	15.60	0	32.94	0
Knee	2.42	0	12.97	0	7.10	0	17.74	0	4.77	0	43.03	0	26.88	0	74.68	0
Ankle	2.19	0	12.55	0	3.00	0	5.54	0	0.00	0	32.84	0	20.55	0	53.40	0

Table 6.3 (cont.). General descriptive results (means and medians) for all the sub-samples according to main locomotor adaptation for all the main weight-bearing joints (the highest mean values of each compartment are shaded).

	Suspensory							
	Eburnation		Osteophytes		Porosity		Combined	
	Mean	Med	Mean	Med	Mean	Med	Mean	Med
Cervical bodies	0.26	0	1.79	0	3.11	0	5.15	0
Upper th. bodies	0.00	0	4.89	0	3.25	0	8.14	0
Middle th. bodies	0.00	0	7.84	0	6.59	0	14.43	0
Lower th. bodies	0.00	0	4.28	0	1.41	0	5.70	0
Lumbar bodies	0.26	0	5.26	0	2.03	0	7.55	0
Cervical apoph	0.26	0	1.25	0	0.41	0	1.95	0
Upper th. apoph	0.00	0	2.29	0	5.90	0	8.19	0
Middle th. apoph	0.00	0	1.25	0	7.27	0	8.52	0
Lower th. apoph	0.00	0	1.96	0	5.26	0	7.22	0
Lumbar apoph	0.00	0	3.44	0	4.16	0	7.59	0
Shoulder	0.44	0	3.95	0	2.19	0	6.58	0
Elbow	0.88	0	13.28	0	6.49	0	20.64	0
Wrist	0.00	0	4.12	0	0.88	0	5.00	0
Hip	0.00	0	5.00	0	4.91	0	9.91	0
Knee	4.74	0	13.16	0	3.07	0	20.97	0
Ankle	0.97	0	2.72	0	2.02	0	5.70	0

6.2.2 Discussion of the distribution of DJD in non-human primates according to locomotor adaptation

The results obtained evidenced that DJD expression was variable among the different sub-samples and that not all of these groups followed the generalised pattern obtained in the first section of this chapter. Skewedness of the data was prevalent for all the sub-samples, as exemplified by the great majority of medians equalling zero.

The five different groups showed different overall values of DJD, suggesting that some groups were more prone to DJD development than others. The knuckle-walkers showed the highest overall values of DJD, followed by the quadrupeds and the suspensory primates. In contrast, the leapers, VCL and slow arboreal quadrupeds showed the lowest average values of DJD (Table 6.3).

The differences in overall severity of DJD expression could be due to differences in locomotor adaptation, but these groups of primates differ greatly in other aspects, such as body mass or longevity. The knuckle-walkers comprise all the African great apes (*Gorilla gorilla*, *Gorilla beringei*, *Pan troglodytes* and *Pan paniscus*), which are among the largest species of extant primates, ranging from an average of 33 Kg of a female bonobo (*Pan paniscus*) to the average of 170 Kg of a male lowland gorilla (*Gorilla gorilla*) (Smith and Jungers, 1997). In contrast, some of the smallest primates recorded are the VCL and slow arboreal quadrupeds. These include some species like the tarsiers (*Tarsius* sp.), with an average body mass of 0.134 Kg, gallagos (e.g., *Gallago alleni*) of 0.277 Kg, and sifakas (*Propithecus* sp.), which can be up to 6.26 Kg (Smith and Jungers, 1997). The other groups of primates are somewhere in between, with the suspensory and quadrupedal primates taking intermediate body mass values (except *Pongo* sp., which is similar to the knuckle-walkers, reaching an average of 78.5 Kg) and the leapers being closer to the VCL and slow arboreal quadrupeds (Smith and Jungers, 1997). Consequently, DJD expression did not seem to be independent to body mass. The group of primates that include the largest taxa also exhibit the highest average severity values of DJD (the knuckle-walkers), whereas the smallest groups exhibited the lowest levels of DJD expression (the leapers and VCL and slow arboreal quadrupeds). Accordingly, the groups that showed intermediate levels of DJD were the groups of intermediate body mass.

Therefore, body mass was a potential driver of DJD that should be considered in the study of DJD development.

The five sub-samples further differed in longevity. Similarly to what was observed with body mass, the groups of primates that exhibited the highest levels of DJD expression were among the longest-lived taxa of primates of the present sample (the knuckle-walkers) (Harvey and Clutton-Brock, 1985). In contrast, the leapers or the VCL and slow arboreal quadrupeds were among the shortest-lived taxa (Harvey and Clutton-Brock, 1985), and exhibited the lowest expressions of DJD. Primates that live longer would reach more advanced ages and potentially more advanced stages of DJD expression, whereas those primates that live comparatively shorter would not have time to develop DJD as severely, entailing that age and longevity were likely to play an important role in DJD development.

The intensity of DJD expression across sub-samples suggests an important role of differences in body mass or longevity. However, differences in the pattern of distribution of relative DJD (which joints are the most affected for each group) suggested that further factors could shape how DJD is expressed in their skeletons.

The **limbs** of knuckle-walkers, quadrupeds and suspensory primates showed a similar pattern to the general one (where eburnation was highest at the knee joint, whereas osteophytosis and porosity were highest at the elbow joint), with the elbow and knee being the most affected joints (Table 6.3). These primate groups showed the highest overall values of DJD expression and their combined sample size was greater than the combined sample size of the primates differing from the general pattern (N=533 for primates coinciding with the general pattern; N=264 for primates deviating from the general pattern). Therefore, it was likely that the general pattern was a reflection of DJD expression in quadrupeds, knuckle-walkers and suspensory primates, at least concerning the limbs.

The three groups that show a similar distribution pattern of DJD (quadrupeds, knuckle walkers and suspensory primates, Table 6.3) perform kinetically similar locomotion at the level of the limbs, in comparison with the group of primates that differ from the general primate pattern exposed in section 6.1 (VCL, slow arboreal quadrupeds and leapers) (chapter 4). The pattern of loading of the limbs and the associated forces and loads that result from locomotion are similar among quadrupeds (including knuckle-walkers) and suspensory primates (with different reliance on forelimb or hindlimb depending on the type of suspensory gait performed) (Bertram, 2004; Raichlen et al., 2009; Granatosky et al., 2016; Finestone et al., 2018). This could suggest that kinematic similarities during locomotion and, thus, similar systems of forces and loads experienced at the level of the limbs, could entail similar patterns of DJD expression, which could further vary depending on locomotor variability within each of these groups (further analysed in chapter 7). In contrast, the other sub-samples (VCL, slow arboreal quadrupeds and leapers) exhibit much lower levels of DJD expression at their limbs as well as different patterns of expression (Table 6.3), in accordance with their kinematic differentiation from the quadrupeds, knuckle-walkers and suspensory primates (chapter 4). The relationships between loading patterns, variability of locomotor behaviour and DJD expression are further assessed in chapter 7.

The expression patterns observed at the **spine** (SDJD) were variable across the different groups considered. None of the sub-samples showed precise coincidences with the general pattern established in section 6.1. This suggested that, contrary to what was observed at the limbs, the general pattern was likely to be a mosaic of the different groups considered and that SDJD could be particularly susceptible to differences in trunk movements associated to the different locomotor adaptations.

The functional differentiation between the vertebral bodies and apophyseal joints, similarly to what was described for the whole sample, was associated to different patterns of DJD expression in different groups of primates. The consideration of the different sub-samples confirmed the association between level of orthograde and the more caudal development of DJD at the vertebral bodies, also reflecting kinematic particularities derived from trunk movements, such as those experienced by the suspensory primates (further developed in chapter 7). In contrast, the most pronograde groups (quadrupeds and the leapers) showed rather cranial expressions of DJD at the vertebral bodies, in comparison with other groups (Table 6.3).

The apophyseal joints showed greater variability in the patterns of expression of DJD across groups (Table 6.3). This was likely to be because the range of trunk movements performed, as suggested in section 6.1, may determine DJD development.

All trunk movements are important for primate locomotion but depending on the locomotor adaptation some movements can be associated to greater stress, potentially inducing greater DJD development. Some groups exhibited higher DJD severity values at the lumbar region, like the knuckle-walkers (osteophytosis lumbar apophyses=24.6; porosity lumbar apophyses=14.15) or the leapers (osteophytosis lumbar apophyses=1.03), suggesting that the most intense stresses were experienced at this region. In contrast, other groups exhibited greater severities of DJD at the thoracic region, like the VCL and slow arboreal quadrupeds (osteophytosis lower thoracic apophyses=1.88) or the quadrupeds (eburnation lower thoracic apophyses=0.12; porosity middle thoracic apophyses=2.11), although the latter exhibited the greatest levels of osteophytosis at the lumbar region (osteophytosis lumbar apophyses=4.11). This suggested that these groups of primates were more likely to experience the greatest stress derived from trunk rotation. The association between specific movements commonly performed by primates and variability of DJD is thus explored in chapter 7.

The results obtained and discussed in this section suggested that DJD development in these groups of primates could be associated to different factors. Firstly, there were obvious differences in severity across the different groups that could be a result of differences in body mass or longevity. Secondly, differences in the pattern of DJD expression were likely to be closely related to locomotor adaptation and the particular locomotor behaviour performed by each of these groups.

6.3 Comparison of DJD at the forelimb and hindlimb

One of the characteristics of the primate gait is that, differently to other quadrupedal mammals, primates greatly rely on the hindlimb for locomotion (e.g., Reynolds, 1985a, 1985b; Demes et al., 1994; Larson, 1998; Schmitt, 1998). The hindlimb usually bears a greater portion of the weight of the animal and it often supports stronger peak SRF (e.g., Larson, 1998; Schmitt, 1998; Demes et al., 1999, 2005; Hanna et al., 2006; Granatosky et al., 2016). Hence, if greater limb reliance entailed greater levels of stress, DJD would be expected to be more prevalent and more severe at the hindlimbs, due to their role as a locomotor drive in primates.

The connection between limb reliance and DJD development was assessed by means of ratios of overall limb DJD expression between the forelimb and the hindlimb. The zero-values were substituted by adding 1 to all the recordings of DJD, thus allowing the calculations of the ratios (*FLHLratio*) for eburnation, osteophytosis, porosity, and combined DJD values (Equation 6.1).

$$FLHLratio = \frac{(glenohumeral + elbow + wrist + 1)}{(hip + knee + ankle + 1)}$$

Equation 6.1

These ratios reflected hindlimb or forelimb dominance in terms of DJD development, depending on whether the ratio was greater or smaller than one. Ratios equalling one could result from two possible scenarios: 1) an individual with healthy forelimbs and hindlimbs or 2) an individual with the same levels of degeneration at the forelimb and the hindlimb. As the interest of these analyses was to see dominance of one limb over the other in terms of DJD, healthy limbs and equally affected limbs provided the same type of information and were not considered. Ratios greater than one were obtained when DJD expression was greater at the forelimb than the hindlimb (forelimb DJD dominance). In contrast, ratios smaller than one were obtained with greater DJD expressions at the hindlimb than the forelimb (hindlimb DJD dominance).

6.3.1 Limb ratios of DJD for the whole primate sample

The ratios obtained by using the **combined values of DJD** showed a high frequency of cases with no differentiation between forelimb and hindlimb DJD expression (N=437) and two clusters of values, one for ratios smaller than one (of hindlimb DJD dominance) and the other for rations greater than one (of forelimb DJD dominance) (Fig. 6.4). The number of cases (or individuals) with hindlimb DJD dominance (N=165) was similar to those with forelimb DJD dominance (N= 195), although there were a greater number of cases of forelimb dominance (Table 6.4).

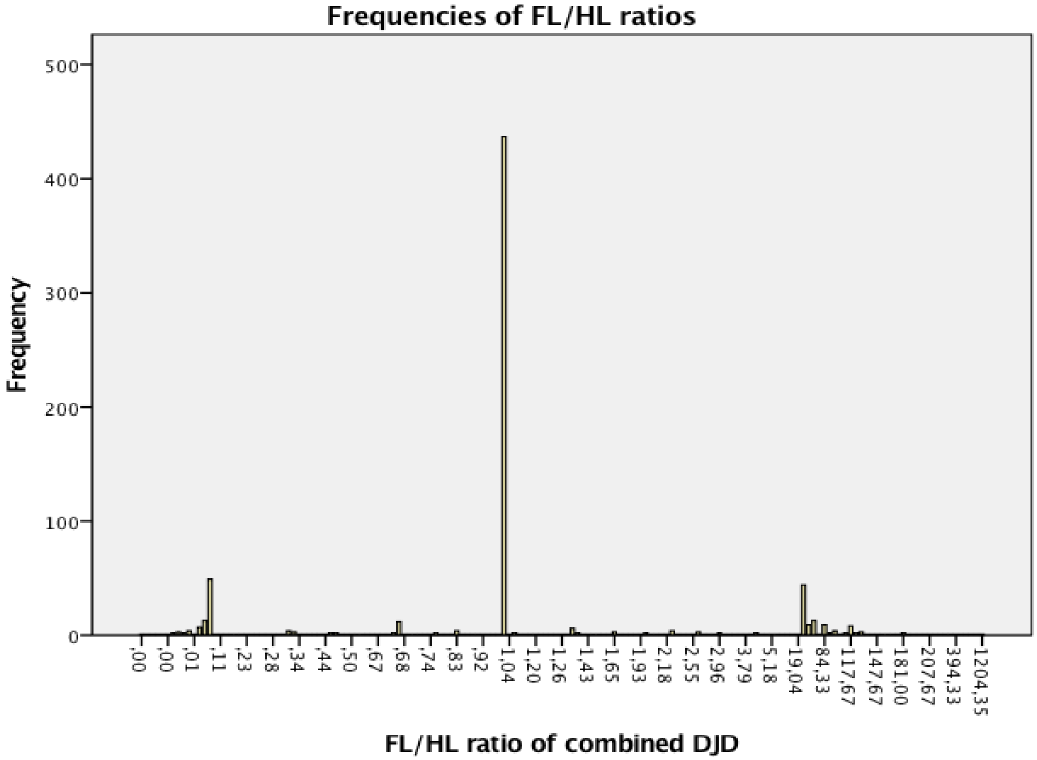


Figure 6.4 Bar chart showing the frequency values of the FL/HL ratios for the combined values of DJD across the whole primate sample

Table 6.4 Number of cases of forelimb-hindlimb ratios greater and smaller than one for different indicators of DJD considering the whole sample of primates. The greater values of each of the DJD indicators are shaded

DJD indicator	FL/HL>1 (N)	FL/HL<1 (N)
Combined DJD	195	165
Eburnation	16	19
Osteophytosis	179	103
Porosity	97	112

The limb ratios for **eburnation** with differentiation between forelimb and hindlimb were very few in comparison with those showing no differentiation (N=35 different to one; 762 equalling one). Of the cases showing limb dominance, 19 cases showed hindlimb DJD dominance and 16 cases showed forelimb dominance (Table 6.4). The limb ratios for **osteophytosis** exhibited a greater number of cases of DJD limb differentiation (N=282). Of these, 179 cases showed forelimb DJD dominance and

103 cases of hindlimb DJD dominance. However, there were still a great number of cases where of no limb differentiation (N=515). **Porosity** showed a greater number of individuals with limb DJD differentiation than for eburnation but less than osteophytosis. However, there were still a great number of cases with no limb differentiation (N=588). The number of individuals exhibiting hindlimb DJD dominance exceeded the number of cases with forelimb dominance (N=112 and 97, respectively).

6.3.2 Limb ratios of DJD for primates of different locomotor adaptations

Limb reliance varies among primate taxa, according to the different locomotor adaptations, as explained in chapter 4. DJD distribution at the limbs varies according to locomotor adaptation, as seen in section 6.2, potentially as a result of the differences in limb reliance. This section presents the limb ratios calculated for the different groups based on locomotor adaptation.

The **combined values of DJD** for different locomotor sub-samples showed different levels of differentiation between limbs in terms of DJD (Table 6.5). Suspensory primates showed the same number of cases of forelimb and hindlimb DJD dominance (N=21). Leapers and VCL and slow arboreal quadrupeds showed more cases of hindlimb DJD dominance (N=29 for leapers; N=15 for VCL and slow arboreal primates) than forelimb dominance (N=21 for leapers; N=8 for VCL and slow arboreal quadrupeds). In contrast, the knuckle-walkers and the quadrupeds showed the opposite. In both groups there were more cases of forelimb DJD dominance (quadrupeds: N=88; knuckle-walkers: N=57) than hindlimb DJD dominance (quadrupeds: N=59; knuckle-walkers: N=41).

Table 6.5 Number of cases of forelimb-hindlimb ratios greater and smaller than one for the combined values of DJD considering the different sub-samples of primates according to their main locomotor adaptation. The greater values of each of the sub-samples are shaded

Combined values of DJD		
Locomotor adaptation	**FL/HL>1 (N)**	**FL/HL<1 (N)**
VCL and slow arboreal quadrupeds	8	15
Leapers	21	29
Quadrupeds	88	59
Knuckle-walkers	57	41
Suspensory	21	21

The ratios obtained for **eburnation** showed very few cases of limb differentiation in expression of eburnation. Most of the samples exhibited equal signs of forelimb and hindlimb dominance, except for the quadrupeds and the suspensory primates (Table 6.6). In the case of the quadrupeds there were more cases of hindlimb (N=10) than forelimb dominance (N=8), whereas in the case of the suspensory primates there were more cases of forelimb (N=5) than hindlimb dominance (N=4). However, the figures were very low and very similar between the cases of ratios greater and smaller than one (Table 6.6).

Table 6.6 Number of cases of forelimb-hindlimb ratios greater and smaller than one for eburnation considering the different sub-samples of primates according to their main locomotor adaptation. The greater values of each of the sub-samples are shaded

Eburnation		
Locomotor adaptation	**FL/HL>1 (N)**	**FL/HL<1 (N)**
VCL and slow arboreal quadrupeds	0	0
Leapers	1	1
Quadrupeds	8	10
Knuckle-walkers	4	4
Suspensory	5	4

The limb ratios for **osteophytosis** showed the same pattern across the different groups, with higher numbers of cases of limb differentiation (Table 6.7). For all the sub-samples there were a greater amount of cases of forelimb dominance (Table 6.7). The quadrupeds were the group showing the greatest number of cases of limb differentiation (N=44 hindlimb and 81 forelimb dominance) and the leapers exhibited the greatest difference between cases of forelimb and hindlimb dominance (N=25 and 4, respectively).

Table 6.7 Number of cases of forelimb-hindlimb ratios greater and smaller than one for osteophytosis considering the different sub-samples of primates according to their main locomotor adaptation. The greater values of each of the sub-samples are shaded

Osteophytosis		
Locomotor adaptation	**FL/HL>1 (N)**	**FL/HL<1 (N)**
VCL and slow arboreal quadrupeds	9	3
Leapers	25	4
Quadrupeds	81	44
Knuckle-walkers	46	39
Suspensory	18	13

The ratios obtained for **porosity** showed fewer cases of limb differentiation than for osteophytosis but more than for eburnation (Table 6.8). The leapers and the VCL and slow arboreal quadrupeds showed a distinct differentiation, with more cases of hindlimb dominance (N=28 for leapers; N=16 for VCL and slow arboreal quadrupeds) than forelimb dominance (N=1 for leapers; N=0 for VCL and slow arboreal quadrupeds). In contrast, the opposite was observed for the remaining groups, with less cases of hindlimb dominance (N=34 for quadrupeds; N=26 for knuckle-walkers; N=8 for suspensory) over forelimb dominance (N=40 for quadrupeds; N=47 for knuckle-walkers; N=9 for suspensory), even though the difference was minimal for the suspensory primates.

Table 6.8 Number of cases of forelimb-hindlimb ratios greater and smaller than one for porosity considering the different sub-samples of primates according to their main locomotor adaptation. The bigger values of each of the sub-samples are shaded

Porosity		
Locomotor adaptation	**FL/HL>1 (N)**	**FL/HL<1 (N)**
VCL and slow arboreal quadrupeds	0	16
Leapers	1	28
Quadrupeds	40	34
Knuckle-walkers	47	26
Suspensory	9	8

6.3.3 Discussion of the results

The aim of this part of the analyses was to assess whether or not there were high levels of differentiation in DJD expression between the forelimbs and the hindlimbs. There were signs of asymmetrical DJD expression for the forelimb and the hindlimb. However, a great number of individuals showed no differentiation in DJD expression between forelimb and hindlimb (N=437). Limb dominance (forelimb or hindlimb DJD dominance) varied depending on the indicator of DJD considered.

6.3.3.1 Limb ratios of DJD for the whole sample

The limb ratios obtained for the whole sample did not show a clear dominance of one limb over the other in terms of DJD expression, even though overall DJD expressions showed a dichotomy in limbs affected. Across the study sample there were similar numbers of cases of forelimb dominance and hindlimb dominance in

DJD expression (N=195 and 165, respectively) (Fig. 6.4). This indicated that there was no clear, consistent limb dominance concerning DJD. Therefore, there probably was no clear relationship between the greater hindlimb reliance characteristic of the primate gait and a greater development of joint degeneration at this limb.

Limb ratios of the different indicators of DJD suggested a slight asymmetry in the different stages of development of the disease. Eburnation was not a prevalent stage of DJD across primates, as seen in the previous analyses in sections 6.1 and 6.2 (Tables 6.1, 6.2 and 6.3). As a result, very few cases showed ratios different to one (N=35), making eburnation only partially informative in terms of DJD limb asymmetry. The slight hindlimb dominance could be the reflection of the high levels of knee eburnation previously observed (Table 6.1). Considering that eburnation is the most severe stage of joint degeneration, this could partially support the link between the hindlimb drive and greater hindlimb degeneration. However, due to the small number of cases considered this was not enough evidence and more data would be necessary in order to confirm this.

The ratios obtained for osteophytosis differed from those for eburnation and porosity (Table 6.4). This was the indicator that showed the clearest asymmetry between limbs with more cases of forelimb than hindlimb DJD dominance (N= 179 and N=103, respectively) (Table 6.4). Regarding porosity there was a smaller difference between the number of cases of forelimb and hindlimb dominance (N=97 and N=112, respectively).

These results suggested that DJD in the broad sense of the disease was not developed in one limb in preference to the other. However, when the different indicators of DJD were analysed separately there seemed to be different prevalence for each indicator at the forelimb and the hindlimb. There was a clear tendency for greater osteophyte development at the forelimb, compared to the hindlimb, while porosity and eburnation were more prevalent at the hindlimb, even though eburnation showed very little difference between limbs. This suggested that the forelimb would develop high levels of early expressions of DJD, whereas the hindlimb would exhibit greater levels of more advanced stages of DJD. Degeneration at the hindlimb was likely to reflect mainly degeneration at the knee, as this was the joint showing the highest expressions of DJD of the hindlimb (Table

6.1). In contrast, DJD of the forelimb was likely to affect mainly the shoulder and the elbow, as observed in the general patterns of expression (Table 6.1).

6.3.3.2 Limb ratios of DJD for the sub-samples according to locomotor adaptation

The lack of a clear, consistent asymmetry between limbs in terms of DJD development did not support the association between limb reliance during locomotion and greater DJD development. However, different primate species can rely on their hindlimbs in different proportions, or even rely more on their forelimbs during locomotion (Reynolds, 1985a; Ishida et al., 1990, 1990; Demes et al., 1994; Schmitt, 1994, 2003; Schmitt and Lemelin, 2004), which led to independent consideration of the different sub-samples according to locomotor adaptation.

Quadrupedal primates, including the knuckle-walkers, rely more heavily on the hindlimb than on the forelimb during locomotion and their hindlimbs bear stronger forces associated to locomotion (Raichlen et al., 2009; Finestone et al., 2018). However, there were more individuals showing greater joint degeneration at their forelimbs compared to their hindlimbs. In contrast, the leapers and the VCL heavily rely on their hindlimbs for locomotion, which was coupled with more cases of hindlimb DJD dominance. The slow arboreal quadrupeds include the slow lorises (*Loris* sp. and *Nycticebus* sp.), which experience an inverted pattern of force distribution during locomotion, therefore, relying more heavily on the forelimb (Ishida et al., 1990; Schmitt, 1994, 1998; Schmitt and Lemelin, 2004; Hanna et al., 2017) and yet, DJD was greater at the hindlimb.

These results continue to challenge the supposition that greater limb reliance during locomotion would entail greater levels of DJD expression. The patterns of mechanical stress did not reflect DJD expression. In fact, almost the opposite was observed for several sub-samples. A potential answer to these expressions of limb DJD could be associated to morphological adaptation and how efficiently different joints have been designed to fulfill different purposes. Joints that are in charge of great amounts of weight bearing generally come with specific adaptations to this role. This makes them more efficient in damping the impact and stresses resulting from weight bearing and the derived forces associated with locomotion, potentially preventing fast, severe degeneration. In contrast, joints that are not designed exclusively for this purpose may be less efficient in dealing with the great forces associated to locomotion, ultimately leading to faster degeneration, which is further analysed in chapters 7 and 8.

While eburnation showed very few differences between limbs, and osteophytosis was consistently more present at the forelimb, the pattern obtained for porosity (Table 6.8) followed the same distribution as the pattern obtained using overall DJD (Table 6.5). This way, the leapers and VCL and slow arboreal quadrupeds showed more cases of hindlimb DJD dominance than forelimb DJD dominance, whereas the quadrupeds and the knuckle-walkers showed the opposite pattern. The suspensory primates showed very similar number of cases of forelimb and hindlimb DJD dominance, with only one more case of forelimb dominance but very few cases of a ratio different to one (N=9 of forelimb DJD dominance; N=8 of hindlimb DJD dominance). Therefore, it was likely that porosity was the DJD indicator responsible for the ratios obtained for overall DJD, as osteophytosis was always more prevalent at the forelimb and eburnation had very low overall prevalence.

These analyses showed that there was certain degree of asymmetry between limbs in terms of DJD expression. However, there was not enough evidence that could support a direct connection between the hindlimb drive characteristic of primate locomotion and greater development of DJD at these limbs. In fact, limb dominance in terms of DJD expression was variable across the five sub-samples of different locomotor adaptations, but it also varied depending on the DJD indicator considered. The forelimb seemed to be more prone to developing osteophytosis, whereas the expression of eburnation and porosity was more variable and comparatively more equally prevalent in both the forelimb and the hindlimb. The results obtained reinforced the great importance of morphological adaptation in the damping effect of forces acting on joints and, ultimately, on the development of DJD. Further exploration on the association of the shape of joints with forces and degree of degeneration can be found in chapter 8.

6.4 Summary and conclusions

This chapter dealt with general descriptive tests in order to provide a broad overview of where and how severely DJD was expressed in the primate skeleton. The patterns of DJD expression observed for this sample of non-human primates were different to those reported for humans, both in terms of intensity and the affected joints.

DJD expression further differed among non-human primates, with different groups of primates exhibiting different levels of severity of DJD, which could be at least partially related to differences in body mass or longevity. Moreover, the pattern of distribution of DJD also varied among the different groups of primates. Generally, the joints that support great mechanical stress and the corresponding loads as a result of differences in locomotion exhibited greater levels of DJD expression, which varied according to locomotor adaptation. In addition, SDJD reflected the functional distinction between the vertebral bodies and the apophyseal joints, suggesting that SDJD expression could be associated to differences in posture and trunk movements.

The tests on DJD expression related to locomotor hindlimb reliance typical of primates could not confirm the connection between limb reliance and DJD development. However, these results put forward the importance of morphological adaptation in terms of dealing with forces, which could determine DJD expression, concluding that DJD cannot be understood without the consideration of the adaptation of a joint and its efficiency dealing with forces.

The main conclusion of these analyses was that DJD differed among primates in distribution across the skeleton and in intensity of severity across taxa. Differences in distribution were likely to be to some extent related to locomotor behaviour, although morphological adaptation can play a key role in determining rate of degeneration. At the same time, other factors like body mass or longevity (and age) could play an important role in determining the intensity of the degeneration process. In the following chapters locomotor behaviour, body mass and age will be treated independently in order to further assess their relationship with DJD expression. Chapter 7 focuses on the effect of locomotor behaviour in DJD development, considering different locomotor adaptations as well as different locomotor strategies.

CHAPTER 7: LOCOMOTOR BEHAVIOUR AND DJD. A MECHANICAL APPROACH TO JOINT DEGENERATION

Chapter 6 explored DJD prevalence among non-human primates, where a general pattern of expression was obtained for the whole sample, and apparent differences from such pattern were reported. Both the general pattern and the deviations from it could potentially relate to the great diversity of primates' locomotor behaviour. This chapter explores the differences in DJD between and within different groups of primates and how differences in joint degeneration may relate to their locomotor behaviour (assessing the effect of differences in locomotor adaptation and in locomotor strategies such as speed or habitat use).

7.1 Locomotor adaptation as a driver of DJD

One of the main goals of this thesis was to explore the effect of locomotion in the development of DJD in non-human primates. Primates are one of the most diverse orders of mammals in terms of locomotor behaviour (chapter 3) and such diversity results in differences in the system of forces acting on the skeleton (chapter 4). Furthermore, primates exhibit a rather generalised skeletal morphology that, in combination with the differing forces acting on their bodies, led to the hypothesis that primates carrying out different locomotor behaviours would present different patterns of joint degeneration. Faster degeneration was expected for those joints bearing comparatively greater forces as a result of locomotion. The analyses of the present section evaluate whether or not the apparent contrasts in DJD expression described in chapter 6 were significant and if this differentiation could be a result of locomotor adaptation. Variability of DJD between and within locomotor adaptations was assessed and contrasted with their diversity in locomotor behaviour.

It was projected that primates that shared locomotor adaptation were more likely to perform more similar locomotor behaviours compared to other taxa and, therefore, probably experienced more similar systems of forces acting on their weight-bearing joints. For this reason, the classification of primates was based on differences in locomotor adaptations (Table 5.2). Five groups or sub-samples were thus obtained: VCL and slow arboreal quadrupeds (N=100), leapers (N=164), quadrupeds (N=310), knuckle-walkers (N=109) and suspensory primates (N=114).

Significance tests with Bonferroni post-hoc corrections for the pairwise comparisons with standard significance values ($p<0.05$) were used. Generally, severity indices (SI) were used (Equation 5.10, chapter 5) but in some parts of the analyses prevalence indices (PI) were also considered (Equation 5.9, chapter 5).

7.1.1 Differences in DJD severity across primates of different locomotor adaptations

The following set of analyses used the combined values of DJD to see where the main differences were among groups of different locomotor adaptations. DJD expression was significantly different among the five groups (answering to locomotor adaptation) at all the considered joints (Table 7.1).

Table 7.1 χ^2 and p-values for differences in DJD development of all the weight-bearing joints or groups of joints among locomotor adaptations (significant differences in bold)

Joint(s)	**χ^2**	**p-value**
Cervical bodies	18.22	**0.001**
Upper thoracic bodies	19.93	**0.001**
Middle thoracic bodies	33.74	**<0.001**
Lower thoracic bodies	48.66	**<0.001**
Lumbar bodies	66.01	**<0.001**
Cervical apophyses	47.41	**<0.001**
Upper thoracic apophyses	39.51	**<0.001**
Middle thoracic apophyses	20.22	**<0.001**
Lower thoracic apophyses	35.24	**<0.001**
Lumbar apophyses	84.75	**<0.001**
Shoulder	91.19	**<0.001**
Elbow	183.15	**<0.001**
Wrist	82.88	**<0.001**
Hip	34.16	**<0.001**
Knee	106.79	**<0.001**
Ankle	84.38	**<0.001**

Pairwise comparisons showed differences affecting all the body compartments: spine, forelimb and hindlimb (Tables 7.2, 7.3). There were groups that were more different in DJD expression than the rest, showing consistent differences with all the other groups. Most of the differences were found in those comparisons involving the knuckle-walkers; they showed significant differences with all the other groups of primates for at least one of the joints of all the compartments (Table 7.2). At the level of vertebral bodies all the differences found concerned only those comparisons involving knuckle-walkers. For the apophyseal joints, at the thoracic region those comparisons concerning suspensory primates as well as the knuckle-walkers showed significant differences with other groups (Table 7.2). At the level of the limbs, aside from the knuckle-walkers, several comparisons concerning the quadrupeds also exhibited significant differences at the forelimb. The results from the hindlimb were variable, showing differences between groups for different joints but with no specific pattern evident.

7.1.2 Differences in DJD expression within locomotor adaptations

Specific locomotor behaviour varies even among primates of the same locomotor adaptation. Therefore, differences in DJD expression were assessed within each of the locomotor adaptations in order to see if variability of DJD could mirror more specific locomotor behaviours. The three indicators of DJD were analysed independently using severity indices (SI) and prevalence indices (PI).

The pattern of differences obtained with PI and SI remained relatively unaltered (Tables 7.4 though 7.8). This was the case for the leapers and the VCL and slow arboreal quadrupeds (Table 7.4). Some variability in the pattern of differences was found for the other three sub-samples of primates. In several cases there were fewer joints showing differences with PI than with SI (for the quadrupeds and the knuckle-walkers). Only in two instances the use of PI detected further differences. These were for porosity at the lower thoracic apophyses of the quadrupeds (Table 7.6) and the shoulder of the suspensory primates (Table 7.8). Due to the greater number of differences detected using SI, the main part of the description and discussion was done considering these indices (Table 7.9).

The group showing the least amount of differences in DJD expression was the leapers, with the only difference found for porosity at the ankle (Table 7.9). The VCL and slow arboreal quadrupeds also exhibited differences among their species for porosity at the ankle as well as at the knee, and differences concerning osteophytosis were only found at the lumbar spine (Table 7.5). The use of PI instead of SI did not evidence further differences among these taxa (Tables 7.5).

The quadrupeds were the group showing the greatest amount of differences (Tables 7.6 and 7.9). Differences in the spine of quadrupeds for osteophytosis were found at the cervical and middle thoracic bodies and the middle thoracic apophyses. There were differences in porosity at the cervical and upper thoracic bodies and at the upper and middle thoracic apophyses. Eburnation showed different severities at the cervical and lumbar regions of the spine for the bodies as well as at the cervical apophyses. For the limbs, all joints except the knee showed some differences for at least some of the indicators of DJD. The ankle joint showed differences in osteophytosis, porosity and eburnation, the shoulder joint differed in osteophytosis and porosity, the elbow joint exhibited differences for porosity, and the hip joint differed in osteophytosis.

Differences in spinal DJD (SDJD) among knuckle-walkers were detected for osteophytosis and porosity, affecting both bodies and apophyses of the thoracic and lumbar regions (Tables 7.7, 7.9). For the limbs differences in osteophytosis were found at the knee, differences in porosity at the ankle and differences in eburnation were found at the elbow joint (Table 7.7).

Suspensory primates only exhibited differences for osteophytosis and porosity, with no differences in eburnation (Table 7.8, 7.9). Differences in SDJD were found throughout the spine, with differences in osteophytosis at the middle thoracic and lumbar vertebral bodies, and cervical and lumbar apophyses. Differences in porosity concerned the cervical, upper and middle thoracic bodies and the middle thoracic apophyses. The elbow was the only joint of the forelimbs showing signs of differences for both osteophytosis and porosity. The joints of the hindlimb showed differences in osteophytosis at the hip and ankle and differences in porosity at the knee joint.

Table 7.2 U statistics and adjusted p-values (with Bonferroni post-hoc corrections) of the pairwise comparisons differences in DJD severity between groups of different locomotor adaptations, where V=VCL and slow arboreal quadrupeds; L=leapers; Q=quadrupeds; K=knuckle-walkers; S=suspensory

Joint		**V-L**	**V-Q**	**V-K**	**V-S**	**L-Q**	**L-K**	**L-S**	**Q-K**	**Q-S**	**K-S**
Cervical bodies	Test statistic	-25.52	-25.04	-61.80	-29.99	0.48	-36.28	-4.47	-36.76	-4.95	31.81
	p-value	1	0.991	**0.002**	1	1	0.072	1	**0.006**	1	0.316
Upper thoracic bodies	Test statistic	-13.00	-10.42	-46.22	-18.61	2.58	-33.22	-5.61	-35.80	-8.18	27.62
	p-value	1	1	**0.01**	1	1	**0.031**	1	**<0.001**	1	0.308
Middle thoracic bodies	Test statistic	-17.78	-20.88	-67.72	-26.65	-3.10	-49.95	-8.87	-46.85	-5.77	41.08
	p-value	1	1	**<0.001**	1	1	**<0.001**	1	**<0.001**	1	0.031
Lower thoracic bodies	Test statistic	21.56	7.87	-59.19	8.16	-13.69	-80.75	-13.40	-67.06	0.29	67.34
	p-value	1	1	**0.008**	1	1	**<0.001**	1	**<0.001**	1	**<0.001**
Lumbar bodies	Test statistic	7.19	19.36	-67.41	14.55	12.17	-74.60	7.36	-86.77	-4.81	81.96
	p-value	1	1	**0.002**	1	1	**<0.001**	1	**<0.001**	1	**<0.001**
Cervical apophyses	Test statistic	16.31	10.88	-40.21	6.24	-5.44	-56.53	-10.08	-51.09	-4.64	46.45
	p-value	1	1	**0.016**	1	1	**<0.001**	1	**<0.001**	1	**<0.001**
Upper thoracic apophyses	Test statistic	-6.48	-14.93	-59.77	-44.85	-8.45	-53.29	-38.37	-44.84	-29.93	14.92
	p-value	1	1	**<0.001**	**0.050**	1	**<0.001**	**0.046**	**<0.001**	0.101	1
Middle thoracic apophyses	Test statistic	-6.31	-23.58	-44.90	-47.15	-17.27	-38.59	-40.84	-21.32	-23.57	-2.25
	p-value	1	0.079	**0.019**	**0.044**	0.835	**0.006**	**0.033**	0.165	0.503	1

Table 7.2(cont.). U statistics and adjusted p-values (with Bonferroni post-hoc corrections) of the pairwise comparisons differences in DJD severity between groups of different locomotor adaptations, where V=VCL and slow arboreal quadrupeds; L=leapers; Q=quadrupeds; K=knuckle-walkers; S=suspensory.

Joint		**V-L**	**V-Q**	**V-K**	**V-S**	**L-Q**	**L-K**	**L-S**	**Q-K**	**Q-S**	**K-S**
Lower thoracic apophyses	Test statistic	7.47	-13.40	-58.97	-40.23	-20.87	-66.44	-47.69	-45.57	-26.83	18.75
	p-value	1	1	**0.003**	0.318	0.681	**<0.001**	**0.024**	**<0.001**	0.467	1
Lumbar apophyses	Test statistic	9.84	0.52	-93.79	-5.67	-9.33	-103.64	-15.52	-94.31	-6.19	88.12
	p-value	1	1	**<0.001**	1	1	**<0.001**	1	**<0.001**	1	**<0.001**
Shoulder	Test statistic	8.20	-52.58	-153.17	-23.85	-60.78	-161.37	-32.04	-100.59	28.73	129.32
	p-value	1	**0.021**	**<0.001**	1	**<0.001**	**<0.001**	0.766	**<0.001**	0.771	**<0.001**
Elbow	Test statistic	-21.20	-96.67	-296.24	-55.81	-75.47	-275.04	-34.61	-199.58	40.86	240.44
	p-value	1	**<0.001**	**<0.001**	0.290	**<0.001**	**<0.001**	1	**<0.001**	0.455	**<0.001**
Wrist	Test statistic	2.74	-44.21	-127.43	-23.16	-46.95	-130.17	-25.91	-83.22	21.04	104.26
	p-value	1	**0.024**	**<0.001**	1	**0.001**	**<0.001**	0.929	**<0.001**	1	**<0.001**
Hip	Test statistic	18.61	-9.99	-59.05	-28.56	-28.60	-77.66	-47.17	-49.06	-18.57	30.49
	p-value	1	1	**0.002**	1	**0.092**	**<0.001**	**0.007**	**0.001**	1	0.454
Knee	Test statistic	23.21	-26.97	-167.26	-14.02	-50.18	-190.47	-37.23	-140.29	12.96	153.24
	p-value	1	1	**<0.001**	1	**0.009**	**<0.001**	0.522	**<0.001**	1	**<0.001**
Ankle	Test statistic	-33.57	-36.70	-158.46	-1.85	-3.14	-124.90	31.72	-121.76	34.86	156.62
	p-value	0.75	0.315	**<0.001**	1	1	**<0.001**	0.796	**<0.001**	0.320	**<0.001**

Table 7.3 Visual summary of the significant differences in DJD severity (represented with tick marks) between groups of different locomotor adaptations (pairwise comparisons with adjusted significance values by means of Bonferroni post-hoc tests), where V=VCL and slow arboreal quadrupeds; L=leapers; Q=quadrupeds; K=knuckle-walkers; S=suspensory. Test statistics and p-values in Table 7.2

Joint	V-L	V-Q	V-K	V-S	L-Q	L-K	L-S	Q-K	Q-S	K-S
Cervical bodies			✓					✓		
Upper thoracic bodies			✓			✓		✓		
Middle thoracic bodies			✓			✓		✓		✓
Lower thoracic bodies			✓			✓		✓		✓
Lumbar bodies			✓			✓		✓		✓
Cervical apophyses			✓			✓		✓		✓
Upper thoracic apophyses			✓	✓		✓	✓	✓		
Middle thoracic apophyses			✓	✓		✓	✓			
Lower thoracic apophyses			✓			✓	✓	✓		
Lumbar apophyses			✓			✓		✓		✓
Shoulder		✓	✓		✓	✓		✓		✓
Elbow		✓	✓		✓	✓		✓		✓
Wrist		✓	✓		✓	✓		✓		✓
Hip			✓			✓	✓	✓		
Knee			✓		✓	✓			✓	✓
Ankle			✓			✓		✓		✓

Table 7.4 χ^2 test and p-values of interspecific differences using severity and prevalence indices (SI and PI) for VCL and slow arboreal quadrupeds

Joint		**Severity indices (SI)**			**Prevalence indices (PI)**		
		Eburnation	Osteophytosis	Porosity	Eburnation	Osteophytosis	Porosity
Cervical bodies	Test statistic (χ^2)			7			7.20
	p-value			0.221			0.206
Upper thoracic bodies	Test statistic (χ^2)			2.600			2.70
	p-value			0.761			0.746
Middle thoracic bodies	Test statistic (χ^2)						
	p-value						
Lower thoracic bodies	Test statistic (χ^2)		4.59	5.146		3.64	5.39
	p-value		0.468	0.398		0.602	0.371
Lumbar bodies	Test statistic (χ^2)		11.95	7.073		9.95	7.39
	p-value		0.035	0.215		0.077	0.193
Cervical apophyses	Test statistic (χ^2)		2.65			2.78	
	p-value		0.755			0.733	
Upper thoracic apophyses	Test statistic (χ^2)						
	p-value						
Middle thoracic apophyses	Test statistic (χ^2)						
	p-value						
Lower thoracic apophyses	Test statistic (χ^2)		2.67			1.38	
	p-value		0.751			0.926	
Lumbar apophyses	Test statistic (χ^2)		14.08			11.59	
	p-value		0.015			0.041	

Table 7.4(cont.). χ^2 test and p-values of interspecific differences using severity and prevalence indices (SI and PI) for VCL and slow arboreal quadrupeds

Joint		**Severity indices (SI)**			**Prevalence indices (PI)**		
		Eburnation	Osteophytosis	Porosity	Eburnation	Osteophytosis	Porosity
Shoulder	Test statistic (χ^2)		6.23	6.815		6.23	6.82
	p-value		0.285	0.235		0.285	0.235
Elbow	Test statistic (χ^2)		7.68			7.68	
	p-value		0.175			0.175	
Wrist	Test statistic (χ^2)		8.35			8.25	
	p-value		0.138			0.143	
Hip	Test statistic (χ^2)		2.29	4.971		2.23	4.88
	p-value		0.808	0.419		0.817	0.430
Knee	Test statistic (χ^2)		4.26	11.491		4.26	11.40
	p-value		0.512	0.042		0.512	0.044
Ankle	Test statistic (χ^2)		4.26	13.007		4.21	12.83
	p-value		0.512	0.023		0.520	0.025

Table 7.5 χ^2 *test and p-values of interspecific differences using severity and prevalence indices (SI and PI) for leapers*

Joint		Severity indices (SI)			Prevalence indices (PI)		
		Eburnation	Osteophytosis	Porosity	Eburnation	Osteophytosis	Porosity
Cervical bodies	Test statistic (χ^2)		1.64	7.12		1.64	6.94
	p-value		0.650	0.068		0.650	0.074
Upper thoracic bodies	Test statistic (χ^2)		5.82	1.42		5.62	1.40
	p-value		0.121	0.700		0.131	0.705
Middle thoracic bodies	Test statistic (χ^2)		5.90	2.26		5.90	2.20
	p-value		0.117			0.117	0.531
Lower thoracic bodies	Test statistic (χ^2)		2.97			2.97	
	p-value		0.396	2.00		0.396	
Lumbar bodies	Test statistic (χ^2)		5.02	0.573		5.10	1.94
	p-value		0.170			0.164	0.585
Cervical apophyses	Test statistic (χ^2)		0.81			0.81	
	p-value		0.847			0.847	
Upper thoracic apophyses	Test statistic (χ^2)		1.49			1.49	
	p-value		0.686			0.686	
Middle thoracic apophyses	Test statistic (χ^2)		1.48			1.48	
	p-value		0.686			0.686	
Lower thoracic apophyses	Test statistic (χ^2)		1.35			1.35	
	p-value		0.717			0.717	
Lumbar apophyses	Test statistic (χ^2)		3.90			3.90	
	p-value		0.272			0.272	

Table 7.5(cont.). χ^2 test and p-values of interspecific differences using severity and prevalence indices (SI and PI) for leapers

Joint		Severity indices (SI)			Prevalence indices (PI)		
		Eburnation	Osteophytosis	Porosity	Eburnation	Osteophytosis	Porosity
Shoulder	Test statistic (χ^2)	2.22	4.24		2.22	4.24	
	p-value	0.529	0.237		0.529	0.237	
Elbow	Test statistic (χ^2)		5.51			5.94	2.28
	p-value		0.138			0.115	0.516
Wrist	Test statistic (χ^2)		2.22	2.28		2.22	
	p-value		0.529	0.516		0.529	
Hip	Test statistic (χ^2)		4.74			4.82	
	p-value		0.192			0.185	
Knee	Test statistic (χ^2)	2.33	4.70	3.35	2.38	5.15	3.21
	p-value	0.506	0.195	0.340	0.498	0.161	0.360
Ankle	Test statistic (χ^2)			23.06			24.09
	p-value			<0.001			<0.001

Table 7.6 χ^2 test and p-values of interspecific differences using severity and prevalence indices (SI and PI) for quadrupeds

Joint		Severity indices (SI)			Prevalence indices (PI)		
		Eburnation	Osteophytosis	Porosity	Eburnation	Osteophytosis	Porosity
Cervical bodies	Test statistic (χ^2)	34.10	24.13	38.42	34.10	24.05	37.48
	p-value	0.002	0.044	<0.001	0.002	0.045	0.001
Upper thoracic bodies	Test statistic (χ^2)		19.65	25.38		19.08	21.07
	p-value		0.104	0.021		0.121	0.072
Middle thoracic bodies	Test statistic (χ^2)		22.56	14.61		22.70	14.61
	p-value		0.047	0.332		0.045	0.332
Lower thoracic bodies	Test statistic (χ^2)		17.94	11.12		18.95	11.19
	p-value		0.160	0.601		0.125	0.595
Lumbar bodies	Test statistic (χ^2)	23.44	7.80	13.66	23.44	7.89	13.59
	p-value	0.037	0.857	0.398	0.037	0.851	0.403
Cervical apophyses	Test statistic (χ^2)	24.22	10.91	14.06	24.22	10.99	14.06
	p-value	0.043	0.693	0.446	0.043	0.687	0.446
Upper thoracic apophyses	Test statistic (χ^2)		18.16	39.55		17.82	40.20
	p-value		0.192	<0.001		0.165	<0.001
Middle thoracic apophyses	Test statistic (χ^2)	19.70	22.90	35.76	19.70	20.66	39.26
	p-value	0.103	0.043	0.001	0.103	0.080	<0.001
Lower thoracic apophyses	Test statistic (χ^2)	14.51	12.01	21.06	14.51	10.39	25.15
	p-value	0.34	0.527	0.072	0.339	0.662	0.022
Lumbar apophyses	Test statistic (χ^2)	9.00	12.76	13.15	9.00	14.97	13.15
	p-value	0.773	0.467	0.436	0.773	0.309	0.436

Table 7.6(cont.). χ^2 test and p-values of interspecific differences using severity and prevalence indices (SI and PI) for quadrupeds

Joint		**Severity indices (SI)**			**Prevalence indices (PI)**		
		Eburnation	Osteophytosis	Porosity	Eburnation	Osteophytosis	Porosity
Shoulder	Test statistic (χ^2)	9.33	39.55	31.16	9.33	41.04	31.64
	p-value	0.809	<0.001	0.005	0.809	<0.001	0.005
Elbow	Test statistic (χ^2)	14.66	18.95	34.69	14.60	20.07	35.01
	p-value	0.402	0.167	0.002	0.406	0.128	0.001
Wrist	Test statistic (χ^2)	27.10	10.28	21.50	27.00	10.17	20.64
	p-value	0.019	0.741	0.090	0.019	0.750	0.111
Hip	Test statistic (χ^2)	22.87	25.41	18.44	22.87	25.00	18.33
	p-value	0.062	0.031	0.187	0.062	0.035	0.192
Knee	Test statistic (χ^2)	9.70	11.61	16.69	8.73	11.44	17.82
	p-value	0.784	0.637	0.273	0.848	0.651	0.215
Ankle	Test statistic (χ^2)	28.91	25.89	27.71	28.91	25.62	27.78
	p-value	0.011	0.027	0.016	0.011	0.029	0.015

Table 7.7 χ^2 test and p-values of interspecific differences using severity and prevalence indices (SI and PI) for knuckle-walkers

Joint		Severity indices (SI)			Prevalence indices (PI)		
		Eburnation	Osteophytosis	Porosity	Eburnation	Osteophytosis	Porosity
Cervical bodies	Test statistic (χ^2)		5.51	5.48		5.51	5.48
	p-value		0.239	0.242		0.239	0.242
Upper thoracic bodies	Test statistic (χ^2)		15.32	2.08		15.32	2.08
	p-value		0.004	0.722		0.004	0.722
Middle thoracic bodies	Test statistic (χ^2)	5.53	4.15	1.41	5.53	4.15	1.41
	p-value	0.237	0.386	0.842	0.237	0.386	0.842
Lower thoracic bodies	Test statistic (χ^2)	5.13	12.69	3.52	5.13	12.69	3.52
	p-value	0.275	0.013	0.475	0.275	0.013	0.475
Lumbar bodies	Test statistic (χ^2)	2.41	8.33	7.06	2.41	8.33	7.06
	p-value	0.66	0.08	0.133	0.660	0.080	0.133
Cervical apophyses	Test statistic (χ^2)	3.31	3.34	0.98	3.31	3.34	0.98
	p-value	0.507	0.502	0.913	0.507	0.502	0.913
Upper thoracic apophyses	Test statistic (χ^2)		0.52	6.00		0.52	6.00
	p-value		0.971	0.199		0.971	0.199
Middle thoracic apophyses	Test statistic (χ^2)	5.53	1.73	4.88	5.53	1.73	4.88
	p-value	0.237	0.786	0.3	0.237	0.786	0.300
Lower thoracic apophyses	Test statistic (χ^2)	2.99	7.24	9.27	2.99	7.27	9.27
	p-value	0.56	0.122	0.05	0.560	0.122	0.055
Lumbar apophyses	Test statistic (χ^2)	5.19	9.08	11.75	5.19	9.08	11.75
	p-value	0.269	0.059	0.019	0.269	0.059	0.019

Table 7.7(cont.). χ^2 test and p-values of interspecific differences using severity and prevalence indices (SI and PI) for knuckle-walkers

Joint		**Severity indices (SI)**			**Prevalence indices (PI)**		
		Eburnation	Osteophytosis	Porosity	Eburnation	Osteophytosis	Porosity
Shoulder	Test statistic (χ^2)	4.45	3.90	7.15	4.45	3.90	7.15
	p-value	0.349	0.419	0.128	0.349	0.419	0.128
Elbow	Test statistic (χ^2)	10.27	7.52	6.16	10.27	7.52	6.16
	p-value	0.036	0.111	0.187	0.036	0.111	0.187
Wrist	Test statistic (χ^2)		1.52	7.30		1.52	7.30
	p-value		0.823	0.121		0.823	0.121
Hip	Test statistic (χ^2)		7.99	3.56		7.99	3.56
	p-value		0.092	0.47		0.092	0.470
Knee	Test statistic (χ^2)	5.18	19.29	3.43	5.18	17.29	3.43
	p-value	0.27	0.002	0.488	0.270	0.002	0.488
Ankle	Test statistic (χ^2)			13.58		3.36	13.58
	p-value			0.009		0.499	0.009

Table 7.8 χ^2 test and p-values of interspecific differences using severity and prevalence indices (SI and PI) for suspensory primates

Joint		**Severity indices (SI)**			**Prevalence indices (PI)**		
		Eburnation	Osteophytosis	Porosity	Eburnation	Osteophytosis	Porosity
Cervical bodies	Test statistic (χ^2)	2.11	1.91	15.75	2.11	1.91	14.78
	p-value	0.715	0.752	0.003	0.715	0.752	0.005
Upper thoracic bodies	Test statistic (χ^2)		9.41	17.90		9.25	17.90
	p-value		0.052	0.001		0.055	0.001
Middle thoracic bodies	Test statistic (χ^2)		10.32	11.47		10.32	11.47
	p-value		0.035	0.022		0.035	0.022
Lower thoracic bodies	Test statistic (χ^2)		8.40	5.57		8.61	5.57
	p-value		0.078	0.234		0.072	0.234
Lumbar bodies	Test statistic (χ^2)	3.00	11.50	4.17	3.00	11.43	4.17
	p-value	0.558	0.021	0.383	0.558	0.022	0.383
Cervical apophyses	Test statistic (χ^2)	6.00	18.66	6.00	6.00	18.66	6.00
	p-value	0.199	0.001	0.199	0.199	0.001	0.199
Upper thoracic apophyses	Test statistic (χ^2)		3.51	7.08		3.53	7.08
	p-value		0.477	0.132		0.474	0.132
Middle thoracic apophyses	Test statistic (χ^2)		6.77	9.70		6.77	9.76
	p-value		0.149	0.046		0.149	0.045
Lower thoracic apophyses	Test statistic (χ^2)		2.96	9.20		2.86	9.47
	p-value		0.565	0.056		0.582	0.051
Lumbar apophyses	Test statistic (χ^2)		19.05	6.75		19.49	6.89
	p-value		0.001	0.149		0.001	0.142

Table 7.8(cont.). χ^2 test and p-values of interspecific differences using severity and prevalence indices (SI and PI) for suspensory primates

Joint		**Severity indices (SI)**			**Prevalence indices (PI)**		
		Eburnation	Osteophytosis	Porosity	Eburnation	Osteophytosis	Porosity
Shoulder	Test statistic (χ^2)	2.80	1.16	7.37	2.80	1.16	10.46
	p-value	0.592	0.884	0.118	0.592	0.884	0.033
Elbow	Test statistic (χ^2)	2.21	18.27	11.76	7.63	18.69	17.04
	p-value	0.697	0.001	0.019	0.106	0.001	0.002
Wrist	Test statistic (χ^2)		9.15	9.48		9.15	9.48
	p-value		0.058	0.050		0.057	0.051
Hip	Test statistic (χ^2)		12.29	6.30		12.48	6.57
	p-value		0.015	0.178		0.014	0.160
Knee	Test statistic (χ^2)	8.55	3.49	22.14	8.55	3.48	22.45
	p-value	0.073	0.479	<0.001	0.073	0.481	<0.001
Ankle	Test statistic (χ^2)	4.43	13.67	3.59	4.43	13.61	3.60
	p-value	0.35	0.008	0.464	0.351	0.009	0.463

Table 7.9 Summary of significant differences of DJD severity among taxa of every locomotor adaptation for the three body compartments (spine, forelimb and hindlimb) and the three indicators of DJD (eburnation, osteophytosis and porosity). Two cases pertain to differences only found with PI as indicated

Locomotor adaptation	**Eburnation**			**Osteophytosis**			**Porosity**		
	Spine	**Forelimb**	**Hindlimb**	**Spine**	**Forelimb**	**Hindlimb**	**Spine**	**Forelimb**	**Hindlimb**
VCL and slow arboreal quadrupeds				Lumbar B Lumbar AP					Knee Ankle
Leapers									Ankle
Quadrupeds	Cervical B Lumbar B Cervical AP	Wrist	Ankle	Cervical B Middle thoracic B Middle thoracic AP	Shoulder	Hip Ankle	Cervical B Upper thoracic B Upper thoracic AP Middle thoracic AP Lower thoracic AP (**with PI**)	Shoulder Elbow	Ankle
Knuckle-walkers		Elbow		Upper thoracic B Lower thoracic B Lumbar B		Knee	Lower thoracic AP Lumbar AP		Ankle
Suspensory				Middle thoracic B Lumbar B Cervical AP Lumbar AP	Elbow	Hip Ankle	Cervical B Upper thoracic B Middle thoracic B Middle thoracic AP	Shoulder (**with PI**) Elbow	Knee

7.1.3 Discussion of role of locomotor adaptation as a driver of DJD

7.1.3.1 Differences in DJD severity across primates of different locomotor adaptations

The results presented confirmed the initial assumption that different primate taxa exhibit different levels of severity and different distribution of DJD across the skeleton. These results supported previous research based on comparative DJD among non-human primates (e.g., DeRousseau, 1988; Rothschild and Woods, 1992, 1993; Jurmain, 2000; Rothschild and Rühli, 2005). Further exploration evidenced where in the skeleton these differences were and how they related to locomotor adaptation.

The search for differences among locomotor adaptations showed that all joints expressed significantly different levels of DJD among the different sub-samples (Table 7.1). This suggested that the joints considered here could develop different levels of DJD depending on how primates move. However, paired comparisons showed that the largest part of the differences observed involved those comparisons that included the knuckle-walkers (Table 7.2). The knuckle-walkers, as seen in chapter 6, exhibited the most severe expressions of DJD (Table 6.3), which could have resulted in the most obvious differences with other groups of primates.

The vertebral bodies showed significant differences in DJD expressions only in those comparisons that involved knuckle-walkers (Tables 7.2, 7.3). Knuckle-walkers, despite being quadrupeds, adopt rather orthograde postures, sometimes reaching full orthogrady during bipedal bouts (e.g., Hewes, 1964; Hunt et al., 1996; Schmitt, 1998; D'Aout et al., 2004; Aiello and Dean, 2006; Fleagle, 2013). This, in combination with their greater body mass, would entail great compressive forces, especially at the more caudal spine, inducing greater DJD development. This confirmed the link between orthogrady and DJD at the vertebral bodies introduced in chapter 6 and was in accordance with Jurmain's (2000) findings, which suggested that SDJD in African apes was a combination of great compression and torsion. The fact that the knuckle-walkers are mainly terrestrial species (Schaller, 1976; Fossey, 1983; Susman, 1984; Doran, 1993, 1996, 1997; Doran and McNeilage, 1998) may further contribute to greater reaction forces resulting from the use of a stiff support (section 7.2).

Great levels of orthogrady were not exclusive to the knuckle-walkers studied in this thesis. Nevertheless, the level of spinal compression associated with more vertical trunk postures was likely to be the greatest for the knuckle-walkers. The VCL can adopt orthograde postures while clinging on a vertical support (Gebo, 1987; Schmidt, 2011). However, this is a rather stationary position from which the animal propels itself. Despite positional behaviour being important for some morphological changes (Dunham et al., 2017), it is the intense forces associated with movement that greatly shape the skeleton of an animal (Hunt et al., 1996; Fleagle, 2013). Therefore, locomotor-related forces would be much more significant in terms of stress than posture-related forces. Moreover, the greater body mass of knuckle-walkers would entail greater pressures as a result of their weight in comparison with the VCL.

Suspensory primates differ less in terms of body mass from knuckle-walkers than the VCL (Smith and Jungers, 1997). Suspensory primates can adopt fully erect trunk postures but, differently to knuckle-walkers, as they hang from the support used during locomotion, their spines are subject to tensile forces rather than compressive ones (e.g., Hunt et al., 1996; Schmidt, 2011; Youlatos, 2017). This seemed to lead to different types of DJD development, as the differences between the knuckle-walkers and suspensory primates were found mainly at the middle and lower regions of the spine, where the knuckle-walkers would experience the greatest compressive stress.

Suspensory primates exhibited different expressions of DJD compared with leapers, the VCL and slow arboreal quadrupeds at the level of the thoracic apophyseal region. The thoracic apophyseal joints are involved with trunk rotation, an action of extreme importance in suspensory primates (Fig. 7.1), especially for the brachiators (Bertram, 2004; Youlatos, 2017). During a brachiation bout primates can perform trunk rotations of up to 180º (Fleagle, 1976; Hunt et al., 1996) and therefore, the stress from such strong movements may have been reflected in the greater development of DJD at the thoracic apophyseal joints. Leapers perform much less trunk rotation than the suspensory primates, especially brachiators, and VCL can perform mid-air rotation but it is a less continuous mode of locomotion than that observed for suspensory primates (Bertram and Chang, 2001; Crompton et al., 2010). Moreover, the slow arboreal quadrupeds perform less intense trunk rotation than the VCLs, as they do not leap. The thoracic apophyses were, therefore, highly susceptible joints to DJD development, as a result of the forces associated to the different levels of trunk rotation.

Figure 7.1 Illustrations showing different types of suspensory progression. Top left: gibbon performing continuous contact brachiation (one swing); top right: gibbon performing ricochetal brachiation (one swing); bottom: spider monkey performing tail-assisted brachiation. Note the intense trunk rotation in all three cases (modified from Mittermeier and Fleagle, 1976; Bertram and Chang, 2001)

Differences found at the level of the limbs once again mainly involved the knuckle-walkers. The hindlimb exhibited some differences but did not seem to reflect a distinct locomotor pattern, maybe as a result of the constant involvement of the hindlimb as an important propulsive compartment for many primate taxa. For the forelimb, there was a clearer pattern of differences involving the quadrupeds, as well as the knuckle-walkers. This suggested that from a forelimb joint degeneration point of view, the quadrupeds were distinct from the rest of the groups. In fact, quadrupeds are characterised by a more equal involvement of the forelimb and the hindlimb in locomotion, so these primates load their forelimbs to greater extend, which could entail different levels of joint degeneration.

The only comparison involving the forelimbs of quadrupeds that did not show significant differences was the one with suspensory primates. Both groups have great involvement of the forelimb during locomotion. However, the quadrupeds' forelimbs are loaded with compressive stress, while the suspensory primates are loaded with tensile forces. This could be expected to result in different patterns of DJD expression, similarly to what was observed at the spine of the knuckle-walkers and the suspensory primates. However, no differences were observed from the compression-tension differentiation between the quadrupeds and the suspensory primates at the level of the forelimb.

The forelimb of suspensory primates is the main propulsive compartment of their body (Hunt et al., 1996; Bertram, 2004; Schmidt, 2011) and as such it is in contact with the support during locomotion (Fig. 7.1). Therefore, this compartment experienced both action and reaction forces resulting from the interaction between the animal and the support, consequently experiencing strong forces and loads on the weight-bearing joints of the forelimb. Hence, the system of forces experienced at the forelimb was likely to be more similar between the quadrupeds and the suspensory primates than that experienced at the spine for knuckle-walkers and suspensory species, which could have led to the lack of differences between quadrupeds and suspensory primates at the forelimb.

7.1.3.2 Differences in DJD within locomotor adaptations

Examination of differences in DJD expression was conducted using SI and PI obtaining very similar patterns of differences within locomotor adaptations (Tables 7.4 through 7.9), suggesting that most of the variability could be detected using either index. However, there were differences in severity that would not have been seen if only PI had been used and, therefore, SI provided greater nuance to the data. This demonstrated that DJD was expressed differently, not only in the amount of times it was present but also in how severely it developed. Considering this, the discussion was done mainly based on the differences spotted with the use of SI (Table 7.9). As the spine and the limbs are different from a functional point of view they were assessed separately.

7.1.3.2a. The spine

The spine of most groups of primates exhibited interspecific differences in SDJD, with the exception of the leapers. The location of such differences varied and in most cases, the more variable regions within each group were likely to be reflecting differences in locomotor behaviour among the species within locomotor adaptation.

The cervical spine showed differences in DJD expression but it rarely did so in isolation. Most of the cases expressing differences in the cervical region for a particular indicator of DJD also showed differences either in the thoracic or the lumbar regions. The different combinations of regions showing differences in DJD often reflected variability in spine movements among species.

The quadrupeds exhibited differences in osteophytosis and porosity development at the cervical and thoracic regions. The cervical spine allows some degree of spinal bending, and the thoracic region is responsible for trunk rotation, therefore differences at these regions could be related to differential performance of these movements in the quadrupeds' locomotor behaviour. Regarding the vertebral bodies, differences in osteophytosis and porosity were found at the cervical region and the more cranial portions of the thoracic spine suggesting that the differential development of DJD was related to differences in the intensity of the pressures derived from sagittal bending movements. High levels of trunk rotation and spinal bending are both essential for climbing. Therefore, variability among quadrupedal species in the amount of climbing performed in their habitual locomotor repertoire could be inducing different levels of DJD development at these regions of the spine.

Further differences were found at the cervical region in combination with eburnation in the lumbar spine (mainly at the vertebral bodies); the lumbar spine did not show significant differences for osteophytosis and porosity. This region of the spine is also involved in sagittal bending, together with the cervical spine. Quadrupeds perform much sagittal bending in their habitual locomotor behaviour and they do so in varying proportion depending on the part of the canopy they exploit. For instance, highly arboreal quadrupeds frequently engage in sagittal bending of the spine in order to climb and interact with the variable network of supports (aided by trunk rotation). Terrestrial quadrupeds, in contrast, require different levels of sagittal bending during running (cursorial behaviours). Cursoriality is an activity that could produce strong enough forces associated to spinal sagittal bending that could induce severe degenerative changes at the cervical and lumbar spine. Therefore, differences in the amount of compressive pressure derived from intense sagittal bending could potentially explain the differences in severity of eburnation at these two vertebral regions.

Suspensory primates showed a relatively similar pattern of SDJD to that observed for the quadrupeds, which could be due to the degree of variability of trunk movements among the suspensory taxa, similarly to what was argued for the quadrupeds. The apophyseal joints showed differences in porosity at the middle thoracic spine and differences in osteophytosis at the cervical and lumbar regions. Therefore, differences in osteophytosis at the cervical and lumbar spine could reflect differences in spinal sagittal bending, whereas the differences in porosity observed at the thoracic spine could reflect differences in trunk rotation.

The pattern of DJD expression throughout the thoracic apophyses in suspensory primates was different to other sub-samples (Table 7.3), but showed very few interspecific differences (Table 7.8). This confirmed the importance of trunk rotation during suspensory locomotion for all the taxa of this group. The average severity of overall DJD at these joints was high (upper thoracic apophyses=8.19; middle thoracic apophyses=8.52; lower thoracic apophyses=7.22, Table 6.3). DJD at the thoracic apophyses was therefore consistently high across taxa, showing differences with other groups but very few significant differences among them, as trunk rotation is an important movement for most of the suspensory taxa.

The differences observed at the vertebral bodies among suspensory primates were mainly located in the cervical and cranial thoracic regions of the spine, showing different levels of porosity, whereas differences in osteophytosis were mainly observed at the middle thoracic and lumbar regions. This could potentially be a result of differing degrees of orthogrady as well as differences in the proportion of tensile-compressive forces. Some species within this group are highly suspensory, such as the gibbons (*Hylobates* sp.) or spider monkeys (*Ateles* sp.) (Fleagle, 1976; Mittermeier and Fleagle, 1976; Mittermeier, 1978; Fleagle and Mittermeier, 1980; Cannon and Leighton, 1994). The orangutans (*Pongo* sp.), perform some quadrupedal locomotion or even assisted bipedalism (e.g., Thorpe and Crompton, 2005, 2006; Thorpe et al., 2007). Therefore, the proportion of tensile stress on the spine of suspensory taxa is variable according to their locomotor repertoire. Differences in the length of the spine may also play an important role in the resistance to compressive and torsional forces (Thompson and Almécija, 2017). The length of the spine in the suspensory primates is overall variable but does not show obvious differences in length at the lumbar region (Williams, 2011). Therefore, it was unlikely that spinal length could explain the differences in DJD expression.

Other sub-samples exhibited interspecific differences at the spine more caudally and with less differentiation of regions than the quadrupeds or the suspensory primates. The knuckle-walkers showed differences in osteophytosis and porosity at the lower thoracic and lumbar regions both for the vertebral bodies and the apophyses. The fact that the greatest differences were found at the more caudal portions could be related to the significant amount of compressive stress at these areas of the spine of the knuckle-walkers (Knüsel et al., 1997; Jurmain, 2000), modulated by their great but differing body mass (Smith and Jungers, 1997).

Differences in the degree of arboreality among species could entail differences in posture and, ultimately, in stress. For instance, bonobos perform frequent arboreal locomotion and, particularly males, include a lot of suspensory behaviours in their locomotor repertoire (Doran, 1993). This would produce an important proportion of tensile stress over compressive one. Therefore, similarly to what was observed in the suspensory primates, this could induce the different levels of DJD development at the lower portions of the spine (Tables 7.7, 7.9).

VCL and slow arboreal quadrupeds only showed differences at the lumbar spine, involving both the vertebral bodies and the apophyseal joints (Table 7.4). Despite the fact that these primates are rather small and, thus, are not subject to as great compressive forces resulting from their weight, these taxa differ greatly in their movements of the spine. Some slow loris species perform lateral bending of the spine instead of the typically primate sagittal bending (Shapiro et al., 2001). The lateral bending, similarly to the sagittal bending, is achieved at the lumbar region and, therefore, the lumbar apophyses would be subject to different forces resulting from the different type of movement, which was also accompanied by morphological particularities of these vertebrae (Shapiro, 2007) and could reflect on differences in the development of DJD at these joints.

The lumbar spine is susceptible to compressive and torsional forces regarding development of SDJD (Jurmain, 2000). A stiffer trunk, resulting from a shorter lumbar region, presumably reduces the stress experienced at the level of the vertebral bodies (e.g., Ward, 1993; Jurmain, 2000; Thompson and Almécija, 2017). The VCL and slow arboreal quadrupeds, compared to other primates, exhibit rather elongated vertebral columns, particularly, at the lumbar region (Ankel-Simons, 2007; McCollum et al., 2009; Williams, 2011). Therefore this compartment could be more susceptible to compressive and torsional forces than other primates of shorter lumbar spines. Moreover, VCL perform 180° body rotations during the aerial phase of a leap, therefore, experiencing great torsional forces at the spine, potentially being reflected on the development of DJD at the lumbar region. During clinging their spines are vertical, which would entail greater compression of the spine. Therefore, different lengths of the lumbar spine coupled with behavioural differences among these taxa could entail differential joint degeneration among these taxa.

The differences observed within every locomotor adaptation groups at the level of the spine could be related to specific trunk movements, which would be variable among their taxa. Thus, differences at the cervical and lumbar regions could be related to differences in sagittal bending of the spine, highly variable during climbing bouts, fast terrestrial running and suspensory progression. Climbing and suspensory progression are also associated to high levels of trunk rotation, achieved at the thoracic spine. This region also showed differences among quadrupeds and, to a lesser extent, the suspensory group.

Differences in the level of orthogrady entailed different intensity of compressive pressures at the lower thoracic and lumbar regions, which came with significant differences among the knuckle-walkers as well as in the suspensory primates. In the case of the latter, this is probably as a result of the differentiation between compressive and tensile stress associated to their suspensory behaviour. Additionally, differences at the lumbar spine could also be related to increased lengths of this region, making it less efficient to deal with compressive and torsional forces and, therefore, more susceptible to varying degenerative changes depending on the stress exerted as a result of locomotion. This was the case of the VCL and slow arboreal quadrupeds that showed differences at the lumbar spine, although such differences could also be related to the characteristic lateral spinal bending seen in some loris species.

7.1.3.2b. The limbs

The limbs are the body compartments that are in direct contact with the supports during locomotion, becoming the main propulsive elements of the primate body. As such, they were expected to show variability in DJD expression related to how primates move and how they position their limbs in relation to the supports used during locomotion, which would condition the forces acting on their skeletons.

The relationship between locomotion, limb positioning and DJD expression was particularly evident for some groups of primates. The quadrupeds showed significant differences at the girdles (shoulder and hip) and the ankle. This could be a reflection of the positioning of the limbs during different types of quadrupedal locomotion. In general terms, arboreal primates adopt an abducted limb posture during locomotion in order to maintain a better balance (Schmitt, 1994) and invert their hands and feet in order to better grasp the supports used to move on, especially if such supports are small branches (Gebo, 2014). Reversely, terrestrial quadrupeds tend to move with adducted limbs in order to obtain a better alignment with the more intense support reaction forces (SRF) and thus reduce the load about their joints (i.e. the moment arms) (Biewener, 1990; Schmitt, 1998). Abduction-adduction is achieved at the shoulder and the hip joints and hand and feet inversion have a direct effect on the ankle and wrist joints. Such positioning may involve differences in the system of forces acting on the limbs, which could result in differences in DJD development. In addition, some arboreal quadrupeds deviate from this pattern and perform adducted quadrupedalism (Meldrum, 1991) reducing the moment arms associated to SRF and providing further variability of DJD if this were related to the intensity of the loads associated to SRF.

Several of the differences were found in the main propulsive limb of the different sub-samples, supporting the link between locomotor variability and DJD variability. Clear examples of this were the leapers as well as the VCL and slow arboreal quadrupeds (Table 7.4). As mentioned in chapter 6, these groups of primates rely mainly on the hindlimb as their main locomotor compartment (Crompton and Andau, 1986; Gebo, 1987, 2011; Crompton and Sellers, 2007) and all the differences observed among these taxa belonged to the hindlimb. The leapers only showed significant differences for porosity at the ankle joint and the VCL and slow arboreal quadrupeds exhibited differences at the ankle and knee joints.

The ankle joint is subject to great stress, especially during leaps. The preparation for a leap is often associated with high levels of dorsiflexion (Gebo, 1987, 2011; Aerts, 1998). The great levels of flexion at the ankle joint (dorsi-and plantarflexion) are often accompanied by foot inversion (Gebo, 2011), particularly in VCL but also in leapers. Most of the porosity found was on the posterio-lateral aspect of the talar articular surface (Fig. 7.2). This suggested that its development was likely to be a result of mechanical stress. During a leap, when the ankle joint is plantarflexed and the foot is inverted, it is possible that the posterior aspect of the tibia may come in touch with the lateral aspect of the posterior talus, which could eventually cause a lesion. Furthermore, landing with an inverted foot can also produce a similar type of impact (Gebo, 2015, pers. Com.). Therefore, different levels of leaping in the habitual behaviour of these primates could result in different levels of porosity at the ankle joint.

Figure 7.2 Example of porosity on the posterior-lateral aspect of the tali of a Galagoides demidoff *(individual M283 from the Powell-Cotton Museum) (photo by Baiges-Sotos)*

The slow arboreal quadrupeds tend not to leap and those that do leap may do so in different proportions, according to the species, leading to differential development of porosity at the ankle joint with the leaping taxa. Moreover, different types of leaping, landing first with forelimb or hindlimb, or differences in speed could contribute towards the different prevalence of porosity at the ankle. The role of speed in DJD development is further developed in section 7.2.

Further differences at the knee joint among taxa of the VCL and slow arboreal quadrupeds could also be explained by differences in behaviour between these two groups. VCL propel themselves by means of very powerful extension of the hindlimb (Crompton and Andau, 1986; Gebo, 1987; Crompton and Sellers, 2007) and generally land hindlimb-first on the new support. This entails great peak reaction forces from the support with great take-off and landing moments acting on the hindlimb joints (Demes et al., 1995), which could result in higher levels of joint degeneration. The slow arboreal quadrupeds, in contrast, rely a lot less on their hindlimbs. Firstly, they use their forelimbs during quadrupedal progression, subjecting these limbs to compressive stress. Secondly, some of these species also exhibit a reverse pattern of forces to that observed in other primate species (Ishida et al., 1990; Schmitt and Lemelin, 2004), by bearing more weight and more intense forces at the forelimb than at the hindlimb. As a result, further differences in DJD at the hindlimb were expected in the comparison between the VCL and the slow arboreal quadrupeds, as the most variable limb in terms of involvement during locomotion. However, differences at the forelimb were not observed.

Other groups of primates exhibit a greater involvement of the forelimb for locomotor purposes, compared to the leapers and the VCL and slow arboreal quadrupeds. However, most species rely more on one limb or the other and, generally, the limb that was more relied upon was the limb showing greater variability of DJD distribution, even though it was not necessarily the limb showing the greatest severities of DJD (chapter 6, section 6.3). As an example, in suspensory primates DJD expression at the elbow joint was the most variable of the forelimb. This compartment is the one establishing direct contact with the support during suspensory progression. Therefore, the forelimb was subject to strong SRF associated to suspensory locomotion and the elbow was likely to be the joint bearing the greatest moment arms associated to SRF. This made this joint more susceptible to changes of limb positioning and magnitude of the SRF. Different degrees of extension of the elbow during suspensory progression (Bertram, 2004; Michilsens et al., 2011; Byron et al., 2017) would entail different intensity of the moment arms. Brachiation is performed with extended forelimbs in comparison with below-branch quadrupedalism (Granatosky et al., 2016), resulting in different alignment with the SRF and thus, different moment arms. This differentiation in moment arms could be reflected in different levels of joint degeneration.

This principle would also be applicable to the elbow joint of both knuckle-walkers and quadrupeds. Both groups of primates exhibit significant differences at this joint, which was probably reflecting variability in moment arms from the different levels of flexion and extension of the forelimb during locomotion. Both groups include species that move arboreally (and thus more flexed) and species that move more terrestrially (and thus more extended) (Schmitt, 1998; Larney and Larson, 2004).

There were also several differences observed at the hindlimb of the knuckle-walkers and the quadrupeds, involving different joints, responding to similar biomechanical principles. The knuckle-walkers showed significant differences at the knee and the ankle joint for osteophytosis and porosity, respectively. This was likely to be a reflection of either difference in body mass or differences in the degree of arboreality and the level of associated limb flexion. However, in the case of the quadrupeds no differences were observed at the knee joint, despite the variability in moment arms associated with differences in arboreality.

DJD at the knee among quadrupeds was found to be relatively high (combined mean=17.7; Table 6.3) but there were no significant differences among quadrupedal taxa in the development of DJD. This could reflect a similar involvement of the knee joint during quadrupedal locomotion. When quadrupeds experience a reduction of the forces that act on their limbs, such reduction is always greater at the forelimb than at the hindlimb, which results in the forelimbs experiencing greater changes in the forces and loads acting on their joints than the hindlimb (Schmitt and Hanna, 2004). The greater range of forces acting on the forelimbs could, thus, be related to the greater variability of DJD expression at this limb.

The hindlimbs of suspensory primates are different, as they are not always in contact with the support, but some species use them more than others (e.g., Fleagle, 1976; Mittermeier, 1978; Hunt et al., 1996; Thorpe et al., 2007; Youlatos, 2017). This distinction could be reflected in the variability of DJD at the joints of the hindlimb, as the use of the hindlimb was often associated with more quadrupedal or even bipedal behaviours. Therefore, the involvement of the hindlimb in locomotion for the suspensory primates would be linked to the application of compressive stress, which could lead to differential levels of expression of DJD at the hindlimb's joints, similarly to what was argued for their spine.

The results obtained evidenced that a high number of the differences observed both among locomotor adaptations and among the taxa within every locomotor adaptation were likely to reflect differences in locomotor behaviour, linked to differences in the forces derived from their activities. This supported the idea that one of the main drivers of DJD expression in non-human primates is of mechanical nature. Therefore, locomotor behaviour is an important causal factor to consider when studying the nature of DJD, at least in non-human primates.

7.2 DJD related to locomotor strategies as modulators of magnitude of support reaction forces (SRF)

The differences found in the previous section were likely to be associated to differences in the system of forces derived from locomotion acting on the skeleton, which seemed to induce different development of DJD. Therefore, modulators of such forces could also play an important role in DJD development.

Locomotor behaviour determines how the different compartments of the body are positioned during travel and, thus, how forces act on the primate skeleton. However, the magnitude of such forces is shaped by both intrinsic and extrinsic factors. As seen in chapter 4 the magnitude of the action force depends mainly on body mass. However, reaction forces can vary depending on differences in locomotor strategies performed by primates. **Speed** is directly related to the magnitude of the SRF. The faster a primate moves the greater is the intensity of the peak reaction forces from the support used (Schmitt, 1999; Bertram and Chang, 2001; Hanna et al., 2006). Similarly, the **diameter of the support** used is positively correlated with the intensity of the SRF. Primates moving on larger supports experience greater SRF than those moving on slender branches or twigs (Schmitt, 2003a, 2003b; Schmitt and Hanna, 2004). Below, these two locomotor strategies (speed and habitat use) are tested as sources of DJD differentiation between different groups of primates performing distinct locomotor strategies.

Significance tests with Bonferroni post-hoc corrections for the pairwise comparisons (when applicable) with standard significance values ($p<0.05$) were run. DJD indicators were treated separately and SIs were used. In the assessment of speed, combined values of DJD were used because of the low severities of DJD exhibited by two of the locomotor adaptations considered (leapers and VCL and slow arboreal quadrupeds), whereas DJD indicators were treated independently in the study of habitat and support use.

7.2.1 Speed

The sample used in this part of the analyses considered three of the five locomotor adaptations, for which a clear differentiation in habitual speed was possible: 1) leapers, 2) VCL and slow arboreal quadrupeds, and 3) suspensory primates. Considering that increased speed during locomotion produced higher peak SRF, differences in DJD expression were expected, with the fast-moving taxa exhibiting higher combined levels of DJD than the slow-moving taxa.

Differences between slow-moving (N=106) and fast-moving (N=272) individuals were found at several joints, belonging to the three body compartments: spine, forelimb and hindlimb (Table 7.10). Most differences at the spine were found at the thoracic region (at the middle thoracic bodies and at the middle and lower thoracic apophyses). The upper thoracic apophyses showed near-significant differences (p<0.1). At the limbs, the elbow and hip joints exhibited significant differences.

Table 7.10 Summary of the joints exhibiting significant differences (p-value in bold, near-significant at upper thoracic apophyses) in DJD expression between slow-moving and fast-moving species, with the average rank values for severity of DJD for the slow-moving and fast-moving sub-samples (the shaded values are the highest of the two)

Joint	**Test statistic (U)**	**p-value**	**Average rank slow-moving taxa**	**Average rank fast-moving taxa**
Cervical bodies	3003.50	0.773	▨ 87.43	86.12
Upper thoracic bodies	2341.50	0.343	▨ 79.97	76.48
Middle thoracic bodies	2021.50	**0.036**	▨ 80.37	72.89
Lower thoracic bodies	2164.50	0.431	▨ 77.96	74.54
Lumbar bodies	2328.50	0.601	76.15	▨ 78.71
Cervical apophyses	2883.00	0.100	▨ 89.84	85.13
Upper thoracic apophyses	2241.50	**0.060**	▨ 82.19	75.56
Middle thoracic apophyses	2027.00	**0.041**	▨ 80.24	72.94
Lower thoracic apophyses	1921.50	**0.007**	▨ 83.75	72.29
Lumbar apophyses	2339.50	0.594	▨ 79.59	77.39
Shoulder	13673.00	0.071	▨ 196.51	186.77
Elbow	12682.50	**0.003**	▨ 205.85	183.13
Wrist	13779.00	0.082	▨ 193.77	187.16
Hip	13168.50	**0.007**	▨ 198.59	184.59
Knee	13684.00	0.207	▨ 194.41	186.18
Ankle	13949.00	0.805	185.85	▨ 187.45

Average ranks (Table 7.10) provided information on to what extent the values of one of the groups tended to score higher in DJD severity than the other groups. Instead of giving information on the actual average of expression or the median value it showed a tendency measure of difference between groups (Daniel, 1990). For all the joints showing significant differences in DJD expression, the slow-moving taxa exhibited higher average ranks than the fast-moving species (Table 7.10). Thus there was a greater tendency of expressing more severe levels of DJD among the slow-moving taxa than among the fast-moving ones.

7.2.2 Habitat and support use

Interactions between moving primates and their habitats are vital in order to understand locomotor behaviour, but the way that primates use their habitats may also contribute to joint degeneration. Primates position their bodies differently, depending on the type of habitat and supports used, thus exhibiting behavioural variability depending on the type of forest and the strata exploited (chapter 3).

The types of supports found in different strata of the forest are associated with different mechanical properties that non-human primates need to assess and deal with during locomotion. Primates found in lowest strata of the forest (i.e. terrestrial taxa) are likely to perform an efficient type of quadrupedalism associated to low energy expenditure but high peak SRF. Arboreal primates, in contrast, deal with a complex network of supports of different degrees of deformability, involving a high energetic cost of locomotion in order to neutralise the sway of branches. They deal with this by adopting different strategies, such as increasing limb excursion in order to reduce the effect of the deformability of the support or use specific parts of branches that can decrease the amount of energy loss (Channon et al., 2011). Despite the energetic cost of arboreal locomotion, these primates experience reduced SRF than those using the ground (Schmitt, 1998).

Differences in DJD between primates exploiting terrestrial and arboreal habitats (Table 5.2) were assessed. As a result of the greater SRF associated with terrestrial locomotion, the most severe expressions of DJD were expected among the terrestrial taxa and the least severe ones in the arboreal taxa, potentially showing intermediate values of DJD in those species with a mixed pattern of habitat use (i.e. semi-arboreal taxa). The differences obtained among habitat use were contrasted with those differences observed among species.

The quadrupeds contain taxa with distinct patterns of habitat use: arboreal primates (80% of their time in trees), terrestrial species (that mainly use the ground) and semi-arboreal species (between 20 and 60% of their time in trees in combination with the ground) (Mekonnen et al., 2018). The knuckle-walkers were treated separately from other quadrupeds in these analyses because they are essentially terrestrial primates with the special case of the bonobos, which show a higher degree of arboreality in their behaviour. However, bonobos are not arboreal primates in the sense that this is understood for the arboreal quadrupeds. Some of the arboreal quadrupeds included in this study rarely use the ground, whereas bonobos do so habitually (Susman, 1984; Doran, 1993, 1996). In addition, the quadrupeds and the knuckle-walkers showed DJD expressions of different severity and their joint treatment could have clouded any possible patterns.

Further exploration on the mechanical differences associated to habitat use and their effect on DJD was done taking the diameter of the supports used into account. Fleagle (1978) observed that the Asian leaf monkeys (*Presbytis* sp.), essentially arboreal primates, performed their leaps from slightly thicker branches than those used for the landing. By doing so, these primates avoided some of the energy loss associated with compliant supports during takeoff, as well as damping part of the impact associated with landing (Demes et al., 1999). The same results were obtained in experimental studies in which primates using smaller supports in diameter (and therefore, more deformable supports) experienced significantly lower SRF than those primates using bigger supports (Schmitt, 2003a; Schmitt and Hanna, 2004).

The effect of support diameter on DJD development was assessed for the quadrupeds, as these are the primates that exhibit the greatest variability of supports used. In addition, these are the species for which the most reliable data could be gathered from published sources and they were classified according to the degree of deformability of the supports most commonly used (chapter 5). Some species were excluded due to a lack of information: *Nasalis larvatus* because no information was available on the type of supports used, only of the height of the canopy most commonly inhabited (Boonratana, 1993, 2000); *Lemur catta*, because only five partial skeletons were available. Similarly to the analyses considering habitat use, those species using stiffer supports were expected to exhibit the greatest levels of DJD as a result of the greater SRF, whereas those species using small branches and twigs as their most commonly used supports were expected to show the lowest levels of joint degeneration.

Differences in DJD between knuckle-walkers exhibiting different habitat use did not greatly mirror the pattern of differences among species (Table 7.11). There were very few differences associated with the differential use of the habitat by the knuckle-walkers and only differences for porosity at the apophyses coincided with the differences among species (Table 7.11).

The quadrupeds showed a very different pattern to that observed for the knuckle-walkers. For osteophytosis most of the differences found among species were observed with the comparison based on habitat use, with the exception of the cervical bodies and the ankle joint. Concerning porosity most of the differences among species were found grouping them by habitat use, except for the elbow and ankle joints. For eburnation the only differences expressed in both comparisons were at the level of the spine but not at the limbs (Table 7.12). In a few cases, further differences were observed by grouping the species according to habitat use that were not observed among species. This was the case of osteophytosis for the upper thoracic bodies, and the middle and lower thoracic bodies for porosity (Table 7.12).

Paired comparisons showed that most of the cases exhibiting significant differences involved the terrestrial and semi-terrestrial species against the arboreal group (Table 7.13). The average ranks for these groups of primates showed that in most cases the arboreal species ranked lower than the semi-arboreal or terrestrial species (Table 7.14) and in the majority of cases the semi-arboreal species showed greater tendency towards high expressions of DJD than the arboreal and terrestrial species. In some cases the highest ranks were expressed by the terrestrial species, as was the case of osteophytosis at the shoulder (rank=182.98 against rank=169.74 of the semi-arboreal) and at the hip (rank=176.12 against rank=152.51 of the semi-arboreal) (Table 7.14). The lowest ranks often pertained to the arboreal species (Table 7.14).

Table 7.11 Test statistics (χ^2 or U) and p-values of differences of DJD expression (significant p-values in bold) for all the weight-bearing joints of the knuckle-walkers 1) among species and 2) among categories of habitat use (arboreal and terrestrial)

Joint		**Eburnation**		**Osteophytosis**		**Porosity**	
		Among species	Between habitat use	Among species	Between habitat use	Among species	Between habitat use
Cervical bodies	Test statistic			5.51	734.50	5.48	600.00
	p-value			0.239	0.691	0.242	0.245
Upper thoracic bodies	Test statistic			15.32	729.50	2.08	619.00
	p-value			**0.004**	0.413	0.722	0.57
Middle thoracic bodies	Test statistic	5.53	664.00	4.15	625.00	1.41	598.00
	p-value	0.237	0.659	0.386	0.363	0.842	0.467
Lower thoracic bodies	Test statistic	5.13	664.00	12.69	648.00	3.52	531.00
	p-value	0.275	0.659	**0.013**	0.662	0.475	0.161
Lumbar bodies	Test statistic	2.41	672.00	8.33	690.00	7.06	439.50
	p-value	0.66	0.661	0.08	0.891	0.133	**0.009**
Cervical apophyses	Test statistic	3.31	714.00	3.34	779.00	0.98	655.50
	p-value	0.507	0.518	0.502	0.311	0.913	0.512
Upper thoracic apophyses	Test statistic			0.52	672.00	6.00	613.00
	p-value			0.971	0.891	0.199	0.549
Middle thoracic apophyses	Test statistic	5.53	664.00	1.73	617.50	4.88	591.00
	p-value	0.237	0.659	0.786	0.282	0.3	0.343

Table 7.11(cont.) Test statistics (χ^2 or U) and p-values of differences of DJD expression (significant p-values in bold) for all the weight-bearing joints of the knuckle-walkers 1) among species and 2) among categories of habitat use (arboreal and terrestrial)

Joint		**Eburnation**		**Osteophytosis**		**Porosity**	
		Among species	Between habitat use	Among species	Between habitat use	Among species	Between habitat use
Lower thoracic apophyses	Test statistic	2.99	672.00	7.24	607.50	9.27	486.50
	p-value	0.56	0.53	0.122	0.35	**0.05**	**0.018**
Lumbar apophyses	Test statistic	5.19	662.50	9.08	450.50	11.75	436.00
	p-value	0.269	**0.023**	0.059	**0.012**	**0.019**	**0.006**
Shoulder	Test statistic	4.45	864.50	3.90	764.00	7.15	635.00
	p-value	0.349	0.646	0.419	0.379	0.128	**0.02**
Elbow	Test statistic	10.27	883.50	7.52	890.50	6.16	905.00
	p-value	**0.036**	0.422	0.111	0.764	0.187	0.658
Wrist	Test statistic			1.52	797.50	7.30	870.50
	p-value			0.823	0.566	0.121	0.826
Hip	Test statistic			7.99	963.00	3.56	854.50
	p-value			0.092	0.171	0.47	0.994
Knee	Test statistic	5.18	893.00	19.29	693.50	3.43	771.00
	p-value	0.27	0.351	**0.002**	0.151	0.488	0.36
Ankle	Test statistic					13.58	946.50
	p-value					**0.009**	0.285

Table 7.12 Test statistics (χ^2) and p-values of differences of DJD expression (significant p-values in bold) for all the weight-bearing joints of quadrupeds 1) among species, 2) among categories of habitat use (arboreal, terrestrial and semi-arboreal) and 3) among groups using different supports of different deformability

Joint		**Eburnation**			**Osteophytosis**			**Porosity**		
		Among quadrupeds	Among habitat use	Among support use	Among quadrupeds	Among habitat use	Among support use	Among quadrupeds	Among habitat use	Among support use
Cervical bodies	Test statistic	34.10	7.56	9.09	24.13	5.63	16.90	38.42	19.37	25.45
	p-value	**0.002**	**0.023**	0.105	**0.044**	0.06	**0.005**	**<0.001**	**<0.001**	**<0.001**
Upper thoracic bodies	Test statistic				19.65	9.76	14.16	25.38	11.17	10.10
	p-value				0.104	**0.008**	**0.015**	**0.021**	**0.004**	0.072
Middle thoracic bodies	Test statistic				22.56	10.44	12.88	14.61	10.96	9.96
	p-value				**0.047**	**0.005**	**0.025**	0.332	**0.004**	0.076
Lower thoracic bodies	Test statistic				17.94	5.85	9.52	11.12	6.73	7.48
	p-value				0.160	0.054	0.09	0.601	**0.035**	0.187
Lumbar bodies	Test statistic	23.44	8.57	7.70	7.80	0.04	0.54	13.66	3.46	6.70
	p-value	**0.037**	**0.014**	0.174	0.857	0.982	0.990	0.398	0.177	0.244
Cervical apophyses	Test statistic	24.22	6.57	7.08	10.91	1.75	5.92	14.06	3.21	7.08
	p-value	**0.043**	**0.038**	0.215	0.693	0.416	0.314	0.446	0.200	0.215
Upper thoracic apophyses	Test statistic				18.16	4.31	6.70	39.55	11.82	13.77
	p-value				0.192	0.116	0.244	**<0.001**	**0.003**	**0.017**
Middle thoracic apophyses	Test statistic	19.70	0.32		22.90	11.74	14.46	35.76	16.60	19.48
	p-value	0.103	0.853		**0.043**	**0.003**	**0.013**	**0.001**	**<0.001**	**0.002**

Table 7.12(cont.) Test statistics (χ^2) and p-values of differences of DJD expression (significant p-values in bold) for all the weight-bearing joints of quadrupeds 1) among species, 2) among categories of habitat use (arboreal, terrestrial and semi-arboreal) and 3) among groups using different supports of different deformability

Joint		**Eburnation**			**Osteophytosis**			**Porosity**		
		Among quadrupeds	Among habitat use	Among support use	Among quadrupeds	Among habitat use	Among support use	Among quadrupeds	Among habitat use	Among support use
Lower thoracic apophyses	Test statistic	14.51	3.23	4.10	12.01	2.99	8.59	21.06	13.34	15.60
	p-value	0.339	0.199	0.535	0.527	0.224	0.127	0.072	**0.001**	**0.008**
Lumbar apophyses	Test statistic	9.00	0.28	2.85	12.76	4.1	7.03	13.15	1.87	4.23
	p-value	0.773	0.870	0.724	0.467	0.126	0.218	0.436	0.393	0.517
Shoulder	Test statistic	9.33	0.28	3.44	39.55	11.16	16.27	31.16	10.20	13.27
	p-value	0.809	0.871	0.633	**<0.001**	**0.004**	**0.006**	**0.005**	**0.006**	**0.021**
Elbow	Test statistic	14.66	2.62	7.34	18.95	5.77	7.55	34.69	3.11	12.79
	p-value	0.402	0.269	0.197	0.167	0.056	0.183	**0.002**	0.211	**0.025**
Wrist	Test statistic	27.10	0.71	2.22	10.28	0.90	3.86	21.50	0.26	3.44
	p-value	**0.019**	0.701	0.818	0.741	0.638	0.570	0.090	0.879	0.632
Hip	Test statistic	22.87	0.55	6.90	25.41	7.63	11.41	18.44	1.97	9.31
	p-value	0.062	0.758	0.228	**0.031**	**0.022**	**0.044**	0.187	0.374	0.097
Knee	Test statistic	9.70	1.28	2.40	11.61	1.57	3.66	16.69	3.93	9.79
	p-value	0.784	0.527	0.791	0.637	0.455	0.599	0.273	0.140	0.082
Ankle	Test statistic	28.91	4.78	7.38	25.89	1.01	11.08	27.71	5.84	8.39
	p-value	**0.011**	0.092	0.194	**0.027**	0.605	**0.05**	**0.016**	0.054	0.136

Table 7.13 Pairwise comparisons between groups concerning habitat use for the joints showing significant differences in DJD (in bold, with adjusted p-values) in the general comparison among habitat use, where A=arboreal, S=semi-arboreal and T=terrestrial use of the habitat.

Joint		**Eburnation**			**Osteophytosis**			**Porosity**		
		A-T	**A-S**	**S-T**	**A-T**	**A-S**	**S-T**	**S-T**	**A-S**	**S-T**
Cervical bodies	Test statistic (U)	0.66	-6.89	-7.55				-5.55	23.77	-18.22
	p-value	1	**0.022**	0.096				1	**<0.001**	**0.042**
Upper thoracic bodies	Test statistic (U)				0.50	-17.36	-16.86	-8.44	-4.22	4.22
	p-value				1	**0.048**	**0.006**	**0.005**	0.351	0.7
Middle thoracic bodies	Test statistic (U)				-10.52	-19.30	-8.78	-4.10	-8.32	-4.22
	p-value				0.310	**0.008**	0.902	0.374	**0.005**	0.687
Lower thoracic bodies	Test statistic (U)							-7.19	-7.77	-0.59
	p-value							0.169	0.140	1
Lumbar bodies	Test statistic (U)	0	-4.78	-4.78						
	p-value	1	**0.011**	0.077						
Cevical apophyses	Test statistic (U)	0	-3.78	-3.78						
	p-value	1	**0.033**	0.191						
Upper thoracic apophyses	Test statistic (U)							2.63	-14.23	-16.84
	p-value							1	**0.003**	**0.01**
Middle thoracic apophyses	Test statistic (U)				-11.01	-11.25	-0.24	1.31	-23.89	-25.20
	p-value				**0.032**	**0.027**	1	1	**<0.001**	**0.004**
Lower thoracic apophyses	Test statistic (U)							-6.42	-16.75	-10.33
	p-value							0.484	**0.001**	0.281

Table 7.13(cont.) Pairwise comparisons between groups concerning habitat use for the joints showing significant differences in DJD (in bold, with adjusted p-values) in the general comparison among habitat use, where A=arboreal, S=semi-arboreal and T=terrestrial use of the habitat.

Joint		**Eburnation**			**Osteophytosis**			**Porosity**		
		A-T	**A-S**	**S-T**	**A-T**	**A-S**	**S-T**	**S-T**	**A-S**	**S-T**
Shoulder	Test statistic (U)				-32.77	-19.53	13.24	-10.25	-21.42	-11.17
	p-value				**0.014**	0.104	1	0.720	**0.006**	0.861
Hip	Test statistic (U)				-22.23	1.38	23.61			
	p-value				**0.02**	1	0.051			

Table 7.14 Average ranks for all the joints showing significant differences in DJD expression among habitat use (A=arboreal; S=semi-arboreal; and T=terrestrial) for eburnation, osteophytosis and porosity. The shaded values indicate the highest ranks

Joint	Eburnation			Osteophytosis			Porosity		
	A	S	T	A	S	T	A	S	T
Cervical bodies	113.16	120.05	112.5				110.25	134.02	115.8
Upper thoracic bodies				104.06	120.92	103.6	104.5	108.72	112.94
Middle thoracic bodies				100.4	119.7	110.92	102.5	110.82	106.6
Lower thoracic bodies							Ø	Ø	Ø
Lumbar bodies	110	114.78	110						
Cevical apophyses	113.5	117.28	113.5						
Upper thoracic apophyses							104.63	118.84	102
Middle thoracic apophyses				101.31	112.56	112.32	101.27	125.16	99.96
Lower thoracic apophyses							102.9	119.65	109.32
Shoulder				150.21	169.74	182.98	151.77	173.19	162.02
Hip				153.9	152.51	176.12			

Further explorations were conducted, searching for differences among the semi-arboreal species and between Old World and New World arboreal quadrupeds, using the combined values of DJD. The three species of semi-arboreal quadrupeds (N=42) exhibited differences at the shoulder, wrist and ankle joints and near-significant differences at the elbow joint (Table 7.15). The paired comparisons showed few differences between the two mangabey species (*Cercocebus agilis* and *C. torquatus*), only showing differences at the shoulder and elbow, but in the comparison between the vervet monkey (*Chlorocebus aethiops*) and the red-capped mangabey (*C. torquatus*) differences were found for almost all the limb joints (except at the hip joint) (Table 7.15). Comparisons between the Old World (N=140, of which 136 with spine) and New World (N=103, of which 40 with spine) arboreal primates showed no significant differences in DJD expression for the present sample (Table 7.16).

Differences in DJD according to the degree of deformability of the supports used commonly showed that a good number of the differences obtained among species were also observed if species were grouped according to the level of compliance of their most commonly used supports (Table 7.12). This was particularly true for osteophytosis, where differences grouping the species according to support deformability reflected all the differences seen among species but also among habitat exploitation strategy. A good number of the differences previously observed for porosity (among species and among strategies of habitat use) were also present in the consideration of the species according to support compliance. The differences for porosity using support use as a grouping factor failed to show the overall differences at the thoracic bodies. No differences for eburnation were found among groups that utilised supports of different compliance.

*Table 7.15 Summary of the significant and near-significant differences in DJD severity (in bold) for all the weight-bearing joints of the semi-arboreal quadrupeds 1) among species, 2) between species (*Cercocebus agilis, Cercocebus torquatus *and* Chlorocebus aethiops*)*

Joint	**Significant differences among semi-arboreal species**		***C. torquatus* vs. *C. agilis***		***C. torquatus* vs. *C. aethiops***		***C. aethiops* vs. *C. agilis***	
	Test statistic (χ^2)	p-value	Test statistic (U)	p-value	Test statistic (U)	p-value	Test statistic (U)	p-value
Cervical bodies	0.95	0.622	23.00	0.535	46.00	0.764	17.00	0.393
Upper thoracic bodies	0.37	0.831	20.00	0.213	44.00	0.583	17.50	0.273
Middle thoracic bodies	2.48	0.289	17.50	0.136	41.50	0.453	17.50	0.274
Lower thoracic bodies	1.42	0.491	10.50	0.24	47.00	0.822	9.00	0.273
Lumbar bodies	0.32	0.852	15.00	0.602	49.00	0.942	12.00	0.564
Cervical AP	0.47	0.791	25.00	0.5	48.00	0.827	20.00	0.456
Upper thoracic AP	3.73	0.155	17.50	0.135	35.50	0.161	20.00	0.456
Middle thoracic AP	3.40	0.183	15.00	0.085	38.50	0.326	17.50	0.274
Lower thoracic AP	1.43	0.488	10.50	0.24	49.00	0.964	9.00	0.275
Lumbar AP	1.31	0.52	15.00	0.602	42.50	0.392	10.50	0.394
Shoulder	8.72	**0.013**	9.00	**0.008**	47.50	**0.002**	51.00	0.323
Elbow	5.06	**0.08**	12.00	**0.018**	65.50	**0.035**	45.00	0.184
Wrist	7.43	**0.024**	21.00	0.105	74.50	**0.022**	57.00	0.584
Hip	0.58	0.747	30.00	0.46	106.00	0.698	57.00	0.584
Knee	3.28	0.194	29.00	0.587	85.00	**0.076**	53.00	0.356
Ankle	10.28	**0.006**	21	0.104	70	**0.005**	60	1

Table 7.16 Summary of the joints exhibiting non-significant differences in DJD expression between New World and Old world arboreal quadrupeds, with the average rank values for severity of DJD both groups (the shaded values are the highest of the two)

Joint	Test statistic (U)	p-value	Average rank New World Monkeys	Average rank Old World Monkeys
Cervical bodies	2410	0.777	85.44	86.78
Upper thoracic bodies	1943.50	0.792	80.28	81.16
Middle thoracic bodies	1794.50	0.648	80.46	78.7
Lower thoracic bodies	2141.50	0.332	85.02	80.65
Lumbar bodies	2830.50	0.272	90.04	85.39
Cervical apophyses	2295.50	0.794	85.01	84.37
Upper thoracic apophyses	2022.00	0.484	82.9	80.56
Middle thoracic apophyses	1761.50	0.946	79.24	78.95
Lower thoracic apophyses	1899.00	0.251	77.26	82.5
Lumbar apophyses	2738.00	0.700	87.78	86.1
Shoulder	7180.00	0.928	121.71	122.22
Elbow	6874.50	0.445	118.74	124.4
Wrist	7249.50	0.901	122.38	121.72
Hip	7442.00	0.357	124.25	120.34
Knee	7800.50	0.110	127.73	117.78
Ankle	6906.00	0.368	119.05	124.17

7.2.3 Discussion of locomotor strategies as modulators of SRF and DJD

Speed and habitat use were factors that could condition DJD development as regulators of magnitude of the SRF. Differences in both factors were reflected in differences in DJD expression for several joints. However, the effect of these factors was not always as initially expected and did not have the same effects across the primate skeleton.

7.2.3.1 The role of speed

Significant differences were found for DJD expression between slow-moving and fast-moving primates for several joints belonging to the three different body compartments. Therefore, differences in DJD at these joints could, at least to some extent, be associated with differences in speed during locomotion. However, contrary to what was initially predicted, the slow-moving taxa exhibited higher levels of severity of DJD for all the joints with different levels of degeneration.

DJD development did not reflect the greater intensity of SRF during fast locomotion. Even though there were differences in joint degeneration related to speed, this was in the opposite direction to what was initially expected. Therefore, the consistently greater levels of DJD expressed in the slow-moving species must be a response to other factors, aside from the magnitude of the SRF.

Most of the joints that showed significant differences were synovial joints, with the exception of the middle thoracic bodies. As explained in chapter 2, synovial joints lie within a joint capsule. The articular facets are covered in hyaline cartilage and the bony elements are submerged in synovial fluid, which reduces friction between the articular surfaces (Norkin and Levangie, 1992). The synovial fluid mainly comprises water, hyaluronate or hyaluronic acid (HA) and a glycoprotein named lubricin. The concentration of the HA determines the viscosity of the fluid and, in humans, the viscosity is partially related to the velocity of action of a joint (Norkin and Levangie, 1992). Viscosity and joint speed are inversely related, so during fast movement joints have less viscous fluid than slow-moving joints, presenting less resistance to movement for the bony elements and allowing their faster motion, ultimately, enhancing the faster action of the joint.

An increase in the viscosity of the synovial fluid in joints of slow-moving taxa would, therefore, entail more resistance to movement of the bony elements, but the increase in fluid viscosity indicates higher concentrations of HA and, therefore, better lubrication of the joint would be expected. However, at least in the case of humans, an increase in the concentration of HA is not necessarily coupled with an increase of concentration of lubricin. Lubricin promotes the entanglement of the strings of HA, increasing the levels of entropy of HA, procuring the synovial fluid with a more flexible HA molecule, reducing the viscosity of the fluid and providing it with the capacity to dissipate the energy that is produced during locomotion, ultimately protecting the hyaline cartilage (Jay et al., 2007). Lubricin is an amphipatic molecule, which bonds the HA with the hyaline cartilage and creates an osmotic barrier for small molecules that maintain the chondrocyte cycle and, consequently, the health of a joint (Jay et al., 2007). If the viscosity of the synovial fluid increases the sub-diffusive behaviour of some molecules within the fluid is reduced, making both the association between HA and lubricin, and the transportation of small molecules slower (including those molecules in charge of joint maintenance).

The interaction between HA and lubricin on a load-bearing surface is triggered by high loads (Jay et al., 2007). There is differentiation between the less loaded phases of the human stride (swing phase) and the moment of greater compressive stress (propulsive phase), in which the joint experiences what is named "boosted lubrication" (Walker et al., 1968).

The present sample showed higher degeneration in the joints of slow-moving taxa. Considering that HA-lubricin association is enhanced by intense load, the greater reaction forces born by the joints of fast-moving taxa could result in a greater stimulation of the molecular association HA-lubricin at the synovial fluid, making HA pliable and able to absorb a greater amount of energy associated with impact, ultimately better preserving the hyaline cartilage and the joint. Moreover, the fact that slow motion of a joint comes with an increase in the concentration of HA, but not necessarily of lubricin could result in a more rigid conformation of the HA (Jay et al., 2007). As a result, the synovial fluid would be less able to dissipate the stress from impact and the higher viscosity would reduce the diffusive behaviour of molecules, affecting both the lubricin and other small molecules in charge of chondrocyte cycle regulation and joint health maintenance. This behaviour of the synovial fluid could potentially explain the higher joint degeneration of the slow-moving primates, in spite of being subject to lesser SRF associated to lesser speed.

Comparisons of the synovial fluid between healthy and pathological joints in humans evidenced that the quantity of fluid is significantly greater in pathological joints than in healthy ones (Balazs et al., 1967; Norkin and Levangie, 1992). However, the quality of the molecular portion differed between healthy and pathological joints and the HA in human joints affected by rheumatoid arthritis had a lower molecular weight than that found in a healthy joint (Balazs et al., 1967). This probably entailed greater difficulty of the HA to produce pliable molecules that can efficiently absorb shear stress. Therefore, once pathological processes are expressed in a joint, despite the measures taken to deal with this, degeneration was likely to increase in severity over time. Moreover, if the quality of the molecular portion of the synovial fluid is variable among mammalian species, in a similar way as it can vary among human joints (healthy and pathological), differences in the efficiency of load bearing could be expected. Little is known about synovial fluid composition in non-human primates and, therefore, further research is necessary in order to clarify the function of the molecular portion of the primate synovial fluid related to joint health and its relationship with speed.

Differentiation in limb positioning during slow and fast locomotion could also explain some of the differences observed, as well as the greater tendency of slow-moving primates to express higher severity levels of DJD. In general, speed is negatively correlated with maximum limb protraction and maximum limb yield, at least for the forelimb (Schmitt, 1998). Therefore, at lower speeds, primates would be expected to perform greater limb excursion (protraction-retraction) as well as adopt more flexed positions (Fig. 7.3). The reduced SRF are partially achieved by increasing the contact time of the limb with the support as well as by increasing limb yield (Larney and Larson, 2004).

Figure 7.3 Representation of the forelimb of a primate performing a stiff gait with increased extension (white representation with a solid line representing the path of the shoulder during the stride) and a compliant gait with increased flexion (dark representation with a dashed line representing the path of the shoulder during a stride) (after Larney and Larson, 2004)

An increase in limb flexion is coupled with greater moment arms about the limb joints (e.g., Biewener, 1990; Schmitt, 1998). Despite the fact that the actual reaction force was greater in magnitude for the fast-moving taxa, the increase in flexion that reduced the magnitude of the force entailed an increase of the load on the joints, by increasing the moment arms. As a result, despite the relationship between SRF and speed being clear, with the magnitude of the force increasing with speed, the amount load on the limb joints coming from the SRF was not necessarily different. The load at the joints of fast-moving taxa would be great due to greater magnitude of the SRF, but the load on the joints of the slow-moving taxa could be equally great due to the increased moment arms about the joints, resulting from the more flexed position.

The greater degeneration of joints in the slow-moving species could therefore be a combination of differences in the synovial fluid and its properties, and a potentially similar amount of load acting on their joints compared to the fast-moving taxa. Further research is necessary in order to confirm these explanations. More information is needed in non-human primate synovial fluid in order to fully comprehend its role, not only as a means of lubricating the joint, but also as a fluid of mechanical properties that permit the dissipation of stress. Further quantifications of SRF and moment arms are essential in order to assess the actual loads acting on the joints and then relating this to DJD expressions.

7.2.3.2 The role of habitat and support use

Experimental research has established that SRFs are greater for primates moving on terrestrial habitats than the forces experienced in arboreal habitats (Schmitt, 1994, 1998). The resultant reaction forces produce bending moments that act on the limb, having an important effect on the joints, involving potential modifications (Schmitt, 2003b). Therefore, in terms of DJD, the greatest levels of severity were expected in the terrestrial species, but this was not fully supported by the results obtained.

The knuckle-walkers did not show many differences in DJD expression according to the way these species used their habitats. In fact, several of the differences found between groups according to habitat use did not coincide with the differences found among species (Table 7.11). Only porosity at the more caudal apophyses reflected the differences found among the different knuckle-walking species. Thus, it was unlikely that the main differences found among these species were a reflection of the way African apes use their habitats, suggesting that the main differences in DJD were likely to be a result of posture or other factors, such as body mass, which is further considered in chapter 8. However, differences in sample size between the groups treated as terrestrial knuckle-walkers (N=90) and arboreal knuckle-walkers (N=19) could make these comparisons unreliable. Further analyses establishing more categories of arboreality, considering percentages of time spent in tress with respect to the ground, could provide further nuance and new information.

The quadrupeds showed a rather different pattern to the knuckle-walkers. There were great similarities in the pattern of differences obtained among species and grouping them according to habitat use (Table 7.12). This suggested that habitat use was shaping DJD distribution among these primates and therefore, at least in the case of the quadrupeds, the way these interact with their habitat was determining the main differences in DJD found among species.

The species of quadrupeds considered include Old World and New World monkeys. While the New World monkeys considered are predominantly arboreal (e.g., Mittermeier and Fleagle, 1976; Mittermeier, 1978; Fleagle and Mittermeier, 1980; Wright, 2007), the Old World monkeys included are highly variable in their habitat use. The ecological origin of Old World primates has been extensively discussed but it seems likely that they experienced at least one transition from arboreal to terrestrial habitats (Gebo and Sargis, 1994; Tosi et al., 2004; Sargis et al., 2008; Elton et al., 2016), leading to an ecological radiation and the variability observed now in extant species. This shaped their skeletal morphology, which mainly reflects ecological adaptations (Fleagle, 1977; Rodman, 1979). The strong link between ecological and morphological variability could be the reason why there was an apparent closer relation between habitat use and DJD in the quadrupeds in contrast with the knuckle-walkers.

The paired comparisons between sub-samples according to habitat use showed that most of the significant differences in DJD expression entailed comparisons between the arboreal primates and either the semi-arboreal or the terrestrial species (Table 7.13). It was the semi-arboreal species that stood out as different compared with the terrestrial primates, suggesting that they had a rather different pattern of DJD expression. The average ranks for the semi-arboreal species expressed the highest values for almost all the joints that expressed significant differences in DJD expression, with the exception of osteophytosis at the limbs, where terrestrial species exhibited the highest values and porosity at the upper thoracic bodies (Table 7.14). This entailed that, contrary to what was expected, the semi-arboreal quadrupeds had the tendency of scoring higher for DJD expression.

The higher tendency of osteophyte development among the terrestrial quadrupeds was in accordance to the hypothesis that stronger SRF would produce higher DJD. However, these were the only joints where the terrestrial primates scored higher than the semi-terrestrial ones. The effect of the reaction forces can be damped by changes in posture (e.g., Biewener, 1990; Demes et al., 1994; Schmitt, 1999), but also by means of different morphological features, such as the presence of some osteological or ligamentous structures at the joints (Schmitt, 2003b). Therefore, the great levels of degeneration observed in semi-terrestrial species were likely to be a combination of factors, but morphological adaptation (or the lack of it) seemed to be an important contributing factor in DJD development among these primates.

Morphological analyses of the guenons (*sensu lato*) (McGraw, 2004) established clear differences between the more terrestrial patas monkey (*Erythrocebus patas*), the semi-arboreal vervets (*Chlorocebus aethiops*) and the more arboreal guenons (*Cercopithecus ascanius*, *C. nictitans* and *C. pogonias*, of the species included in this thesis) (Gebo and Sargis, 1994). The morphology of *E. patas* was similar to that of a terrestrial cursor, whereas the semi-arboreal *C. aethiops*, despite presenting some traits typical of terrestrial exploitations, was morphologically closer to the arboreal guenons than it was to the terrestrial primates (Gebo and Sargis, 1994). The mangabeys included in this study contained one mainly arboreal species (*Lophocebus albignea*), with arboreally adapted morphologies, and two semi-arboreal species (*Cercocebus agilis* and *C. torquatus*), which showed some adaptations to terrestrial behaviours but retained many arboreal traits (Nakatsukasa, 1994).

The partial adaptation to terrestrial locomotion observed in the postcranial skeleton of semi-arboreal species (Gebo and Sargis, 1994; Nakatsukasa, 1994; Fleagle and McGraw, 1999) could entail a reduced capability of dealing with the intense SRF associated with terrestrial locomotion, potentially resulting in higher development of DJD. Thus, the exploitation of terrestrial habitats with arboreally adapted skeletons can make a primate less efficient in dealing with the more intense forces that come with the interactions with stiff supports, and this reduced efficiency could be reflected in a faster or more severe development of degenerative changes.

Different levels of adaptation to terrestrial behaviours are noticeable even among the semi-terrestrial species considered in this study. Vervets are morphologically very close to the arboreal guenons (Gebo and Sargis, 1994; Sargis et al., 2008), whereas the semi-arboreal mangabeys exhibit greater adaptation to terrestrial behaviours than seen in the vervets (Nakatsukasa, 1994). The significance analyses of the semi-arboreal species showed differences in DJD at the limbs among the three species of semi-arboreal primates (Table 7.15) and the paired comparisons showed that these differences were probably the result of the comparison between *C. torquatus* and *C. aethiops*. These two species showed differences at all the joints of the limbs except the hip joint (Table 7.15), supporting the fact that differences in the postcranial adaptations to terrestriality were mirroring differences in DJD. *C. torquatus* is the most terrestrial of the mangabeys (Jones and Sabater Pi, 1968), which is coupled with its more terrestrial morphology, in contrast with the more arboreal morphology of *C. aethiops* (Nakatsukasa, 1994). However, the vervets perform a great amount of terrestrial activities despite its arboreal morphology (McGraw, 2004), which could induce accelerated DJD, leading to differences with the better-adapted red-capped mangabeys (*C. torquatus*). However, greater sample sizes would be required to confirm these differences (Table 5.2).

One of the behavioural characteristics of terrestrial and semi-arboreal species is that they all perform terrestrial quadrupedal running, for which these species exhibit different levels of adaptation. Terrestrial quadrupeds are morphologically characterised as terrestrial cursors (e.g., Gebo and Sargis, 1994; Nakatsukasa, 1994; Stein and Casinos, 1997). However, semi-terrestrial species also perform fast terrestrial quadrupedalism, which is reflected in differences in mobility of their body compartments. During fast quadrupedal terrestrial locomotion the degree of sagittal bending of the spine is different between terrestrial and semi-terrestrial species as a strategy to compensate for the differences in morphology (Hurov, 1987; Zihlman and Underwood, 2013). In order to perform an equally long stride to undertake efficient cursoriality, semi-terrestrial species need to perform more intense spinal bending in order to compensate for their shorter limbs (compared to terrestrial species) (Fig. 3.13). In a comparison between *E. patas* and *C. aethiops*, Hurov (1987) observed that the intervertebral discs of the vervets were significantly thicker than those of the patas monkeys. This would partially damp the stress associated to the intense bending of the spine of these primates during fast terrestrial quadrupedal locomotion but was probably an adaptation to arboreality.

Thicker intervertebral discs are characteristic of the arboreal species (Hurov, 1987), as the discs damp the impact derived from intense torsional stress associated to climbing activities. Considering that the reaction forces are greater during terrestrial activities than in arboreal activities (Schmitt, 1998) it is likely that with similar spinal morphologies, the semi-arboreal species developed more severe DJD than the arboreal quadrupeds, as the former would be exposed to greater loads during running than the arboreal quadrupeds during climbing. In fact, in almost all the differences concerning the spine, it is the semi-arboreal species that present the highest tendencies of expressing severe DJD (Table 7.14).

Semi-arboreal species also perform a highly diverse repertoire of locomotor behaviours, increasing the variability of the forces that these primates experience. This could potentially contribute to the great differentiation of the semi-arboreal species from the terrestrial and arboreal quadrupeds and could also entail greater levels of joint degeneration, in addition to the changes associated to morphological differences.

Semi-arboreal and terrestrial species showed greater tendency towards higher levels of DJD development than the arboreal quadrupeds (Table 7.14). Therefore, arboreal primates were clearly distinct from the semi-arboreal and terrestrial quadrupeds. The lowest ranks of the arboreal quadrupeds were as initially predicted, as these are the group of quadrupeds that deal with the lowest SRFs as a result of the interaction with deformable supports. However, this sub-sample includes Old World and New World monkeys (Table 5.2, chapter 5), and previous research on DJD in New World monkeys reported that these exhibited fewer degenerative changes than the Old World monkeys (Rothschild and Woods, 1993).

The lower incidence of DJD among New World Monkeys could either be a result of the very arboreal nature of many New World monkeys in comparison with Old World monkeys (which show greater ecological diversity) or it could be due to phylogenetic distinctiveness. In the present sample, there are two New World species of quadrupeds: *Cebus albifrons* and *Sapajus apella*, which are highly arboreal primates (Fleagle and Mittermeier, 1980; Youlatos, 2001; Wright, 2007), despite the fact that *C. albifrons* uses the ground much more often than *S. apella* (Janson and Boinski, 1992). If there were a clear differentiation between New World monkeys and Old World monkeys, the inclusion of these two species could potentially bias the results towards lower prevalence of DJD that would not be applicable to all arboreal quadrupeds.

Further testing for differences between the Old World and New World arboreal quadrupeds showed no differences between these two groups for any of the weight-bearing joints (Table 7.16). This suggested that it was likely that the differences that Rothschild and Woods (1993) observed were due to the lack of differentiation between the arboreal and more terrestrial Old World primates, dismissing the idea that differences in DJD among monkeys of different continents are due to phylogeny. Therefore, the lower levels of DJD development for the arboreal quadrupeds were likely to respond to the way these primates use their habitat, probably as a consequence of the reduced SRF experienced in the arboreal strata of the forest.

Further reduction of SRF could be associated with a reduction in the diameter of the supports used during locomotion. This could be a reflection of the increased deformability of the supports, which would damp some of the impact (Demes et al., 1999; Channon et al., 2011). However, it could also be achieved by an increase of limb yield (Schmitt, 1999) or a greater engagement of the extensor hindlimb musculature (Reynolds, 1985a, 1985b). Regardless of the mechanism by which this was obtained, the reduction of SRFs was greater with a reduction of the support diameter (Schmitt, 2003a; Schmitt and Hanna, 2004). Therefore, significant differences in the expression of DJD were expected depending on how deformable the supports most commonly used were.

Many of the differences observed among species of quadrupeds or among groups of quadrupeds that exploit different habitats were also observed when grouping the species according to support use (Table 7.12). All the differences observed for osteophytosis among species and among groups of different habitat use were also observed in comparisons reflecting support use. This suggested that the differences seen in osteophytosis among species were likely to be reflecting, not only the way different quadrupeds use their habitats but also most likely, the way they use the supports available. It was probable that the use of small, highly compliant branches (reducing SRF), in contrast with the use of very stiff supports, like boughs or the ground (increasing SRF), entailed differences in the development of osteophytosis.

The number of differences observed for porosity according to support use was not reflecting all the differences observed in the previous comparisons among species and considering habitat use (Table 7.12). Therefore, the effect of support compliance was not as great in the development of porosity as it was for osteophytosis. In addition, no differences for eburnation were found with support use as a grouping factor, implying that differences in the types of supports used did not entail any differences in the development of eburnation.

These results indicated that the use of supports of different degrees of compliance during habitual quadrupedal locomotion might have different effects on the development of different indicators of DJD. There seemed to be a strong relationship between support deformability and osteophyte development, whereas no relationship was observed between support use and eburnation. This differential effect could be a reflection of how mechanical stress associated with SRF may have an important effect during the early stages of joint degeneration, but not necessarily in the more advanced stages of the disease. The earlier signs of DJD (osteophytosis and, to a lesser degree, porosity) seemed to reflect differences in support use and, specifically, in the level of compliance of these supports. However, the effect of support use seemed to only be relevant in the earlier expressions, as for more severe levels of degeneration (eburnation), support use did not seem to accurately reflect the differences observed among the species, suggesting that severe expressions of DJD were likely to respond to other causal factors.

DJD development among knuckle-walkers did not seem to be particularly affected by habitat use. However, the way that quadrupeds use their habitat was of extreme importance in terms of joint degeneration, as most of the differences observed among species were also observed if these primates were grouped according to the way they interact with their environments. The results obtained supported the relationship between SRF and DJD, but emphasised that morphological adaptation played an important role in the efficiency in dealing with SRF. Phylogenetic differences did not seem to contribute towards DJD for the quadrupeds, while support use played an important role in the development of the earlier stages of DJD: osteophytosis and, to a lesser extent, porosity. The later stages of degeneration, despite being linked to locomotor behaviour, were likely to be induced by other factors.

7.3 Summary and conclusions

This chapter evaluated the effect of different aspects of primate locomotor behaviour in terms of DJD development. Locomotor adaptation and locomotor strategies that modulate SRF were taken into account as potential drivers of DJD. The results obtained suggested that the system of forces acting on the primate body that derive from locomotion was likely to shape the pattern of prevalence and severity of DJD.

Primates of different locomotor adaptations showed significant differences in DJD development, indicating that the way that primates move could entail differences in DJD expression. Further variability was observed among species within each locomotor category and most of the differences observed were likely to respond to variability of locomotor behaviour within each locomotor group. Therefore, patterns of variability of DJD were related to specific movements that were performed in varying degree by different primates. Differences on the loads that joints bear (defined as varying moment arms) as a result of different positions adopted in different types of locomotion were likely to play a significant role in determining DJD.

The link between forces and DJD was further confirmed in the consideration of speed and habitat use as sources of variability of DJD. Slow and fast moving taxa of primates exhibited differences in DJD at some synovial joints and the severity of its expression was possibly linked to the mechanical properties of the synovial fluid, which are enhanced by intense forces associated with fast movement of the joints. However, differences in limb postures could also have been determinant in the differences in DJD. Habitat use was closely related to DJD expression in quadrupeds, despite not being particularly informative for the knuckle-walkers. This suggested that different factors could have a different effect on DJD development in different groups of primates. In fact, the close relationship between habitat use and DJD in quadrupeds could be a result of their ecological diversity and their ecomorphological adaptations. Morphological adaptation was a key aspect on the efficiency of the quadrupeds to deal with the intense forces related to locomotion.

The degree of deformability of the supports used during locomotion and the intensity of the reaction forces associated, played an important role in the development of the earlier stages of DJD (osteophytosis and, to a lesser degree porosity). However, support deformability was not clearly associated with the later stages of the disease (eburnation). Eburnation was probably induced by other factors, which could be of mechanical nature, such as body mass, or related to life history, such as age.

In conclusion, variability of DJD could be mostly explained in relation to the diversity of locomotor behaviour across primates. However, locomotor behaviour did not explain all the differences observed in DJD, suggesting the involvement of other factors in DJD development. Some of these factors are assessed in the following chapter, where the effect of body mass and age is evaluated in relation to DJD expression at the weight-bearing joints of the primate limbs.

CHAPTER 8: EFFECT OF BODY MASS AND AGE ON DJD

DJD expression in the primate body differed in distribution and severity across the sample of study (chapter 6). While the distribution patterns of DJD were at least partially related to variability of locomotor behaviour and the associated forces (chapter 7), differences among sub-samples in overall severity of DJD were likely to respond to other factors, such as body mass or age (chapter 6).

The leapers, vertical clingers and leapers (VCL) and slow arboreal quadrupeds exhibited lighter overall expressions of DJD than the knuckle-walkers, while the quadrupeds and the suspensory primates exhibited intermediate levels of DJD expression (chapter 6). These differences in severity of expression of DJD among different sub-samples could partially be a result of the effect of locomotion on specific joints. However, the group showing the highest expressions of DJD comprised the largest primates of the sample, as well as the longest-lived ones. In contrast, those that showed the lightest expressions of DJD were the smallest and the shortest-lived, suggesting that factors such as body mass or age were likely to play a key role in DJD development.

This chapter explores the effect of body mass and relative age on DJD expression. The spine was excluded from this part of the study, as it is a highly complex system of joints, with different joints performing different functions (e.g., Norkin and Levangie, 1992; Ankel-Simons, 2007; Gebo, 2014). Instead the focus was on the limbs, as these joints perform both weight bearing and mobility functions, making these body compartments more suited for these analyses.

Body mass was inferred from femoral head measurements (chapter 5) and its effect on DJD expression was assessed in different ways. Firstly, inferred body mass was contrasted with overall DJD expression found at the forelimb and hindlimb. Secondly, body mass was related to pressure exerted on two main weight-bearing joints (shoulder and knee) and contrasted to DJD expression at these joints. Lastly, the potential effect of sexual dimorphism was taken into account, by looking for differences in DJD expression between males and females.

The effect of longevity was analysed by assessing the effect of relative age in DJD expression, establishing correlations between limb DJD expression and relative age. This was done for the whole sample as well as for the five different sub-samples.

8.1 Relationship between body mass and DJD

The following analyses were based on a total of 740 individuals. Explorations on the relationship between body mass and overall limb severity of DJD (Equation 8.1 and 8.2) or pressure and overall joint severity of DJD (Equations 5.11, chapter 5) mainly consisted on non-parametric correlation tests (Spearman's ρ) accompanied by graphic representations (scatterplots). The effect of sexual dimorphism was analysed by searching for differences in DJD expression between males and females, using non-parametric significance tests in a total of 695 individuals, of which 313 were females and 382 were males.

$$Forelimb\ DJD = Shoulder\ DJD + Elbow\ DJD + Wrist\ DJD$$

Equation 8.1

$$Hindlimb\ DJD = Hip\ DJD + Knee\ DJD + Ankle\ DJD$$

Equation 8.2

(where the values of DJD for each joint were calculated as shown in Equation 5.11).

Body mass across this primate sample was highly variable, ranging from 60-63 g of the dwarf galago (*Galagoides demidoff*) to an average of 170 Kg of adult male lowland gorillas (*Gorilla gorilla*) (Smith and Jungers, 1997). Therefore, differences in scale across the sample were considerable and transformations of the data (Log10) were necessary.

8.1.1 Relationship between body mass and severity of DJD

The correlations between transformed body mass (from now on referred to as body mass) and overall DJD were significant both at the forelimb and the hindlimb (forelimb $\rho=0.444$, $p<0.001$; hindlimb $\rho=0.326$, $p<0.001$). However, the correlation coefficients were not particularly high in either case[1].

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[1] Correlation analyses run with transformed DJD data (Log10), in order to reduce variability of DJD expression, provided the same results as for non-transformed data and thus transformations for DJD expressions were not presented in this chapter.

The graphic representations of DJD development against body mass showed a very weak quadratic distribution of the data but provided good information on the levels of expression of DJD in relationship to body mass (Fig. 8.1 and 8.2). The majority of cases exhibited low to intermediate DJD severity values, but some cases showed extreme DJD expression, contributing towards the weak fit of the quadratic equation ($R^2=0.146$). The highest levels of DJD at the forelimb were found in individuals of intermediate body mass, while for the largest individuals the highest values of DJD expression were lower, in comparison (Fig. 8.1). The species showing the greatest ranges of expression of DJD were *Cercocebus torquatus, Chlorocebus aethiops*, *Pan paniscus* and *Pan troglodytes*. These were followed by *Cebus albifrons*, *Cercocebus agilis* and *Lophocebus albigena*, which exhibited high values of DJD expression but lower than the previously listed species (Fig. 8.1).

The values of DJD expression at the hindlimb increased with body mass, so the highest severity values of DJD expression were observed in the largest individuals (Fig. 8.2). Most of the cases took low to intermediate values of DJD expression, entailing a weak fit with the quadratic equation ($R^2=0.121$). The species showing the greatest ranges of DJD expression were *Cercocebus torquatus*, *Gorilla beringei*, *Gorilla gorilla* and *Pan troglodytes*. *Ateles* sp. and *Pan paniscus* also exhibited high levels of DJD expression at the hindlimb, but lower than the first group of species.

DJD at the different joints of the limbs showed different levels of correlation with body mass but all were significant (Table 8.1). While the correlation coefficients obtained remained low, the joints showing the strongest correlations of each limb were the elbow ($\rho=0.424$, $p<0.001$) and knee ($\rho=0.313$, $p<0.001$) joints, with similar correlation factors to those obtained for the overall limbs (forelimb DJD $\rho=0.444$, $p<0.001$; hindlimb DJD $\rho=0.326$, $p<0.001$).

Table 8.1 Correlation coefficients (ρ) and significance values (p-value) of the correlations considering transformed body mass (Log10) as the independent variable and combined DJD at the different limb joints as the dependent variables

Dependent variable	**Spearman's rho (ρ)**	**p-value**
DJD at the shoulder joint	0.328	< 0.001
DJD at the elbow	0.424	< 0.001
DJD at the wrist	0.274	< 0.001
DJD at the hip	0.238	< 0.001
DJD at the knee	0.313	< 0.001
DJD at the ankle	0.184	< 0.001

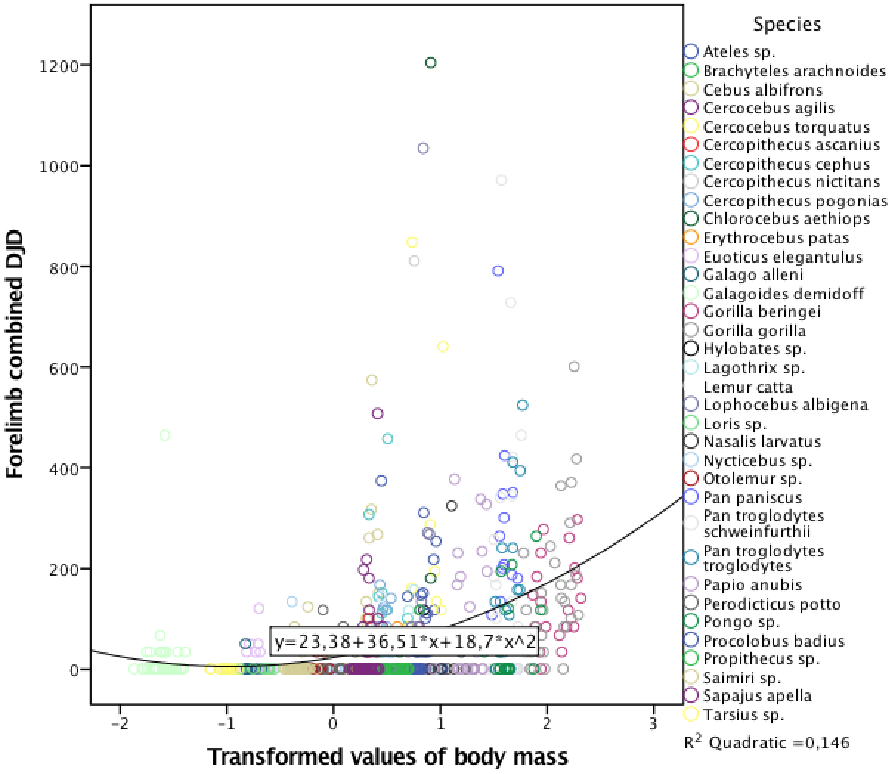

Figure 8.1 Bivariate scatterplot with transformed body mass (Log 10) as independent variable and combined values of DJD at the forelimb as the dependent variable, showing a general increase in DJD as body mass increases, with cases labelled by species

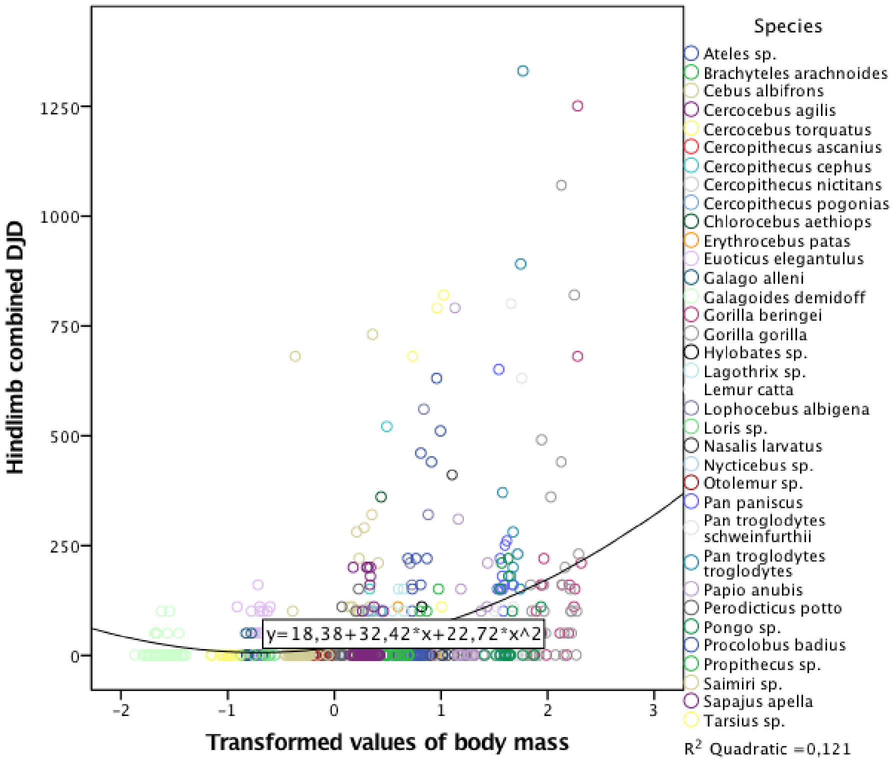

Figure 8.2 Bivariate scatterplot relating transformed body mass (Log 10) as independent variable and combined values of DJD at the hindlimb as the dependent variable, showing a general increase in DJD as body mass increases, with cases labelled by species

8.1.2 Pressure and severity of DJD on two main weight-bearing joints

Body mass is an indicator of the weight of an animal (i.e. mass under the action of gravity). Body weight, as a force, determines the amount of stress that a joint experiences, which could potentially result in different expressions of DJD. Stress, understood as mechanical pressure, is negatively correlated with the surface onto which a force is applied. Therefore, the effect of weight on the joints during locomotion is dependent on 1) the size of the joints supporting the force and 2) the amount of weight born by each limb during locomotion. The goal of this part of the analyses was to assess whether or not differences in joint dimensions among taxa entail an increase or a reduction of pressure born on two main weight-bearing joints (shoulder and knee joints) and if this was reflected in different average DJD expression at these joints.

Estimated pressure in Pascals (Pa) was calculated for the shoulder and knee joints of each individual from the inferred values of body mass (chapter 5). Average values of pressure and DJD expression were used for each taxon (listed in Table 5.2), as the interest was on the potential differences among taxa and not among individuals. Using averages avoided problems of differences in sample size across taxa and significantly reduced the number of cases with zero-values for DJD expression. All the variables considered were Log10 transformed, which entailed the exclusion of those species with healthy shoulders or knees. As a consequence, these analyses considered the relationship between the average amount of pressure and average DJD only for those taxa that exhibit some level of joint degeneration at the shoulder and knee joints.

The calculated amounts of pressure differed between the shoulder and knee joints (Table 8.2). Both the range of values (differences between minimum and maximum) and the average pressure were much higher at the shoulder than at the knee.

Table 8.2 Minimum, maximum and average calculated pressures (P) in Pascals (Pa) at shoulder and knee

	Minimum P (Pa)	Maximum P (Pa)	Average P (Pa)
Shoulder	5.08	689.46	155.16
Knee	15.44	261.32	80.19

Calculated pressure at both the shoulder and knee were significantly and positively correlated with severity of DJD at these joints across taxa (Table 8.3). The correlation coefficients were moderate, showing a stronger correlation between the two variables at the knee joint than at the shoulder (Table 8.3). There was a positive, linear increase of DJD at higher pressures on both the shoulder and knee joints (Fig. 8.3 and 8.4) but the tendency lines had different slopes, with a more evident increase for the hindlimb than the forelimb (slope shoulder=0.45; slope knee=1.02).

Table 8.3 Correlation coefficients (ρ) and significance values (p-value) for the correlations between transformed pressure (Log10) as the independent variable and transformed DJD (Log10) as the dependent variable, at the level of the shoulder and knee

Dependent variable	Spearman's rho (ρ)	p-value
DJD at the shoulder	0.428	0.029
DJD at the knee	0.570	0.005

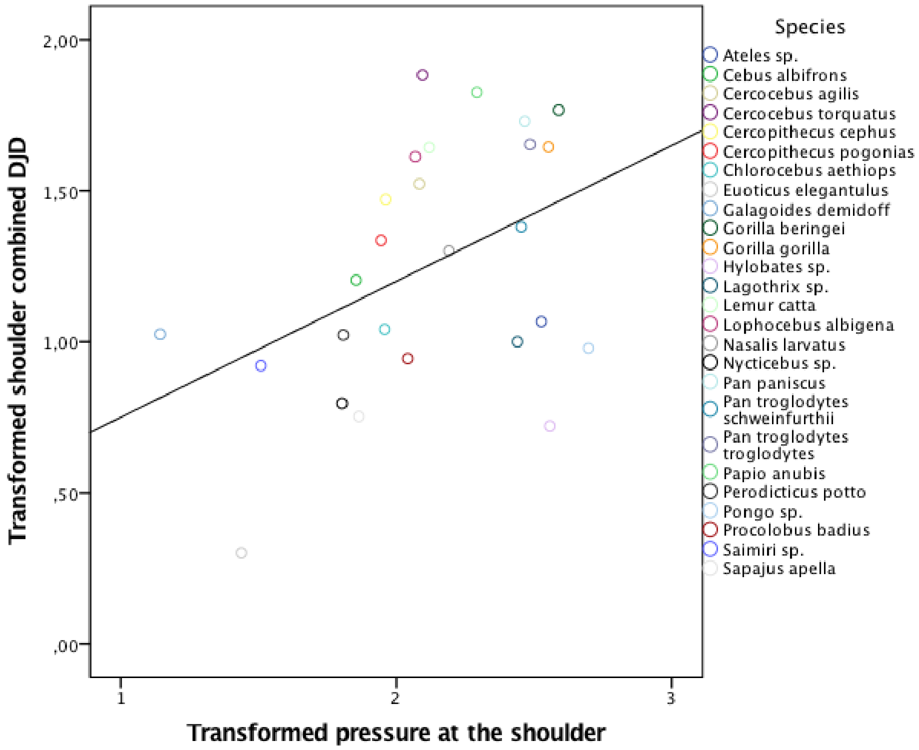

Figure 8.3 Bivariate scatterplot relating transformed pressure at the shoulder (Log 10) and transformed severity of DJD at the shoulder with cases labelled by species and tendency line showing the positive direction of the correlation (slope=0.45)

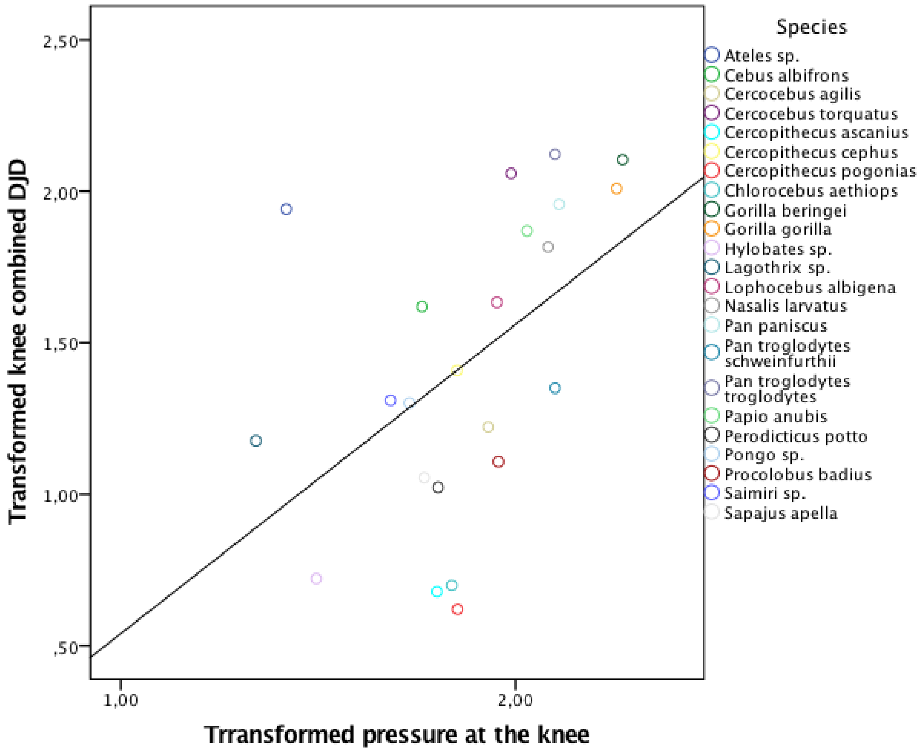

Figure 8.4 Bivariate scatterplot relating transformed pressure at the knee (Log 10) and transformed severity of DJD at the knee with cases labelled by species and tendency line showing the positive direction of the correlation (slope=1.02)

8.1.3 Influence of sexual dimorphism on DJD development

An intra-specific source of variability of body mass is the differences in size between males and females. Some primate species are highly sexually dimorphic, exhibiting great differences in body mass (e.g., DeRousseau, 1988; Smith and Jungers, 1997). This entails differences in weight and, potentially, on pressure at the joints that could result into differences in severity of DJD.

Two of all the weight-bearing joints studied in this thesis showed significant differences in DJD expression between males and females: the shoulder and elbow joints. The differences observed did not affect all the indicators of DJD. The shoulder joint only exhibited differences concerning osteophytosis, whereas the elbow joint showed differences in osteophytosis and porosity expression (Table 8.4).

Table 8.4 U statistics and p-values of those joints showing significant differences in the distribution of DJD between males and females for at least one of the DJD indicators (the significant values are shaded) considering the whole sample of primates

Joint	**Eburnation**		**Osteophytosis**		**Porosity**		**Combined**	
	U	**p-value**	**U**	**p-value**	**U**	**p-value**	**U**	**p-value**
Shoulder	59713	0.839	63115	0.028	60903.5	0.346	64110	0.011
Elbow	60069	0.644	64927	0.013	62664	0.049	65293	0.011

Further analyses were run for the shoulder and elbow joints considering sex differentiation in five sub-samples (VCL and slow arboreal quadrupeds, leapers, quadrupeds, knuckle-walkers and suspensory primates). The results showed significant differences in DJD expression for the quadrupeds and the suspensory primates (Table 8.5). The quadrupeds exhibited differences in osteophytosis at the elbow joint (U=9856; p=0.008) and differences for the combined DJD values at the shoulder (U=9433.5;p=0.032) and elbow joints (U=9809.5;p=0.014). The suspensory primates only showed significant differences between males and females for combined DJD at the elbow (U=1727;p=0.022).

Table 8.5 U statistics and p-values of those joints showing significant differences in the distribution of DJD between males and females for at least one of the DJD indicators (the significant values are shaded) considering the different sub-samples of primates

Sub-sample	**Joint**	**Eburnation**		**Osteophytosis**		**Porosity**		**Combined**	
		U	**p-value**	**U**	**p-value**	**U**	**p-value**	**U**	**p-value**
Quadrupeds	Shoulder	8585	0.439	9189	0.088	8885	0.214	9434	0.032
	Elbow	8580	0.814	9856	0.008	8984	0.150	9810	0.014
Suspensory	Elbow	1525	0.109	1627	0.116	1598	0.071	1727	0.022

8.1.4 Discussion of the results

8.1.4.1 Inferred body mass and DJD expression

The results obtained reported significant positive correlations between body mass and DJD development at the limbs (ρ=0.444, p<0.001 for the forelimb; ρ=0.326, p<0.001 for the hindlimb). As a result, there were better chances for bigger individuals to develop severe expressions DJD than for smaller primates, implying that body mass played a significant role in DJD expression. However, the correlation coefficients obtained were relatively low, suggesting that body mass was unlikely to be the only variable contributing to DJD.

Healthy joints or with light expressions of DJD were common across primates, regardless of their body mass (Fig. 8.1 and 8.2). The highest levels of DJD expressions at the hindlimb were observed in the largest individuals, even though these comprised fewer cases than those exhibiting lighter expressions of DJD (Fig. 8.2). In contrast, in the case of the forelimb, the individuals showing the highest severity levels of DJD were individuals with intermediate values of body mass (Fig. 8.1). Most of the species showing the highest values of DJD exhibited a mixed use of their habitat, exploiting both arboreal and terrestrial forest strata (*Cercocebus torquatus*, *C. agilis*, *Chlorocebus aethiops* and *Pan paniscus*). As discussed in chapter 7, their higher expressions of DJD could be a result of their locomotor behaviour in combination with their morphological and postural adaptations (or the lack of adaptations), and not necessarily a reflection of body mass.

The association between body mass and DJD differed between limbs, with stronger correlations found at the forelimb than at the hindlimb (ρ=0.444 and ρ=0.326, respectively). This suggested that the forelimb was likely to be more susceptible to changes in body mass concerning DJD expression (probably of osteophytosis or porosity). In fact, excluding the extreme cases of DJD expression at the forelimb and hindlimb, overall limb DJD expression at the forelimb was substantially greater than at the hindlimb, showing values of overall limb DJD expression of around 400 at the forelimb and 250 at the hindlimb (Fig. 8.1 and 8.2).

Different joints within each of the limbs exhibited further differences concerning the body mass-DJD association (Table 8.1). The joints that showed the best correlations were the elbow (ρ=0.424) and shoulder (ρ=0.328), followed by the knee (ρ=0.313). The joints of the forelimb showed more similar correlation coefficients, although the elbow joint showed the strongest association between DJD and body mass (shoulder ρ=0.328; elbow ρ=0.424; wrist ρ=0.274), suggesting that the whole forelimb was more evenly influenced by body mass concerning DJD development. In the hindlimb, the knee was the joint showing higher correlations with body mass, with the hip (ρ=0.238) and the ankle (ρ=0.184) showing the weakest correlations (Table 8.1).

The joints of the forelimb, showed the highest averages of early development of DJD (osteophytosis and porosity) in a comparison with their homologous joints of the hindlimb, particularly the shoulder and elbow (average osteophytosis at shoulder=8.58; at elbow=17.11; average porosity at shoulder=6.36; at elbow=8.75, Table 6.1). However, the greatest evidence of later DJD development was observed at the knee (average eburnation at knee=2.48, Table 6.1). Therefore, it was likely that the strongest correlations observed between body mass and DJD expression at the forelimb (both for the whole limb and for independent joints) were a result of the more gradual but consistent development of DJD. This would entail a closer relationship between body mass and DJD for the earlier stages of joint degeneration (often seen at the forelimb) than for the more advanced, extreme expression (seen more often at the hindlimb, especially at the knee).

These results suggest that different factors can have a different effect among body compartments (in this case, forelimb and hindlimb), or even among joints of a same compartment. In the hindlimb case, the knee joint was the most influenced by differences in body mass in terms of DJD expression, probably as a result of the great involvement of this joint in weight-bearing functions. In contrast, DJD at the other joints of this limb was likely to be induced by other factors, judging by the lower correlation coefficient with body mass compared to that obtained at the knee (Table 8.1).

8.1.4.2 Pressure and DJD expression

The relationship between pressure and DJD was assessed at the shoulder and knee joints. The amount of calculated pressure born at the shoulder and knee was different for the two joints (Table 8.2). Both the range and the average pressure supported at the shoulder joint were much higher than those observed at the knee joint (Table 8.2). This demonstrated a difference in function between the two joints. The low average pressure at the knee was an indicator that this joint is comparatively larger than the shoulder with respect to the overall size of a primate (average pressure at knee=80.192 Pa; average pressure at shoulder=155.164 Pa). Moreover, the narrower range of estimated pressures obtained for the knee joint (minimum pressure=15.439 Pa; maximum pressure=261.322 Pa) indicated that this joint scaled closely with overall body mass and thus was more reflective of a weight-bearing role. In contrast, the shoulder joint did not scale as closely to body mass as the knee joint, reflected by the broader range of pressures experienced at the shoulder joint (minimum pressure=5.08 Pa; maximum pressure=689.459 Pa). The size of the shoulder joint was probably a reflection of a species' ability to perform a great range of movement with their forelimbs, which is essential for the arboreal mode of life (e.g., Larson, 1993; Schmitt, 1998, 1998; Aiello and Dean, 2006; Cachel, 2015).

The correlation between pressure and DJD was stronger at the knee than at the shoulder (ρ=0.57; p=0.005 and ρ=0.428; p=0.029, respectively), showing a reverse correlation pattern to that observed using body mass, where the correlation with DJD was slightly stronger at the shoulder than at the knee, although similar (ρ=0.328 and ρ=0.313, respectively). Moreover, the correlation coefficient obtained in the association of pressure and DJD at the knee was the greatest observed throughout these analyses. This entailed that, despite the narrower range of pressures experienced at the knee in comparison to the shoulder, as pressure increased, so did severity of DJD. Moreover, DJD increased at a faster rate at the knee than at the shoulder, as evidenced by the steeper tendency line of the distribution of the data of the knee (slope=1.02), compared to that obtained for the shoulder (slope=0.45).

The stronger correlation between pressure and DJD at the knee joint could be due to the fact that hindlimbs are generally more heavily loaded with the animal's weight than the forelimbs during locomotion in the majority of primate species, with the main exception being the suspensory species (e.g., Reynolds, 1985; Biewener, 1990; Demes et al., 1994; Larson, 1998; Schmitt, 1998). This could entail great levels of pressure that could induce more severe expressions of DJD. In fact, the knee was the joint exhibiting the highest average values of the later stages of joint degeneration (average eburnation knee=2.48, Table 6.1), which could be a consequence of the intense pressures exerted. The knee has associated structures that absorb shock (i.e. menisci and patella), which could delay the development of DJD (Palastanga et al., 1998). However, despite the adaptations present at the knee joint to deal with weight, significant increases in pressure would probably produce very intense loads that would be accompanied by higher levels of severe degeneration, reflected by the steeper correlation line between pressure and DJD at this joint than at the shoulder (slope of tendency line at shoulder=0.45; slope of tendency line at knee=1.02, Fig. 8.3 and 8.4).

The great range of pressures experienced at the shoulder joint entailed a more disperse distribution of the data in the representation of the correlation (Fig. 8.3), resulting in lower correlation coefficients than those obtained at the knee joint. The shoulder joint was not exclusively used for weight bearing and, therefore, it experienced lower load than the knee. The shoulder showed lower levels of expression of the later stages of DJD than the knee (average eburnation at shoulder=0.31; average eburnation at knee=2.48, Table 6.1). Nevertheless, changes in body mass came with great differences in pressure at the shoulder (Table 8.2). Therefore, despite showing weaker correlations between DJD and pressure than those of the knee joint, the shoulder was highly susceptible to changes in body mass, resulting in the slightly stronger correlations with body mass than seen in the knee (Table 8.1). In other words, the fact that the shoulder joint is less adapted for this single purpose (i.e. weight bearing) makes it more susceptible to changes in body mass, even though the pressures born entailed lesser loading than that experienced at the knee.

The use of pressures in order to understand DJD expression in particular joints should be more accurate than the use of body mass. This is due to the potential uneven distribution of weight between the forelimb and hindlimb during primate locomotion (e.g., Reynolds, 1985; Ishida et al., 1990; Demes et al., 1994; Larson, 1998; Schmitt, 1998). Moreover, the analyses of pressures considered the functional role of the joint, by dealing with joint dimensions and the pressures they experience, reflecting the functional purpose of a joint. However, in order to confidently use pressures instead of body mass, further examination is required involving the elbow instead of the shoulder joint, which was not possible in this study due to methodological limitations that were already described (chapter 5). Moreover, the calculation of pressure was only approximate, using precise measurements of joint sizes but inferred forces that were attributed arbitrarily using a theoretical model that was based on published information from previous research (e.g., Reynolds, 1985; Schmitt, 1998; Schmitt and Hanna, 2004) (presented in chapter 5). Therefore, this information should only be treated as a starting point and further research needs to be done in order to obtain robust models that provide fully reliable results.

8.1.4.3 Sex and DJD expression

Biological sex was treated as another potential causal factor for DJD, especially as a source of differences in body mass in some primate species that are highly sexually dimorphic, as suggested by DeRousseau (1988). She reported differences in prevalence of osteoarthritis (OA) between males and females of rhesus macaques (*Macaca mulatta*) but none among gibbons (*Hylobates lar*), suggesting that it was due to the greater sexual dimorphism of the macaques in comparison with the gibbons. However, very few differences in DJD expression were obtained in the present study, with the only differences found at the shoulder and elbow joints (Table 8.4). These differences mainly concerned osteophytosis and, thus, would probably only be relevant in the first stages of development of DJD and not particularly informative in more advanced stages of degeneration. Therefore, DJD expression was unlikely to be significantly influenced by sex and thus, DJD should not be expected to be more or less severe in males or females of the present sample of non-human primates.

The search for differences between males and females for the different sub-samples treated independently only showed differences at the shoulder and elbow joint for among the quadrupeds and the suspensory primates (Table 8.5). Suspensory primates only exhibited significant differences between males and females for the combined values of DJD at the elbow, but not for any of the independent indicators of DJD. Suspensory primates did not particularly differ in body size between males and females, with the exception of the orangutans (Smith and Jungers, 1997). Therefore, the differences in this group could either be a reflection of differences among the orangutans, potentially biasing the results with their greater sexual dimorphism, or attributed to other factors. For the quadrupeds differences were found for the combined values of DJD at the shoulder joint, and for osteophytosis and the combined values of DJD at the elbow joint. Similarly to the suspensory primates, the differences were few. Although some of these species are sexually dimorphic (Smith and Jungers, 1997), there was great variability of DJD expression among these taxa (chapter 7) and the differences observed here could be a result of other factors.

It appears unlikely that the differences observed between males and females were a result of differing body size, as many of the species considered in the sub-samples exhibiting differences were not particularly dimorphic (Smith and Jungers, 1997). The most dimorphic sub-sample, the knuckle-walkers (Smith and Jungers, 1997), did not show any differences in DJD prevalence between males and females. Therefore, it was possible to state that sex was not informative enough in terms of DJD development and, thus, it was unlikely to be an important causal factor of joint degeneration among the analysed list of taxa.

8.2 Relationship between age and DJD

Some of the differences in severity of DJD observed in chapter 6 could be a reflection of differences in longevity among species (Harvey and Clutton-Brock, 1985). DJD has long been associated to advanced age in humans (e.g., Rogers et al., 1987; Hukuda et al., 2000; Waldron, 2008; Aufderheide and Rodríguez-Martín, 2011). In non-human primates, DJD seemed to be present during the first stages of adulthood and at old ages, going through a period of stasis in the middle adulthood (DeRousseau, 1988; Nakai, 2003). However, possibly as a result of the few osteological collections with individuals of known age, there have not been many studies that specifically assessed the role of age in DJD development in non-human primates, despite having been considered in the studies of well-known populations (e.g., DeRousseau, 1985; Jurmain, 1989; Lovell, 1990; Nakai, 2003).

The relationship between age and DJD expression was further analysed in this thesis at the level of the limbs (Equations 8.1 and 8.2) for the whole sample of primates and for the different sub-samples according to locomotor adaptation. Correlations between relative age (obtained as explained in chapter 5) and DJD development were conducted by means of non-parametric correlation tests (Spearman's ρ) accompanied by graphic representations (scatterplots).

8.2.1 *Relative age and severity of DJD*

Relative age and DJD expression for the whole sample correlated significantly at the forelimb and the hindlimb ($\rho = 0.238$; $p<0.001$ and $\rho = 0.163$; $p<0.001$, respectively), exhibiting an increase in DJD expression at advanced stages of the individuals' lives (Fig. 8.5 and 8.6). However, the correlation coefficients were low.

Correlations between relative age and DJD at individual joints of the limbs were all significant (Table 8.6). The coefficients obtained for the forelimb joints were similar ($\rho=0.203$ at shoulder; $\rho=0.209$ at elbow; $\rho=0.197$ at wrist), whereas the coefficients at the hindlimb joints were more variable. The correlation between relative age and DJD at the hip was the strongest of the compartment ($\rho=0.202$), reaching similar values to those at the shoulder joint ($\rho=0.203$). The knee and ankle joints showed substantially lower correlation coefficients ($\rho=0.111$ at knee; $\rho=0.092$ at ankle).

Table 8.6 Correlation coefficients between relative age and severity of DJD for the forelimb and hindlimb as well as for the independent joints of each of these compartments

Dependent variable	Spearman's rho (ρ)	p-value
Combined DJD at the forelimb	0.238	< 0.001
Combined DJD at the hindlimb	0.163	< 0.001
Shoulder	0.203	< 0.001
Elbow	0.209	< 0.001
Wrist	0.197	< 0.001
Hip	0.202	< 0.001
Knee	0.111	0.006
Ankle	0.092	0.023

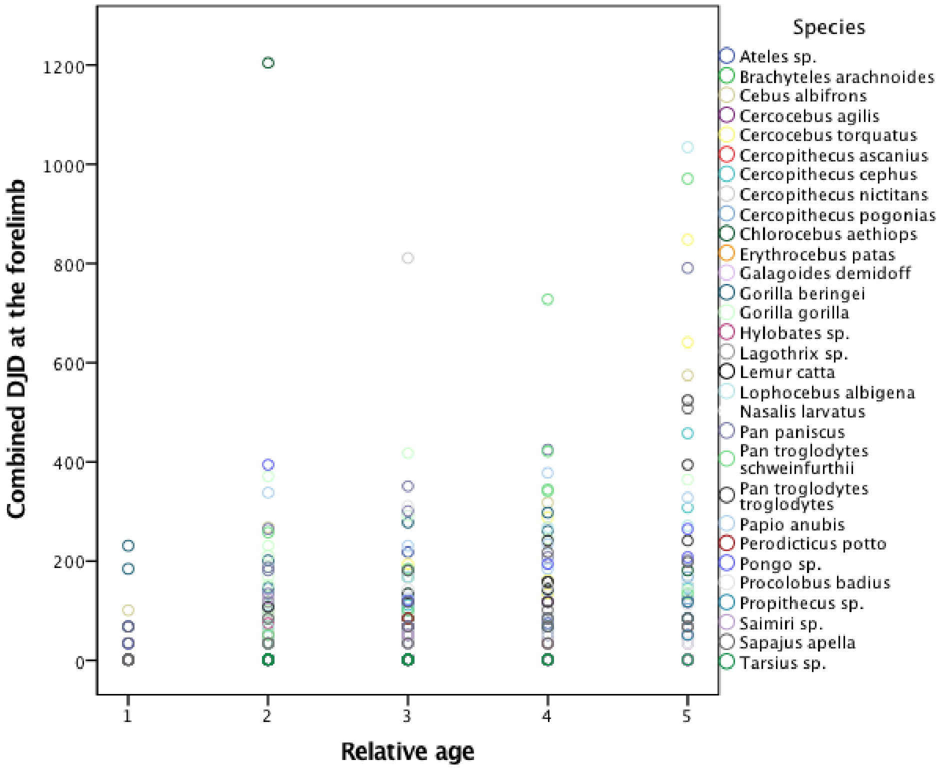

Figure 8.5 Scatterplot relating relative age and combined DJD at the forelimb, where an increase of DJD is shown towards the later stages of life (stage 4 and particularly stage 5)

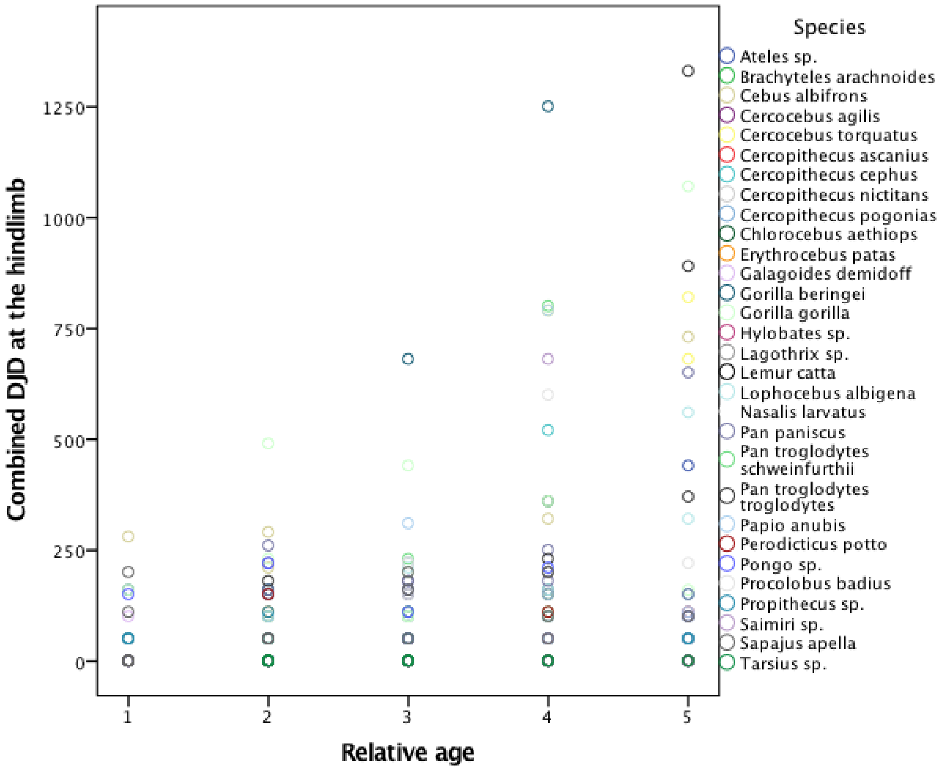

Figure 8.6 Scatterplot relating relative age and combined DJD at the hindlimb where an increase of DJD is shown towards the later stages of life (stages 4 and 5)

The different sub-samples showed several significant but highly variable correlations between relative age and severity of DJD (Table 8.7). The quadrupeds and knuckle-walkers presented the highest correlation coefficients between relative age and DJD for both forelimb and hindlimb (quadrupeds: forelimb ρ= 0.419; p<0.001; hindlimb ρ= 0.283; p<0.001; knuckle-walkers: forelimb ρ= 0.454; p<0.001; hindlimb ρ= 0.319; p=0.001). The leapers did not show significant correlations for either limbs. The suspensory primates only showed significant correlations at the hindlimb (ρ= 0.238; p=0.017) and the VCL and slow arboreal quadrupeds at the forelimb (ρ= 0.226; p=0.017).

Table 8.7. Correlation coefficients between relative age and severity of DJD for the forelimb and hindlimb for each of the sub-samples of primates according to locomotor adaptation. Significant results are in bold.

Locomotor adaptation	**Forelimb**		**Hindlimb**	
	Spearman's rho (ρ)	**p-value**	**Spearman's rho (ρ)**	**p-value**
VCL and slow arboreal quadrupeds	0.336	**0.017**	-0.036	0.802
Leapers	0.068	0.530	0.071	0.513
Quadrupeds	0.419	**< 0.001**	0.283	**< 0.001**
Knuckle-walkers	0.454	**< 0.001**	0.319	**0.001**
Suspensory	0.113	0.188	0.238	**0.017**

8.2.2 Discussion of the results

This section deals with two general questions related to the role of age: 1) whether or not older individuals exhibited more severe DJD at their limb joints, and 2) whether or not the sub-samples including the longest-lived taxa exhibit a stronger relationship between relative age and DJD expression.

DJD, as a degenerative process, implies some cumulative effect over time, often being associated with older ages. Previous research on DJD has found higher prevalence in older individuals for both human and non-human primates (e.g., DeRousseau, 1985; Rogers et al., 1987; Nakai, 2003; Waldron, 2008; Aufderheide and Rodríguez-Martín, 2011). As a result, DJD would be expected to appear, or at least to develop further, towards the end of an individual's life. For those species that live longer, adults reach more advanced ages and thus their joints could get comparatively older. Hence, stronger correlations between relative age and DJD were expected for those groups of primates that live longer.

The first assumption, relating older stages of life with more severe DJD expression, was partially supported by the results. Relative age and DJD correlated significantly and positively at both limbs but with low correlation coefficients (forelimb $\rho = 0.238$; hindlimb $\rho = 0.163$), suggesting that DJD expression increased in age (Fig. 8.5 and 8.6). The correlation was stronger for the forelimb than the hindlimb, suggesting that in general terms age-related degeneration would be found in greater proportion at the forelimb than at the hindlimb. However, DJD found at both limbs could only be partially explained by age: the low correlation coefficients strongly supported that other factors contributed to the expression of DJD.

The positive correlations between DJD and age at the limbs, despite being significant, were not constant (i.e. linear). The effect that age had on the joints was not progressive over time. The scatterplots showed that the expression of DJD was stable during the first stages of adulthood and it was only in the latest stages (stage 5 at the forelimb and 4 and 5 at the hindlimb) that severity of DJD increased (Fig. 8.5 and 8.6). This suggested that some degeneration took place at the earlier stages of adulthood, possibly even during adolescence, and the only obvious increase in severity occurred after some time of stable DJD expression, following a trend previously described for non-human primates by other researchers (DeRousseau, 1985; Nakai, 2003).

Age, consequently, did not seem to be related with the early development of DJD observed during the younger stages of the life of primates. It seemed likely that in the first years of adulthood, possibly even before, DJD was developed as a result of other factors, some of them mechanically related, as seen with the closer correlations between body mass and DJD for the earlier stages of the disease expression at the forelimb (section 8.1.4), or locomotor behaviour (chapter 7). Early DJD expression was followed by a period of time of little change, during which DJD severity may increase at a slow rate until the individual reached older ages, when severity of DJD significantly increased. This increase was possibly a result of the combined effect of the mechanical input, which is present throughout a primate's life, and skeletal ageing processes. However, the reason behind such ageing processes cannot be answered with the present data.

The correlation between age and DJD expression was different for the different joints considered (Table 8.6). The forelimb joints showed similar correlation coefficients (shoulder ρ=0.203; elbow ρ=0.209; wrist ρ=0.197), suggesting that DJD at these joints was linked to ageing processes to a similar extent. However, in the hindlimb the hip joint showed the highest correlation coefficient of all the joints (hip ρ=0.202; knee ρ=0.111; ankle ρ=0.092). Therefore, compared to the knee and the ankle, DJD expression at the hip joint was highly affected by age and ageing processes, making DJD development at the hip a better indicator of ageing than the other joints of this limb. However, all the correlations showed low coefficients suggesting that DJD expression was likely to be determined by age but in combination with other factors.

It can therefore be concluded that relative age plays a significant role in DJD development, especially at older ages and to different extents for each joint. However, the correlations between age and DJD varied across the five sub-samples considered (Table 8.7). The sub-samples containing shorter-lived taxa (i.e. leapers and VCL and slow arboreal quadrupeds) exhibited either non-significant correlations or rather weak ones. In contrast, quadrupeds and the knuckle-walkers, consisting of longer-lived taxa (Harvey and Clutton-Brock, 1985), showed the strongest correlations between age and DJD. These results suggested that primates that live longer lives were likely to exhibit stronger correlations between relative age and DJD expression, experiencing a greater effect of ageing processes on their joints. However, the suspensory primates are as long-lived as the quadrupeds or even the knuckle-walkers in the case of the suspensory apes, and the correlations between age and DJD expression were non-significant in the case of the forelimb and significant but not very strong for the hindlimb (ρ=0.238). This suggested that, while taxa that live longer may have greater chances of developing more severe expressions of DJD at later stages of their lives (as seen among the quadrupeds and knuckle-walkers), this was not true for all the long-lived species considered (i.e. suspensory primates). Therefore, the effect of age was probably dependent on other factors related to DJD expressions, and not only depended on how long a primate lives.

The assessment of relative age among different sub-samples of primates was sometimes challenging from a methodological point of view. The post-canine dentition of strepsirhines and haplorhines was different in size and shape. This made the assessment of molar wear and dentine exposure complicated, especially among the strepsirhine sample, often resulting in missing information. Therefore, the low or non-existing correlations between age and DJD in the mainly strepsirhine group could possibly be a result of small sample size, combined with the low levels of DJD expression in leapers and VCL and slow arboreal quadrupeds. As a result, more accurate dental wear information among these primates should be implemented in order to confirm or challenge the present results.

8.3 Summary and conclusions

This chapter dealt with two intrinsic potential causal factors of DJD: body size and age. DJD development was significantly correlated with both of these factors, but the rather low correlation coefficients suggested that other factors are likely to be involved in joint degeneration.

Few significant differences of DJD expression were found between males and females, and these were unlikely to be associated to differences in body mass as a result of sexual dimorphism. Nevertheless, there were differences in the analyses of DJD of the limbs in relation to body mass, where the forelimb was more susceptible to body mass variation than the hindlimb, with good correlations between the variables for the shoulder, elbow and wrist. This was related to the early and gradual expression of DJD at this limb (in accordance with the results obtained in chapter 6). In contrast, the hindlimb showed slightly weaker overall correlations. The knee was the main contributor to such correlations. In fact, when pressure and DJD were considered at the shoulder and knee, the knee showed the strongest associations, evidencing its specialised role as a weight-bearing joint by exhibiting a lower range of pressures born but high severity expressions of DJD associated to great levels of loading.

Relative age was significantly related to DJD development. Confirming previous results of other researchers (DeRousseau, 1985; Nakai, 2003), DJD only increased at later ages but this factor did not seem to affect all groups of primates in the same way. Some of the sub-samples considered did not exhibit significant correlations between age and DJD or, when significant, they were very weak for some groups. However, this could be due to methodological challenges.

The results obtained suggested a closer relationship between body mass and the first stages of DJD expression, likely to be related to mechanical stress on the joints. In contrast, relative age was associated to more extreme expressions of DJD, increasing severity of expressions at the later stages of an individual's life.

These results also evidenced the heterogeneity of DJD development and associated causal factors, not only across taxa but also within the primate skeleton. This was particularly obvious at the level of the hindlimb where, of the two factors considered in this chapter, degeneration at the knee joint seemed to respond mainly to loading (with high correlations between pressure and DJD), whereas degeneration at the hip seemed to be more related to ageing.

In summary, the results obtained in this chapter confirmed the partial effect of body mass and age in DJD expression, probably related to different stages of the disease. The following chapter consists of a multivariate approach to DJD in non-human primates testing the effect of all the factors considered in chapters 7 and 8 (locomotion, body mass and age) in order to observe the differential contribution of each of these variables and their potential combined effects on DJD expression.

CHAPTER 9: MODELS OF DJD DEVELOPMENT AT THE LIMBS OF QUADRUPEDS AND SUSPENSORY PRIMATES

Previous chapters discussed prevalence of DJD across the primate sample and a few of its potential causes. The distribution of DJD in the primate skeleton was assessed, reaching a generalised primate pattern of DJD distribution but also observing deviations from this pattern for some groups. The differences observed were suggested to be a result of differences in locomotor behaviour, body mass and/or longevity, which were then assessed individually as potential causal factors of DJD in an exploratory phase in search for patterns. Thus, different locomotor adaptations, as well as different locomotor strategies (concerning differences in habitat and support use for some groups of primates, and differences in speed in other groups) were studied as potential drivers of DJD. Body mass, pressure at two of the main weight-bearing joints and relative age were also assessed as potential causal factors with DJD expression and could be involved in joint degeneration.

All the results presented up to this point suggested that DJD is a multifactorial phenomenon and all the variables studied contributed to DJD variability. However, the effect of each of the factors considered was variable and often partial, depending on the group of primates and the body compartment analysed. In fact, none of these variables seemed to fully reflect the development of DJD and the variability in severity observed between and within groups.

In this chapter all the previously analysed factors are brought together in a set of multivariate analyses to better and more fully explain DJD distribution in the limbs of two groups of primates. The relationship between all the different variables as potential drivers of DJD is evaluated by means of statistical models. The main goal was to assess which of these factors more heavily contribute towards DJD expression and how these factors may interact among them, resulting in expression of DJD. If good models are obtained, DJD predictions could be possible by assessing the variables tested (age, body mass and locomotor behaviour). Such predictions could have great implications for the study of the fossil record as, through robust models, by assessing DJD on a primate skeleton, inferences could potentially be made on the type of locomotor behaviour performed, body mass and even relative age of the individual considered, providing great insight on its eco-morphological characteristics. This knowledge could also be applied to improve living conditions of captive primates.

Generalised linear models (GLM), a regression-type set of models, were used. Due to the nature of the response variable (i.e. combined DJD severity), the models used a generalised algorithm with an inverse link function, assuming a Gamma distribution of the data after the necessary transformations of the original data (chapter 5). The variables included in these models were: transformed combined DJD at the forelimb and hindlimb as response variables (i.e. dependent variables) and relative age, locomotor strategy and inferred body mass as predicting variables (i.e. independent variables). Due to the non-parametric nature of relative age, sex and locomotor strategy, these were included in the model as factors, whereas body mass had to be considered a covariate as a result of its scalar nature.

Wald's inference statistic was used because this method is based on an asymptotic normality distribution. Therefore, under the H_0: $\beta = 0$;

$$\left(\frac{b_j}{se(b_j)}\right)^2$$

has a χ_1^2 distribution for large samples (Myers et al., 2012) (Fig. 9.1), where, β = predicted value, b = observed value and *se* = standard error. Standardised deviance residuals were used, as Pierce and Schafer (1986) suggested that deviance residuals were the best fitted for models based on the exponential distribution family (in Myers et al., 2012), such as the Gamma-distribution based models used in this thesis.

These models were run on two sub-samples: the quadrupeds and the suspensory primates (sample size: N=294 and N=114 respectively), and the compartments considered were the limbs, in order to be consistent with the analyses on chapter 8 for body mass and age that were also based on these compartments. These groups were selected as the best examples of the two locomotor strategies tested in chapter 7: speed and support use. The quadrupeds were chosen for two reasons. Firstly, they are the group of primates that showed the greatest variability in terms of habitat and support use of the groups considered in this thesis. Secondly, they were chosen over the knuckle-walkers because they displayed a closer relationship between support use and DJD development, explaining most of the differences observed among species by means of habitat and support use differentiation. The suspensory primates were selected because they exhibited the highest levels of DJD average severity at the limbs, compared to the leapers, the VCL and slow arboreal quadrupeds (forelimb DJD of VCL and slow arboreal quadrupeds=8; leapers=10.51; suspensory=32.22 and hindlimb DJD of VCL and slow arboreal quadrupeds=13.70; leapers=16.89; suspensory=36.58). Moreover, suspensory primates display a forelimb-reliant type of locomotion, which could modify the interactions between factors, resulting from mechanical differences. Post-hoc tests were run on the estimated marginal means, as detailed in chapter 5.

Figure 9.1 Chi-square distribution graphs for the probability density function of χ_1^2, with the independent variable depicted in the x-axis and the density of fk(x) in the y-axis (modified from Lane et al.. 2014)

9.1 Generalised linear models for DJD on the limbs of quadrupedal primates

Quadrupedal primates exhibited species differences in the distribution and severity of DJD at both forelimbs and hindlimbs. Some of these differences seemed to be related to differences in habitat use, and for the earlier indicators of DJD (osteophytosis and porosity) most of the differences found were likely to respond to differences in the type of support used (Table 7.7). However, not all the differences were explained by support use. Relative age correlated significantly with severity of DJD (forelimb ρ=0.419; p<0.001; hindlimb ρ=0.283; p<0.001). Differences in body mass were also likely to account for some of these differences in DJD, as significant correlations were found between body mass and overall limb DJD for primates in general (forelimb ρ=0.444; p<0.001; hindlimb ρ=0.326; p=<0.001). However, when these correlations were tested for only the quadrupeds, the correlation between body mass and DJD was non-significant at the hindlimb (ρ=0.09; p=0.134) and significant but not with a very strong correlation at the forelimb (ρ=0.211; p=<0.001).

All the variables considered up until this point appear to have an important role in DJD development. However, none of them were sufficiently strong on their own as a sole causal factor of DJD. Each of these variables could explain some of the variability observed but none of them could be appointed as the main cause of joint degeneration when treated independently. Nonetheless, before these variables were considered together some relationships among them need to be considered.

Observational studies of sympatric species reported that primates of different body mass tend to use supports of certain diameters and thus of different deformability. Several researchers reported that larger primates tend to use boughs or big branches during locomotion, whereas the smallest primates tend to use twigs or small branches (Fleagle and Mittermeier. 1980; Gebo and Chapman. 1995a). However, some exceptions have been reported. For instance, large-bodied spider monkey (*Ateles paniscus*) used small supports through the adoption of a suspensory behaviour. Among quadrupeds the relationship between body mass and support size was not always clear. Larger species of guenons and colobines did not always use bigger supports than the smaller ones (McGraw. 1998a). Despite this, the possible relationship between support diameter (directly linked to deformability) and body mass had to be considered here as a potential interaction that could entail joint effects in the models.

A clear relationship was observed between body mass and support use for the individuals of this sample (Fig. 9.2 and 9.3). A strong and significant negative correlation existed between these two variables ($\rho=-0.847$; $p=<0.001$). For this reason the interactive effect of support deformability and support use was taken into account. Hence, the models run included as predictors: age, support deformability, body mass and support deformability * body mass interaction.

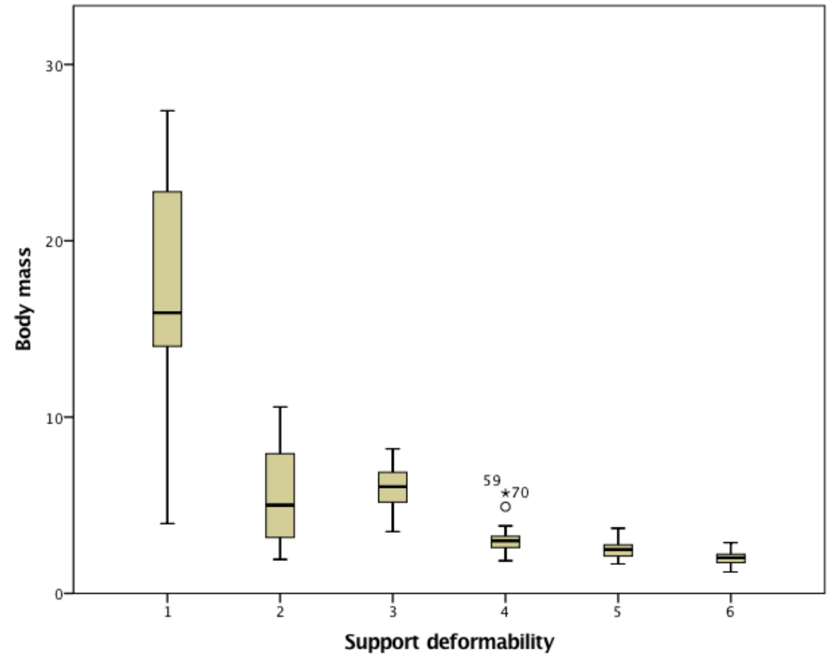

Figure 9.2 Boxplot depicting the relationship between body mass in Kg (Y axis) and support deformability (X axis) for the quadrupedal primates

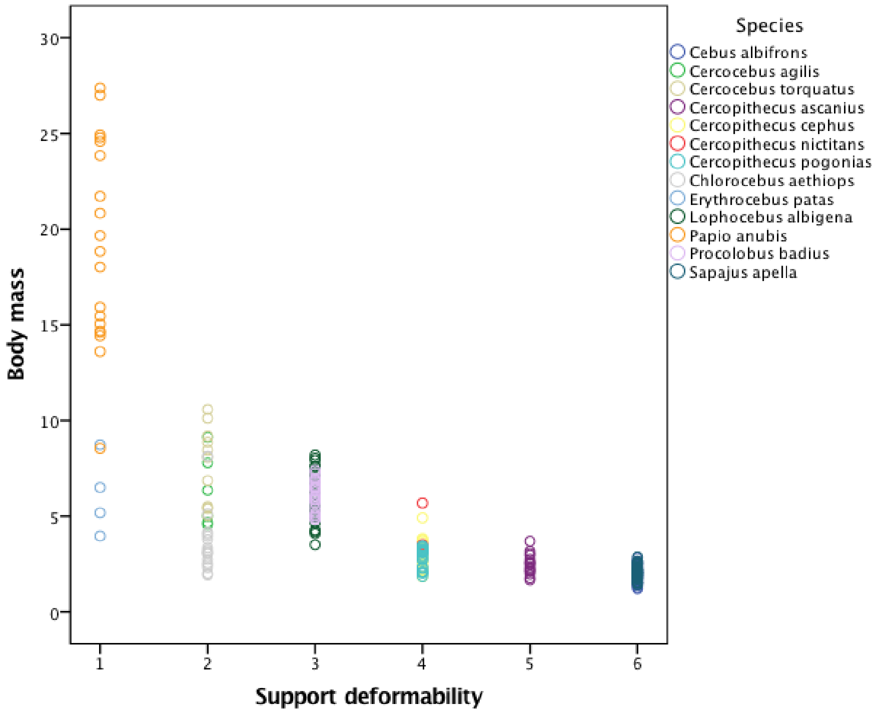

Figure 9.3 Scatterplot depicting the relationship between body mass in Kg (Y axis) and support deformability (X axis) for the quadrupedal primates with cases labelled by species in order to see the variability in body mass for each of the species considered

9.1.1 The forelimb

The model obtained for the forelimb of quadrupeds was overall significant and had good values for the indicators of goodness of fit (i.e. low values) (Table 9.1). The tests of the model effects showed that age and support deformability contributed significantly towards DJD variability at the forelimb of the quadrupeds (χ^2=34.52; p<0.001 and χ^2=16.76; p=0.005. respectively). The interaction between body mass and support deformability also showed a significant contribution to the response variable (χ^2=22.03; p=0.001), despite the non-significant effect of body mass on its own (Table 9.2). Boxplots for DJD at forelimb according to support use clustered by age showed a general decreasing tendency along the x-axis (degree of support deformability) but an increasing tendency according to age within each level of support deformability (Fig. 9.4). Level 5 of support deformability was under-represented, showing great contrast with level 6.

Table 9.1 Summary of the model for the forelimb of quadrupeds showing three different indicators of goodness of fit, the overall statistic (likelihood ratio X2) and overall p-value

GLM forelimb of quadrupeds		**Value**
Goodness of Fit indicators	Akaike's information criterion (AIC)	416.41
	Bayesian information criterion (BIC)	475.30
	Log Likelihood * (-2)	382.41
Likelihood ratio χ^2		84.10
Significance (p-value)		<0.001

Table 9.2 Summary of the tests of model effects for the forelimb of quadrupeds

Forelimb quadrupeds		
Term of the equation (predictors and intercept)	**Wald χ^2**	**p-value**
Intercept	7.74	0.005
Age	34.52	<0.001
Support deformability	16.76	0.005
Body mass	0.02	0.891
Body mass * support deformability	20.72	0.001

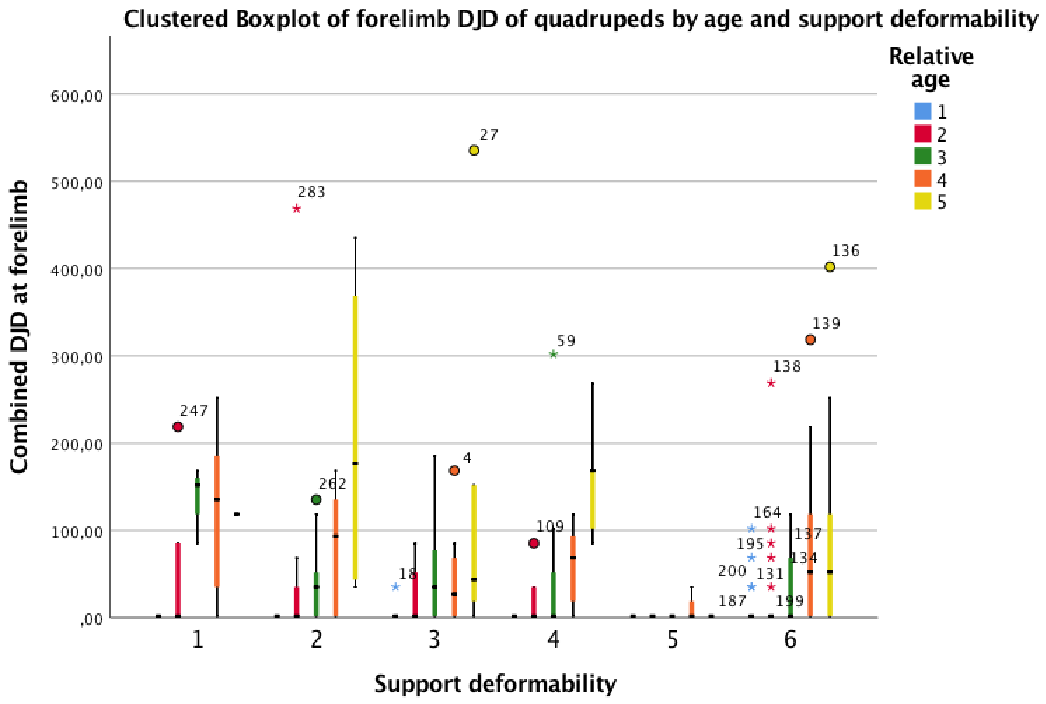

Figure 9.4 Clustered boxplot depicting the relationship between combined DJD at the forelimb (Y axis) and support deformability (X axis) for the quadrupedal primates, using relative age category as the clustering factor

Estimated marginal means (EMM) were calculated for age and support deformability (Tables 9.3 and 9.5) and paired comparisons were done by repeated contrast. The tests for age were overall significant (χ^2=34.52; p<0.001) but the only comparison showing significant differences was between age categories 1 and 2 (Table 9.4). Concerning the EMM for support deformability, the tests were also overall significant (χ^2=20.55; p=0.001) and the only paired comparison showing significant differences was between levels 5 and 6 of support deformability (Table 9.6). The comparison between levels 1 and 2 reached near-significance.

Table 9.3 EMM for Age at the forelimb of quadrupeds

Age category	Mean (EMM)	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
Level 1	2.23	0.53	1.19	3.27
Level 2	1.53	0.46	0.62	2.44
Level 3	1.26	0.46	0.37	2.16
Level 4	1.06	0.46	0.16	1.96
Level 5	0.94	0.45	0.05	1.83

Table 9.4 Paired comparisons (by repeated contrast) of the different age levels EMM at the forelimb of quadrupeds (significant differences in bold)

Age Repeated Contrast	Contrast Estimate	Std. Error	Wald Chi-Square	Sig.
Level 1 vs. Level 2	0.70	0.28	6.43	**0.011**
Level 2 vs. Level 3	0.27	0.15	3.00	0.083
Level 3 vs. Level 4	0.20	0.13	2.59	0.108
Level 4 vs. Level 5	0.12	0.12	1.04	0.307

Table 9.5 EMM for Support deformability at the forelimb of quadrupeds

Support deformability	Mean (EMM)	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
Level 1	0.56	0.29	0.00	1.12
Level 2	1.19	0.18	0.84	1.55
Level 3	1.26	0.22	0.83	1.69
Level 4	0.83	0.21	0.43	1.24
Level 5	5.26	2.63	0.11	10.41
Level 6	-0.68	0.49	-1.65	0.28

Table 9.6 Paired comparisons (by repeated contrast) of the different support use levels EMM at the forelimb of quadrupeds (significant differences in bold)

Support deformability Repeated Contrast	Contrast Estimate	Std. Error	Wald Chi-Square	Sig.
Level 1 vs. Level 2	-0.64	0.33	3.64	0.06
Level 2 vs. Level 3	-0.07	0.28	0.06	0.82
Level 3 vs. Level 4	0.43	0.29	2.17	0.14
Level 4 vs. Level 5	-4.43	2.63	2.84	0.09
Level 5 vs. Level 6	5.94	2.66	4.98	**0.03**

The representation of the observed against the predicted values of the model (Fig. 9.5) closely followed the linear function built by the model. The lower values were more distant from the tendency line, showing a decreased fit of the model for lower values than for medium or higher ones. The distribution of the residuals was far from optimal. In strong models the distribution of the residuals should be random obtaining a cloud of points around the zero. This was not the case in the models obtained for DJD at the forelimb, where a clear trend in the data was observed, suggesting a bias in the residuals (Fig. 9.5). Consequently, the parameter estimates were inconclusive and were not included here but can be found in appendix 2.

9.1.2 The hindlimb

The model obtained for the hindlimb was overall significant with good fitness (Table 9.7). The model effect tests showed a significant contribution to the response variable of age (χ^2=23.43; p<0.001), support deformability (χ^2=12.71; p=0.026) and the interaction between support compliance and body mass (χ^2=11.44; p=0.043). The effect of inferred body mass without the interaction was non-significant (Table 9.8). The clustered boxplots for the hindlimb showed a relatively stable expression of DJD across categories of support deformability but exhibited variability in expression along age within each level of support deformability (Fig. 9.6).

Table 9.7 Summary of the model for the hindlimb of quadrupeds showing three different indicators of goodness of fit, the overall statistic (likelihood ratio X2) and overall p-value

GLM hindlimb of quadrupeds		**Value**
Goodness of Fit indicators	Akaike's information criterion (AIC)	384.81
	Bayesian information criterion (BIC)	443.70
	Log Likelihood * (-2)	350.81
Likelihood ratio χ^2		46.00
Significance (p-value)		<0.001

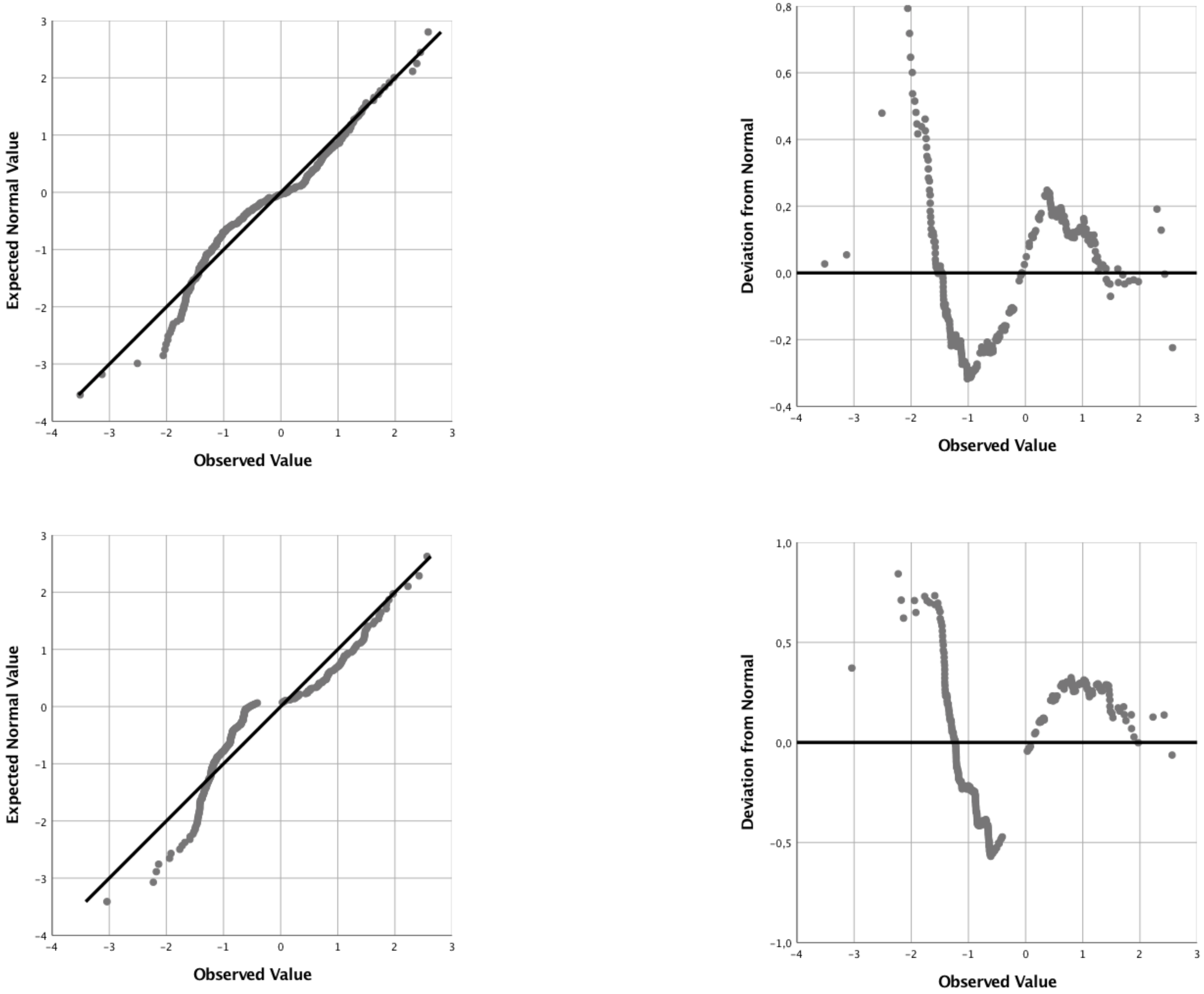

Figure 9.5 Graphic depiction of the fitness of the models and distribution of the residuals for quadrupeds. Top graphs pertain to the forelimb, bottom graphs pertain to the hindlimb. The left graphs are a representation of the fitted values (observed vs. predicted) and right graphs represent the distribution of the residuals in relation to the observed values)

Table 9.8 Summary of the tests of model effects for the hindlimb of quadrupeds

Hindlimb quadrupeds		
Term of the equation (predictors and intercept)	**Wald χ^2**	**p-value**
Intercept	15.78	<0.001
Age	23.43	<0.001
Support deformability	12.71	0.026
Body mass	0.594	0.441
Body mass * support deformability	11.44	0.043

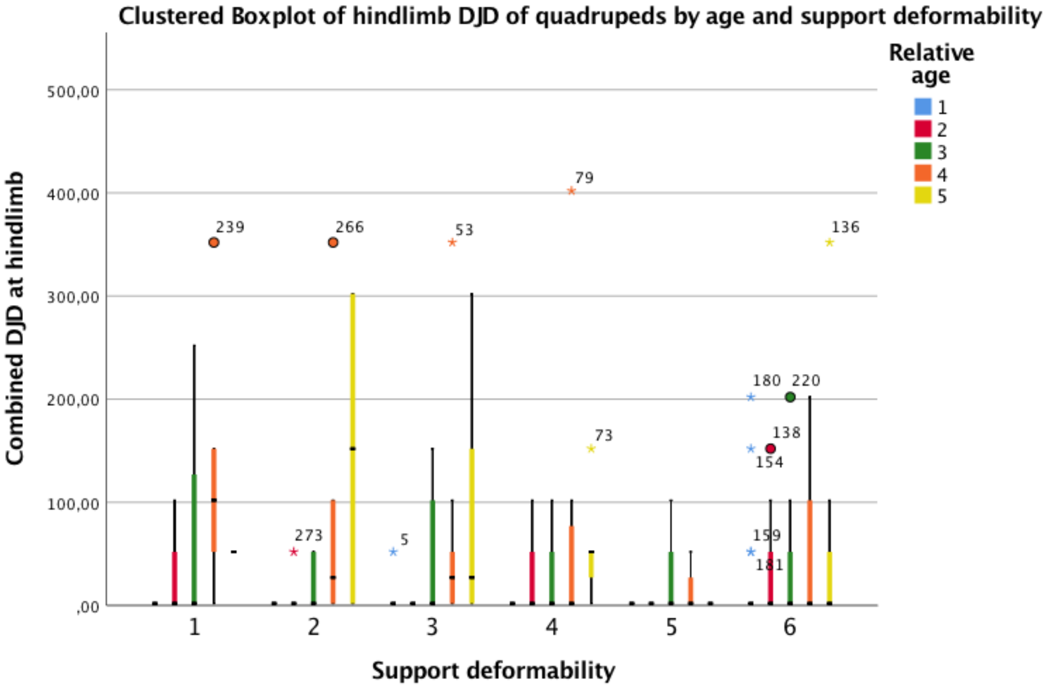

Figure 9.6 Clustered boxplots depicting the relationship between combined DJD at the hindlimb (Y axis) and support deformability (X axis) for the quadrupedal primates, using relative age category as the clustering factor

EMM were calculated for age and support deformability (Tables 9.9 and 9.11), as both have a significant effect on the response variable (Table 9.8). The paired comparisons with repeated contrast were overall significant for age (χ^2=23.43; p<0.001) but not for support deformability (χ^2=7.52; p=0.185). As a result, only the paired comparisons for age are meaningful and thus presented here. The only significant differences in EMM for the different levels of age were for the comparison between levels 2 and 3 (Table 9.10).

Table 9.9 EMM for age at the hindlimb of quadrupeds

Age category	Mean (EMM)	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
Level 1	1.76	0.36	1.05	2.48
Level 2	1.38	0.29	0.81	1.94
Level 3	0.91	0.26	0.40	1.42
Level 4	0.78	0.27	0.25	1.31
Level 5	0.72	0.28	0.17	1.26

Table 9.10 Paired comparisons (by repeated contrast) of the different age levels EMM at the hindlimb of quadrupeds (significant differences in bold)

Age Repeated Contrast	Contrast Estimate	Std. Error	Wald Chi-Square	Sig.
Level 1 vs. Level 2	0.39	0.30	1.71	0.191
Level 2 vs. Level 3	0.47	0.19	6.31	**0.012**
Level 3 vs. Level 4	0.13	0.15	0.70	0.402
Level 4 vs. Level 5	0.06	0.16	0.17	0.685

Table 9.11 EMM for Support deformability at the hindlimb of quadrupeds (note that the tests were not overall significant and thus these means are just for guidance)

Support deformability	Mean (EMM)	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
Level 1	0.73	0.40	-0.05	1.50
Level 2	1.51	0.26	1.00	2.01
Level 3	1.23	0.26	0.73	1.74
Level 4	2.03	0.40	1.26	2.81
Level 5	0.17	1.14	-2.06	2.40
Level 6	1.00	0.76	-0.50	2.49

The distributions of the fitted values and the residuals was similar to that obtained for the forelimb (Fig. 9.5). The distribution of predicted and observed values was not too far from the linear resulting functions of the model, also showing a reduced fit for the lower values. However, the distribution of the residuals followed a clear trend instead of the expected random distribution that would entail a cloud of points. Parameter estimates can be found in appendix 2.

9.1.3 Discussion of the GLM on the limbs of quadrupedal primates

The models obtained for the forelimb and the hindlimb of quadrupedal primates were significant. Therefore, the variables included in each of the models could explain the variability of the response variable: combined DJD. The fitness of the models was good, with low values of the Akaike's and Bayesian information criteria as well as the log likelihood values (Table 9.1 and 9.7). The distribution of the predicted and observed values was close to the linear function that resulted from each of the models run, despite the slightly weaker fit for the lower values. Consequently, the relationship between variables was sufficiently accurate to report the link between them.

The distribution of the residuals should be improved. A strong model would show a random distribution of the residuals, creating a cloud of points in a plot relating the observed values and the corresponding residuals. This was not the case of the models obtained for DJD at the limbs of quadrupeds. The residual data points followed a clear trend in all the models presented here (Fig. 9.5), notably decreasing the prediction power of the models. The main implication is that these models **should not be used for predictions**, as they are not sufficiently robust for this purpose. The parameter estimates obtained (appendix 2) would not necessarily provide precise distances between cases. Consequently, these models are sufficiently strong to be used as exploratory tools, revealing the relationship between the variables considered, but are not good as predictive tools.

9.1.3.1 The forelimb

The model obtained for the forelimb showed a clear contribution towards DJD expression of age, support deformability and the interaction between support deformability and inferred body mass (Table 9.2). These results support the independent findings presented in previous chapters. Differences in the use of supports with different levels of compliance among quadrupeds explained a good proportion of the variability of DJD observed among species (Table 7.12) and relative age correlated significantly with DJD at the forelimb ($\rho=0.419$; $p<0.001$).

Differences in support use accurately reflected the variability of DJD for the earlier stages of the disease (i.e. osteophytosis and, less precisely, porosity), but did not seem to answer for the differences in eburnation, the more severe stage of joint degeneration. However, a pronounced increase in severity of DJD was observed in primates towards the later stages of an individual's life (Fig. 8.5). Age contributed significantly to an increase of severity of DJD that was already present, and therefore could be related to the development of eburnation. Consequently, support use (linked to support deformability) and age could potentially be complementary in terms of DJD, with the former being responsible for earlier stage degeneration and the latter possibly answering to an increase in severity of DJD already developed as a result of the interactions with the supports use. This relationship can also be observed in the clustered boxplots presented (Fig. 9.4), where a general decreasing tendency is observed with support deformability but within each level of support use, DJD increased with age. Thus, previously reported results and the graphic representations supported the fact that age and support deformability were somehow complementary, being the main contributing factors in DJD development at the forelimb, evidenced by their significant effects in the model, while other independent variables (i.e. body mass) did not seem to play a significant role on its own (Table 9.2).

The EMM and the corresponding repeated contrasts were overall significant for both age and support deformability. However, in neither of these cases were there significant differences for all the possible comparisons (Tables 9.4 and 9.6). In the case of age, the only significant differences found were between levels 1 and 2. Therefore, a distinction can be made between the youngest individuals and the rest of primates of this group, despite the increasing tendency in the data (Table 9.4; Fig. 9.4). The post-hoc tests for support deformability showed significant differences between the last levels of deformability (5 and 6) and near significant differences between the first ones (1 and 2) (Table 9.6). There was a distinction between the terrestrial primates and the semi-arboreal ones (with higher EMM for the semi-arboreal ones, supporting the discussion of chapter 7; Table 9.5). The other distinction was between generally arboreal primates (levels 2 through 5) and the arboreal ones moving on twigs and very thin branches (level 6), those that interact with the most deformable supports. However, this difference could be a result of under-representation of level 5 (Fig. 9.4) and should be considered with caution.

The the interaction between body mass and support use provided further nuance to the relationship between variables. In this case, body mass had a significant contribution towards forelimb DJD, in combination with support deformability (Table 9.2). This suggested that, although support use played a key role in DJD development, it was to some extent dependent on body mass. The strong correlation between support deformability and body mass (ρ=-0.847) indicated that these two variables were strongly related with each other but the significant effect shown by the model provided information on how the relationship between the two variables could affect DJD expression.

Every reaction force depends on an action force, according to the third of Newton's Laws (chapter 4). This was the key to understanding the relationship between body mass, which determined weight (i.e. action force), and support deformability, which modulated the SRF (i.e. reaction force), and how these conditioned DJD. In a neutral system of forces, the SRF would be equal in magnitude and have opposite direction to the force of weight. However, in the case of moving primates, several mechanisms are put in place, which modulate SRF.

A reduction of SRF was observed experimentally in primates moving on arboreal and terrestrial supports (Schmitt and Hanna, 2004; Franz et al., 2005), especially as the diameter of the arboreal supports decreased (Schmitt, 2003). This was probably partially achieved by the damping effect of a compliant support (Demes et al., 1999; Channon et al., 2011), but it was also likely to be achieved by an increase in limb yield during locomotion (Schmitt, 1999; Larney and Larson, 2004). The increase of limb yield is accomplished by an increase in the amount of flexion at the limb joints, which results in greater moment arms (i.e. load), as the perpendicular distance between the joints and the SRF increases (Biewener, 1990; Schmitt, 1998).

These forces and loads are vectors, the magnitude of which is initially dependant on the magnitude of the original action force. Thus, changes in the magnitude of the SRF as a result of changes in body mass have a direct effect on the intensity of the moments of force on the forelimb's joints (and load). This meant that, even if a reduction of the magnitude of the SRF was achieved by increasing flexion, there was still a great effect of body mass on the final magnitude of the SRF and, ultimately, of the moment arm which would be increased by the greater levels of flexion. In other words, for two monkeys of different body mass with the same degree of limb flexion moving on similar diameter branches (therefore, experiencing similar SRF and moment arms), the larger primate would bear greater absolute load because the action force (i.e. weight) was greater to begin with. Consequently, the amount of load born by a joint would be dependent on body mass even though it can be greatly shaped by the different strategies adopted.

Support deformability was of great importance in the determination of the SRF experienced by a moving quadruped. However, as the reduction of SRF was probably obtained by differences in the amount of limb flexion, the effect of body mass was great in the determination of final load acting on the joint. For this reason, the interaction between these two variables was key in the development of DJD at the forelimb, while body mass on its own was not significant. In fact, the main differences in the paired comparisons are between terrestrial and semi-arboreal quadrupeds and the arboreal primates in contrast with those moving on the most deformable supports (Table 9.6), so in groups that show great differences in limb flexion.

The isolated effect of body mass was countered by the adoption of different postures during locomotion. The bigger species were terrestrial or moved on large supports (Fig. 9.3), and performed a good alignment of the limb joints with the reaction force, reducing moment arms and load. However, among the arboreal quadrupeds the effect of body mass was more likely to be important but subtle, as a modulator of load. It probably contributed to the intensity of moment arms but only as a result of the reduction of forces that was experienced by moving on smaller, more deformable supports. Therefore, the effect of support use should not be understood without consideration of body mass, as in terms of forces, one depends on the other and was particularly important among arboreal quadrupeds as a result of the different levels of limb flexion adopted and the associated loads.

9.1.3.2 The hindlimb

The model obtained for the hindlimb was similar to that seen for the forelimb in terms of goodness of fit and their explanatory power. Age, support deformability and its interaction with body mass had a significant effect on DJD expression, while body mass on its own did not (Table 9.8). Age correlated significantly with DJD at the hindlimb even though it did not present a very high correlation coefficient ($\rho=0.283$. $p<0.001$). Body mass, however, exhibited a non-significant correlation with DJD at the hindlimb ($\rho=0.090$. $p=0.134$) and support use seemed to reflect variability in osteophytosis at the level of the hindlimb, but the differences observed in porosity and eburnation did not seem to be reflected by the use of supports of different levels of compliance (Table 7.12).

The effect of age was obvious for the forelimb and was also significant at the hindlimb. In fact, the effect of age was likely to be important throughout the animal's life, but as seen in previous chapters, there seemed to be a clear difference at a more advanced stage in life. The EMM and their paired comparisons show overall significance but the only significant comparison was that contrasting relative age category 2 and 3, with a significant increase in DJD between these two categories (Table 9.10). Thus, two distinct subsets could be defined, suggesting that there were significant differences in the EMM between the younger individuals (categories 1 and 2) and the middle-aged and older individuals (categories 3 through 5). In contrast, the effect of support deformability and their EMM and the repeated contrasts were not overall significant and thus the paired comparisons obtained were inconclusive.

It was thus possible that age was one of the main factors contributing to variability of DJD in the hindlimb of quadrupeds, as ageing processes would come with an increase in severity of DJD initially expressed as a result of other factors, ultimately increasing the variability of DJD expression. In fact, this relationship could be observed in the boxplots obtained of DJD for different levels of support deformability clustered by age (Fig. 9.6). At the same time, even though support deformability seems to have an overall significant effect on hindlimb DJD variability (Table 9.8), this effect could not be attributed to differences between levels of support deformability (non-significant post-hoc comparisons). Moreover, the graphic representations with the original data did not show an obvious increasing or decreasing tendency of DJD across the different levels (Fig. 9.6), which was further confirmed by the lack of directionality of the EMM (Table 9.11).

It was likely that the significant effect of the interaction between body mass and support deformability reported by the model could better explain how support deformability may contribute to DJD, despite the non-consistent post-hoc results obtained for support use on its own. The same relationship between body mass, SRF and moment arms discussed for the forelimb was experienced at the hindlimb. The use of different habitats and supports of different diameter entailed a reduction of the SRF both at the forelimb and the hindlimb (Schmitt, 1999; Larney and Larson, 2004). However, the reduction of SRF was always greater at the forelimb than at the hindlimb (Schmitt, 2003; Schmitt and Hanna, 2004). This came with greater variability of SRF experienced at the level of the forelimb than at the hindlimb, which was probably coupled with greater variability of limb yield, flexion at the forelimb and, consequently, of moment arms (i.e. loads). As a result, the forelimb of quadrupeds was likely to experience greater variability of loads about their joints than the hindlimb and, as these loads are ultimately dependent on body mass, the forelimb was comparatively more susceptible to changes in body mass than the hindlimb. Contrarily, as the increase of limb yield in relation to decreasing support diameter was greater at the forelimb than at the hindlimb, the effect of support deformability was probably less important at the hindlimb, thus explaining the non-significant paired comparisons obtained for this compartment but the overall significance of this factor in the main effects of the model.

The inclusion of the interaction in the models showed the significant effect of support use as a means of reduction of SRF and as a source of DJD variability, reinforcing the link between intensity of SRF and DJD development. The system of forces acting on the forelimb and hindlimb of quadrupedal primates is similar and, as a result, the effect that the tested variables have on DJD development also showed similarities.

Relative age significantly contributed to DJD variability in both limbs, as DJD increased in severity towards the later stages of an individual's life (Figs. 9.4 and 9.6), but with the most significant differences found in the distinction between young and middle-aged individuals (levels 1 and 2 at the forelimb; levels 2 and 3 at the hindlimb, Tables 9.4 and 9.10). Support deformability also played an important role in DJD variability but this was particularly important when considered in combination with body mass, as joint modulators of load on the limb joints, especially at the hindlimb. Thus one variable should not be considered without the other, despite the apparently irrelevant role of body mass.

These results support the conclusions that have been reached in previous chapters of this thesis for the quadrupeds but have given further insight on how much each of these variables account for DJD development and how they interact among them in order to understand the disease.

9.2 Generalised linear models for DJD on the limbs of suspensory primates

Suspensory primates are distinct from the other groups in the way they interact with their habitat for locomotor purposes. These primates exhibited lower levels of severity of DJD at their limb joints compared with quadrupeds or knuckle-walkers, but higher levels than those belonging to the leapers, VCL and slow arboreal quadrupeds (average forelimb combined DJD of suspensory=36.58; VCL and slow arboreal quadrupeds=8.00; leapers=10.51; quadrupeds=52.57; knuckle-walkers=163.49; suspensory=32.22 and average hindlimb combined DJD of VCL and slow arboreal quadrupeds=13.70; leapers=16.89; quadrupeds=45.76; knuckle-walkers=161.01).

Suspensory primates showed significant differences in DJD development at the level of the forelimb with other groups of primates of different locomotor adaptations, but they did not differ too much with other groups at the level of the hindlimb (Table 7.2). The elbow, knee and hip joints were some of the joints showing the greatest levels of variability among different species of suspensory primates (Tables 7.3 and 7.4).

Differences between fast and slow moving species were noted for primates in general (Table 7.10). Differences between fast and slow moving suspensory primates were found at the elbow (U=1204.50; p=0.003), hip (U=1336.50; p=0.025) and ankle (U=1382.50; p=0.012) joints, suggesting that at least some of the differences obtained in DJD were likely to be related to differences in speed.

Speed was treated as a modulator of magnitude for SRF and, therefore, it would be dependent on the action force, which is determined by body mass. General correlations between body mass and DJD expression in primates were significant at the forelimb (ρ=0.444; p<0.001) and the hindlimb (ρ=0.326; p<0.001). However, if only suspensory primates were considered these two variables did not correlate significantly at either limb (forelimb ρ=0.166, p=0.107; hindlimb ρ=0.099, p=0.339).

Speed and body mass showed a weak correlation that approached a significant level (ρ=-0.199; p=0.054). It seemed that slow locomotion was performed by species of differing body mass, contrary to fast locomotion, which seemed to be performed mainly by smaller species (Fig. 9.7). However, when the cases were labelled by species, the greater values of body mass observed for the slow-moving species were mainly due to the effect of the orangutans (*Pongo* sp.), while the rest of species were of rather similar size but equally performed fast and slow locomotion (Fig. 9.8). Despite this, the interaction between speed and body mass was included in the models, as the intensity of the SRF should be somehow dependant on the magnitude of the action force (i.e. weight) and the modulators of the SRF (i.e. speed).

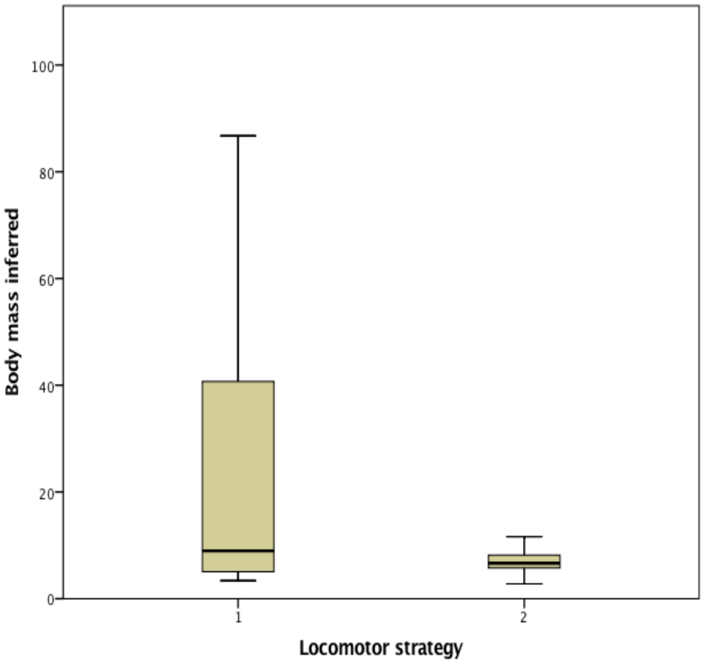

Figure 9.7 Boxplot depicting the relationship between body mass in Kg (Y axis) and speed (X axis, where 1=slow-moving species and 2=fast-moving species) for the suspensory primates

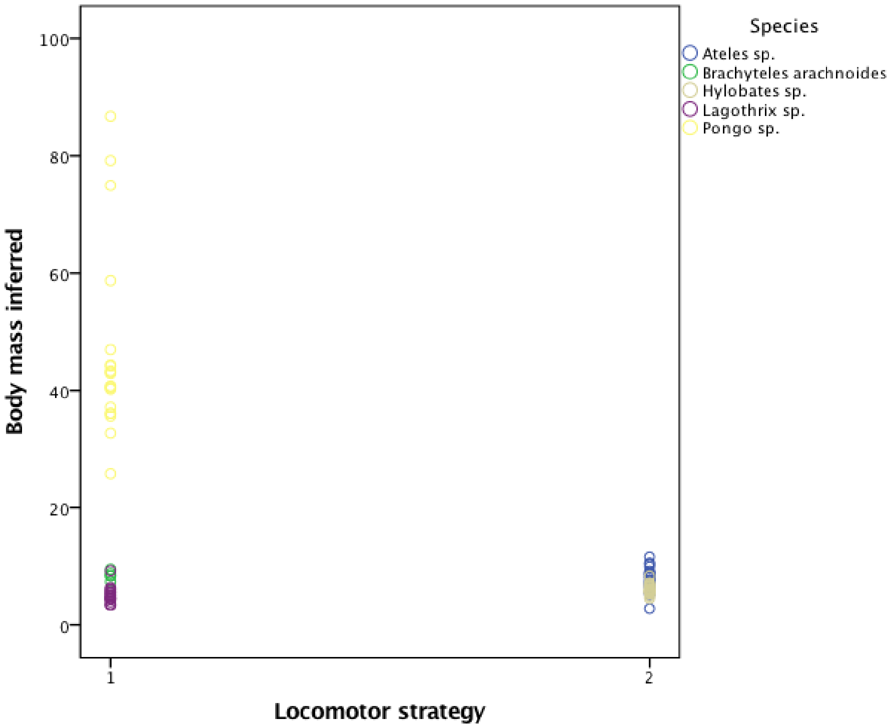

Figure 9.8 Scatterplot depicting the relationship between body mass in Kg (Y axis) and speed (X axis) for the suspensory primates with cases labelled by species in order to see the variability in body mass for each of the species considered, where 1=slow-moving species and 2=fast-moving species

The effect of age was important for primates in general (chapter 8) but it differed among groups of primates. Age and DJD did not correlate significantly at the forelimb of the suspensory primates (ρ=0.113; p=0.188) and they only correlated weakly but significantly at the hindlimb (ρ=0.238; p=0.017).

The models run for the forelimb and hindlimb of suspensory primates considered interactions between potentially correlated factors, including as predictors: age, speed, body mass, and speed * body mass.

9.2.1 The forelimb

The model obtained for the forelimb was overall significant and its indicators of goodness of fit were low, showing good fitness (Table 9.12). This model showed a significant effect of speed on the response variable (χ^2=4.25; p=0.039), while all the other factors did not reach significance, including the interaction (Table 9.13). Clustered boxplots showed a great difference in DJD expression according to speed, with higher expressions found for the slow-moving group (Fig. 9.9). DJD seemed to increase with age at the later levels of this variable, but only for the slow-moving group and no evidence of this was observable within the fast-moving level (Fig. 9.9).

Table 9.12 Summary of the model for the forelimb of suspensory primates showing three different indicators of goodness of fit, the overall statistic (likelihood ratio X2) and overall p-value

GLM forelimb of suspensory primates		**Value**
Goodness of Fit indicators	Akaike's information criterion (AIC)	115.93
	Bayesian information criterion (BIC)	137.59
	Log Likelihood * (-2)	97.93
Likelihood ratio χ^2		20.36
Significance (p-value)		0.005

Table 9.13 Summary of the test of model effects for the forelimb of suspensory primates

Forelimb suspensory primates		
Term of the equation (predictors and intercept)	**Wald χ^2**	**p-value**
Intercept	18.58	<0.001
Age	7.61	0.107
Speed	4.25	0.039
Body mass	2.11	0.147
Body mass * speed	2.00	0.158

EMM were calculated only for speed, as this was the only variable significantly contributing to the response (Table 9.14). However, the overall test was non-significant (χ^2=0.52; p=0.472) and so paired comparisons were not as informative, mainly because this is a variable with only two levels (slow and fast).

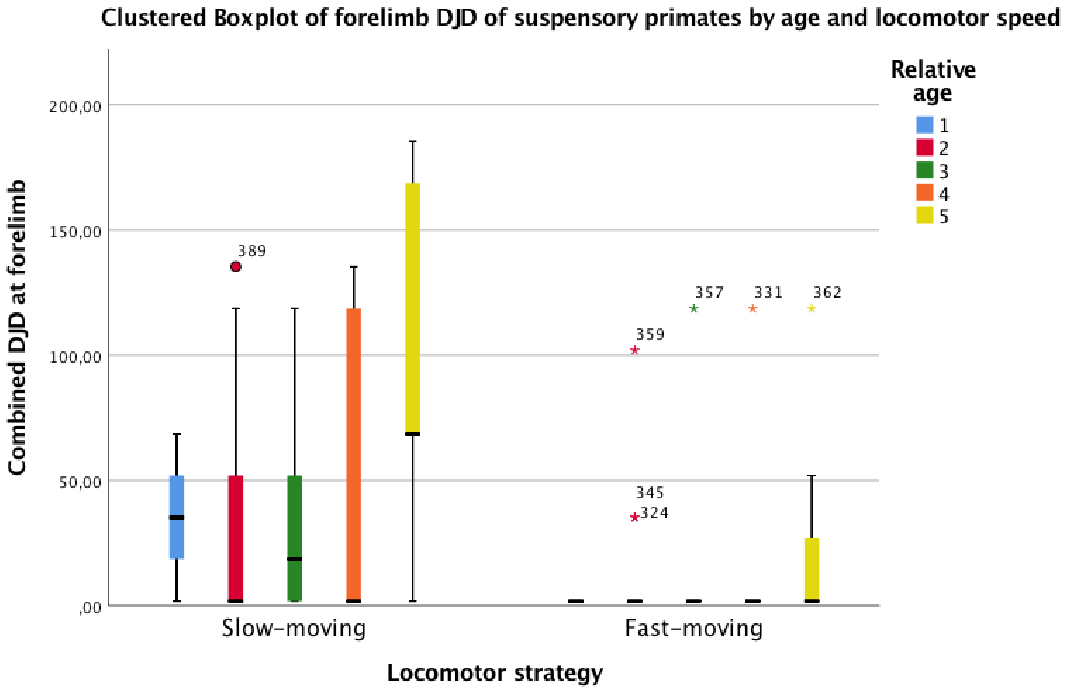

Figure 9.9 Clustered boxplot depicting the relationship between combined DJD at the forelimb (Y axis) and speed (X axis) for the suspensory primates, using relative age category as the clustering factor

Table 9.14 EMM for speed at the forelimb of suspensory primates (note that the tests were not overall significant and thus these means are just for guidance)

Speed	**Mean (EMM)**	**Std. Error**	**95% Wald Confidence Interval**	
			Lower	**Upper**
Level 1	0.99	0.14	0.73	1.26
Level 2	0.27	1.00	-1.69	2.23

The distribution of the observed against the predicted values deviated slightly from the linear function (Fig. 9.10). The lower values of DJD exhibited the greatest distance with the linear model function, showing a worse fit than the intermediate and higher values. The residuals were not randomly distributed (Fig. 9.10).

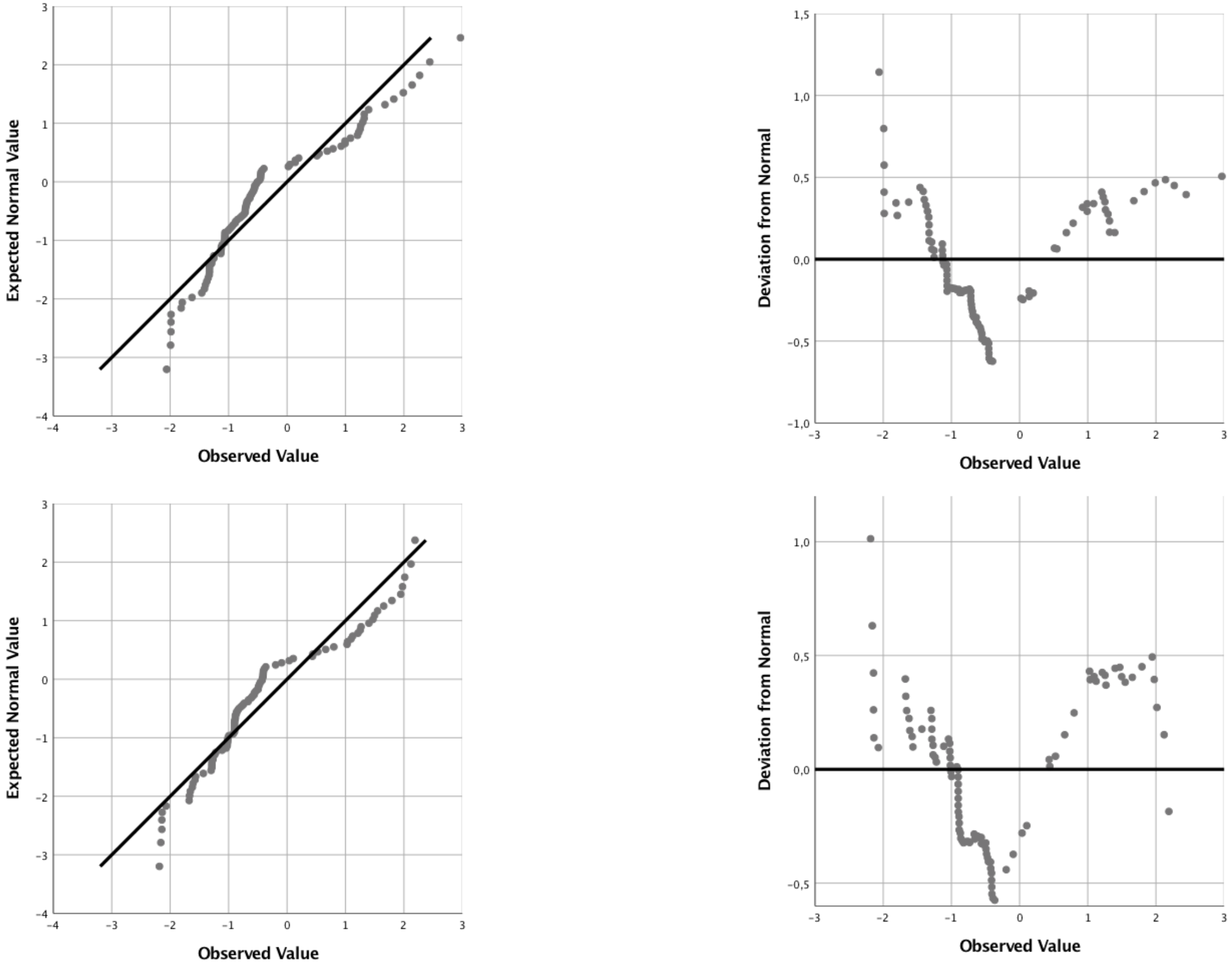

Figure 9.10 Graphic depiction of the fitness of the models and distribution of the residuals for suspensory primates. Top graphs pertain t forelimb, while bottom graphs pertain to the hindlimb. The left graphs are a representation of the fitted values (observed vs. predicted) and right graphs represent the distribution of the residuals in relation to the observed values)

9.2.2 The hindlimb

The model obtained for the hindlimb was overall significant and exhibited good fitness values (Table 9.15). Age was the only variable showing a significant contribution on the response variable (χ^2=15.12; p=0.004). The rest of the factors, including the interaction, showed no significant contribution to the variability of the response (Table 9.16), even though speed was not too far from significance (χ^2=3.26; p=0.071). Clustered boxplots showed different expressions of DJD between the slow- and fast-moving groups, with overall lower levels found at the fast-moving group (Fig. 9.11). There were different levels of expression of DJD for the different age categories within both the fast and the slow-moving groups, but with no linear trend observable (Fig. 9.11).

Table 9.15 Summary of the model for the hindlimb of suspensory primates showing three different indicators of goodness of fit, the overall statistic (likelihood ratio X2) and overall p-value

GLM forelimb of suspensory primates		**Value**
Goodness of Fit indicators	Akaike's information criterion (AIC)	115.53
	Bayesian information criterion (BIC)	137.19
	Log Likelihood * (-2)	97.53
Likelihood ratio χ^2		24.10
Significance (p-value)		0.001

Table 9.16 Summary of the tests of model effects for the hindlimb of suspensory primates

Hindlimb suspensory primates		
Term of the equation (predictors and intercept)	**Wald χ^2**	**p-value**
Intercept	17.75	<0.001
Age	15.12	0.04
Speed	3.26	0.071
Body mass	1.45	0.229
Body mass * speed	1.47	0.226

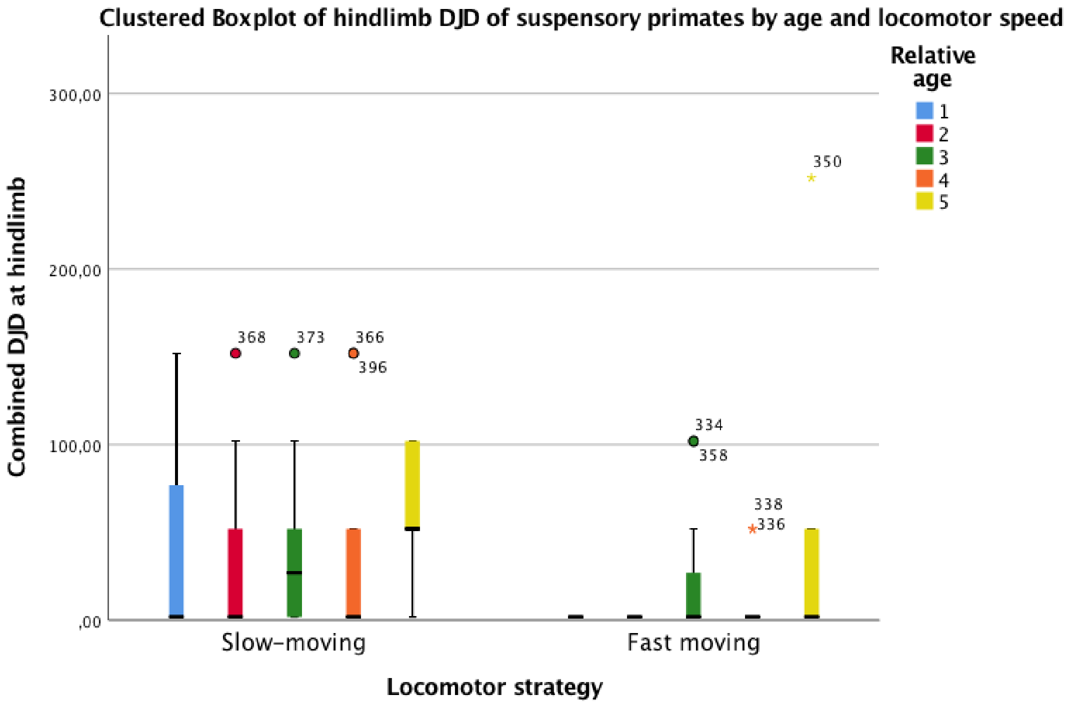

Figure 9.11 Clustered boxplot depicting the relationship between combined DJD at the hindlimb (Y axis) and speed (X axis) for the suspensory primates, using relative age category as the clustering factor

EMM were calculated for age as well as speed (Tables 9.17 and 9.19), even though the latter was only near-significant in the overall model (Table 9.16). However, the paired comparisons with repeated contrast were only conducted for age, as this was the only significant factor in the model and because this is a multi-level categorical variable (Table 9.18). The overall tests for age were significant (χ^2=15.12; p=0.004) and in the repeated contrasts only the comparisons between categories 2 and 3, and 4 and 5 showed significant differences (Table 9.18).

Table 9.17 EMM for age at the hindlimb of suspensory primates

Age category	**Mean (EMM)**	**Std. Error**	**95% Wald Confidence Interval**	
			Lower	**Upper**
Level 1	1.20	0.72	-0.22	2.61
Level 2	1.28	0.56	0.19	2.38
Level 3	0.47	0.54	-0.59	1.52
Level 4	0.82	0.52	-0.21	1.85
Level 5	0.21	0.52	-0.81	1.22

Table 9.18 Paired comparisons (by repeated contrast) of the different age levels EMM at the hindlimb of quadrupeds (significant differences in bold)

Age Repeated Contrast	Contrast Estimate	Std. Error	Wald Chi-Square	Sig.
Level 1 vs. Level 2	-0.08	0.56	0.02	0.883
Level 2 vs. Level 3	0.81	0.31	6.77	**0.009**
Level 3 vs. Level 4	-0.35	0.31	1.28	0.258
Level 4 vs. Level 5	0.61	0.31	4.01	**0.045**

Table 9.19 EMM for speed at the hindlimb of suspensory primates (note that the tests were not overall significant and thus these means are just for guidance)

Speed	Mean (EMM)	Std. Error	95% Wald Confidence Interval	
			Lower	Upper
Level 1	1.10	0.15	0.80	1.40
Level 2	0.49	1.01	-1.48	2.46

The trends observed for the fitted values and the distributions of the residuals were very similar to those obtained at the forelimb (Fig. 9.10). The fitted values were distributed around the projected line and the worst fit was observed for the lower values. Similarly, the residuals were not randomly distributed (Fig. 9.10)

9.2.3 Discussion of the GLM on the limbs of suspensory primates

The two models obtained for the suspensory sample were overall significant and exhibited strong indicators of goodness of fit (Tables 9.12 and 9.15). Thus, the variables considered could explain variability of DJD expressed at the limbs of suspensory primates. The distribution of the residuals was not random, as would be expected from a strong regression-based model. All models showed a distribution of the residuals that followed a trend. Therefore, similarly to the models obtained for the quadrupeds, these **should not be used as predicting models**. These models were powerful enough to assess the relationships between variables in relation to the response but the equations obtained would not produce reliable predictions. Therefore, the parameter estimates obtained were not fully reliable, as they would not reflect the real distances between categories (to be found in appendix 2).

9.2.3.1 The forelimb

The forelimb model for suspensory primates showed a significant contribution of speed towards variability of the response variable. No effect was seen for age, body mass, or the interaction between body mass and speed. The little or no contribution of such variables to forelimb DJD could be a result of the locomotor particularities of the suspensory primates.

The forelimbs of suspensory primates support more tensile than compressive stress, which entails that most of the DJD exhibited at these joints was likely to be exclusively a result of the loads derived from the SRF. The reduction or sometimes the complete lack of compressive forces experienced at the forelimb would greatly diminish the direct effect of body mass at these joints concerning DJD, and body mass would only contribute as a modulator of the SRF. In fact, the correlation between body mass and DJD was not significant at the forelimb of suspensory primates ($\rho=0.166$; $p=0.107$). Therefore, it was unlikely that body mass was directly related to DJD at the forelimb.

Suspensory behaviour has long been understood as a strategy adopted by relatively large-bodied species of primates in order to efficiently exploit arboreal habitats, avoiding branch failure (Fleagle and Mittermeier, 1980; Youlatos, 2001, 2017; Fleagle, 2013). This idea is further supported by the present results, showing further implications of this locomotor strategy in relation to joint health. The difference in strategy, which led to a change in the type of stress born at the joints (i.e. tensile stress instead of compressive), was very effective in terms of neutralising the effect of the large body mass of these primates at the level of their joints. Not only it reduces the amount of compression-related degeneration but by reducing the amount of earlier DJD it also diminishes the effect that age has in terms of severe DJD expressions.

The lack of DJD directly related to body mass resulting from the reduction of compressive stress would probably slow down the overall process of joint degeneration, which ultimately led to a non-significant effect of age. In general terms age contributed to DJD as a factor that increased the severity of degeneration, while the earlier stages of DJD development were not dependent on age (explored in chapter 8). The reduction of degeneration at the earlier stages of a suspensory primate's life thus entailed less variability of early DJD and, consequently, also at later stages of an individual's life. In fact, age did not correlate significantly with DJD at the forelimb (ρ=0.113; p=0.188).

The variability of joint degeneration was likely to be linked to differences in loads resulting from the SRF and the associated moment arms, with speed being an important modulator of such force. Differences in speed were often accompanied by differences in the positioning of the animal during locomotion. Fast-moving species of suspensory primates tend to move with more extended limbs, whereas the slow-moving species do so with more flexed joints (Bertram et al., 1999; Bertram, 2004), involving differences in the moment arms about the joints and, consequently, of loads. In fact, differences in DJD related to speed were mainly seen at the elbow joint of suspensory primates (U=1204.50; p=0.003). As discussed in chapter 8, differences in speed could also entail differences in the mechanical properties of the synovial fluid of the joint (Norkin and Levangie, 1992; Jay et al., 2007), which could result in different levels of efficiency of a joint in dealing with forces and maintaining its health. The overall repeated contrasts were non-significant, and so was the comparison between fast and slow-moving suspensory primates. However, the EMM obtained (Table 9.14) were notably greater for slow-moving species than for the fast-moving ones (0.992 and 0.270 respectively), supporting the present discussion. This is further visible in the clustered boxplots, where great differences in prevalence of DJD are obvious between the two levels of speed (Fig. 9.9).

The interaction between speed and body mass was less clear among suspensory primates (ρ=-0.199; p=0.054) (Fig. 9.7 and 9.8) and its inclusion in the model carried no significant effect on the response variable. This was probably a result of the close alignment of the limb with the stronger reaction forces during fast locomotion, diminishing the effect of the force as a result of the reduction in moment arms and load about the joints (as the perpendicular distance between the SRF and the joint decreased). Therefore, despite the reaction forces being greater for fast-moving species, the interaction between the action and reaction-related factors (body mass and speed) did not condition DJD expression.

9.2.3.2 The hindlimb

The model obtained for the hindlimb showed a significant effect of age and near significant effect of speed on DJD development, with no effect of body mass or the interaction between speed and body mass (Table 9.16). The hindlimb of suspensory primates can experience greater levels of compression than the forelimb. Most of these primates perform bipedal or quadrupedal locomotion as part of their locomotor repertoire (e.g., Fleagle, 1976; Thorpe et al., 2007), during which the hindlimbs are loaded with compressive forces. Consequently, DJD at this limb was likely to show some similarities with the quadrupeds in the way different variables contribute to joint degeneration. However, the proportion of compressive locomotion was much lower in the suspensory primates than it was on the quadrupeds and the effect of the variables varied accordingly.

The increase of compressive locomotion at the hindlimb compared to the forelimb of these primates could involve a greater proportion of compressive-related DJD at these joints. If compression involved greater levels of early DJD at the hindlimb than at the forelimb (as seen by the slightly greater EMMs, Tables 9.14 and 9.19), its severity would increase with age, supporting the significant correlation between these two variables ($\rho=0.238$; $p=0.017$). In fact, while combined levels of average osteophytosis and porosity were similar at the forelimb and the hindlimb, for the later stage of degeneration (i.e. eburnation) there was a clear differentiation between the two limbs (forelimb osteophytosis=21.35; hindlimb osteophytosis=20.88; forelimb porosity=9.56; hindlimb porosity=10.01; forelimb eburnation=1.32; hindlimb eburnation=5.71, chapter 6).

The EMM and repeated contrasts for age were overall significant (Tables 9.17 and 9.18) and showed significant differences between levels 2-3 and 4-5, conforming three different homogenous subsets for this sample. These results suggest different expressions of DJD between the youngest individuals (levels 1 and 2), middle-aged individuals (levels 3 and 4) and the oldest group (level 5), coinciding with the distribution of age reported by previous authors (DeRousseau, 1988; Nakai, 2003) as well as by the overall sample of this study (chapter 8). Consequently, the effect of age at the hindlimb of suspensory primates was similar to the pattern described typical of compressive locomotion. Different DJD expressions for different age categories were also visible in the clustered boxplots, particularly obvious for the slow-moving species (Fig. 9.11).

Speed did not contribute significantly to DJD expression at the hindlimb (although it reached near significance), in contrast to what was observed at the forelimb. However, it was possible that part of the variability of hindlimb DJD expression was linked to differences in magnitude of the SRFs. EMM of the slow-moving species was notably higher than those of the fast-moving species (Table 9.19), despite the non-significant paired comparison for the hindlimb. The potential effect of speed was confirmed by the clustered boxplots obtained; where higher overall levels of expression could be observed in the slow-moving group (Fig. 9.11). This contrast was likely to be a consequence of the difference in the magnitude of SRF, combined with the different levels of joint health maintenance observed in synovial joints as a result of the mechanical properties of the synovial fluid depending on speed of joint motion (Norkin and Levangie, 1992; Jay et al., 2007). However, it could also result from differing moment arms derived from SRF as a result of limb positioning with high and low speed locomotion.

SRF was closely related to body mass, as previously discussed. However, neither speed, nor body mass played a significant role in DJD variability for these primates' hindlimbs (Table 9.16). In fact, the correlation between DJD and body mass at the hindlimb was not significant ($\rho=0.099$; $p=0.339$) and this, similarly to what happened at the forelimb, could be a result of the reduction of compression stress in comparison with other groups of primates that habitually rely on their hindlimbs for locomotion. Furthermore, the interaction between body mass (determining the action force) and speed (a modulator of the reaction force) did not contribute significantly to variability of DJD at the hindlimb. Therefore, similarly to what was observed at the forelimb, despite the fact that speed and body mass could interact to some extent in the determination of SRF, their combined effect was not significant and did not contribute to DJD development in this compartment of the suspensory sample.

The forelimb and hindlimb of suspensory primates behaved overall in a similar way in terms of DJD variability and the effect of different factors as the potential drivers of joint degeneration. Speed was the main factor contributing to DJD variability at the forelimb and showed near-significant effects at the hindlimb, whereas other factors, such as body mass did not play a significant role. There could be an interaction between speed and body mass but it did not have a significant effect on DJD development. In contrast, age was more relevant at the level of the hindlimb than it was at the forelimb. This was likely to be a result of a greater proportion of compressive types of locomotion affecting the hindlimb compared to the forelimb. Hindlimb-reliant locomotion could entail greater levels of compression-related DJD, which could potentially increase in severity at more advanced stages in life. The lack or reduction of compressive stress often experienced at the forelimb would therefore reduce the effect of age as a factor increasing severity of DJD at this compartment. These results highlighted the advantages of suspensory behaviours, which not only allow large-bodied primates to exploit high strata of the forest, but it seemed to better preserve the health of their joints, neutralising some of the degenerative effects observed in typically compressive-driven locomotion.

9.3 Summary and conclusions

The analyses presented above brought together the different variables that had been previously considered as potential drivers of DJD and sources of variability among species. Different groups of primates exhibit differences in DJD expression, but they also differ in the way the different predictor variables contributed to DJD expression across the sample. Both sets of limbs reacted similarly, but with some particularities according to the mechanical challenges each of the limbs face. Most of the variability in the effect of the different contributing factors to DJD seemed to be closely related to mechanical differences of locomotion. Therefore, primates of different locomotor adaptations should be considered separately in order to understand DJD development, and the analyses should be done independently for the body compartments that may perform mechanically different functions.

Most of the variability in the expression of DJD for the samples selected answered to differences in locomotor strategies adopted during locomotion. Support use and speed played an important role in DJD development at the limbs. There was a link between support deformability and body mass (as modulators of the reaction and action force, respectively), whereas the relationship between locomotor strategy and body mas was not deciding in terms of DJD development for suspensory primates. In fact, the contribution of body mass and locomotor strategy as a combined factor (interaction) showed significant effects on the quadrupeds, but provided no significant contribution towards DJD for the suspensory primates. This could be due to the differentiation between compressive and tensile forces during their locomotion. Age often contributed towards DJD variability, as suggested in chapter 8, but always in combination with other factors.

The models obtained provided a good insight on how the different variables considered in this thesis contribute to DJD development, but more importantly, they showed how factors interact in order to explain DJD variability across quadrupeds and suspensory primates. Unfortunately, these models did not provide a complete picture of what causes DJD in non-human primates, as evidenced by the non-random distribution of the residuals. The models are probably incomplete and in order to improve their predictive power further variables should be considered, so aside from the factors already analysed there might be other variables that could partially determine joint degeneration in non-human primates.

CHAPTER 10: GENERAL DISCUSSION AND CONCLUSIONS

The present study provided a general overview of how DJD develops in the non-human primate skeleton. DJD development was assessed in a broad range of primate taxa (N=35), reflecting the locomotor, ecological and taxonomical variability of this order. Where, how, when and why DJD appeared were the aspects taken into account in the evaluation of joint degeneration. This final chapter brings together all the results previously discussed in an attempt to present an in-depth view of how DJD may have developed in the present sample of non-human primates. The results obtained in the present study are not exhaustive in the exploration of DJD. Some ideas for future research are thus proposed, opening new lines of enquiry that could lead to a deeper understanding of the role of the factors considered in this thesis, as well as newly considered ones.

A first description of the data collected for this study (chapter 6) produced a general pattern of distribution of DJD in non-human primates but also reported certain differentiations from such pattern for some of the primate groups considered. This apparent variability of DJD was proposed as a response to differences in locomotor behaviour, body mass and longevity, factors that were then explored independently in chapters 7 and 8. The final stage of the research consisted in pooling all these factors together by means of statistical models in order to see how each of them contributed to DJD development and how they interacted with each other as causal factors for joint degeneration (chapter 9).

10.1 Locomotor behaviour as a driver of DJD

Locomotor behaviour was proposed as one of the main features of DJD causality. As such, studying locomotor behaviour as a determinant factor of DJD was the main goal of this thesis. This assumption relied on the fact that different types of locomotion entailed different systems of forces acting on the primate body, exerting different stresses and loads on the weight-bearing joints, potentially inducing different rates of joint degeneration. As locomotor behaviour was treated from a mechanical perspective, two different aspects were considered: 1) locomotor adaptation, which would determine the angle of incidence of forces and the intensity of stress in different body compartments, and 2) locomotor strategy, which would condition the magnitude of the support reaction forces (SRF), modulating the intensity of the load born by the weight-bearing joints and, potentially, DJD.

The analyses on variability of DJD according to locomotor adaptation and locomotor strategy concluded that both aspects of locomotion were important factors related to DJD expression, entailing that the system of forces derived from locomotion did shape DJD expression. Primates of different locomotor adaptations exhibited different patterns of DJD expression for the three body compartments considered (spine, forelimb and hindlimb), leading to the rejection of the null hypothesis of question 1 (Q1, chapter 1) and confirming the alternative hypothesis that primates of different locomotor adaptations exhibit different patterns of DJD expression.

Most of the differences noted involved the knuckle-walkers. Other groups of primates also showed significant differences at several body compartments, most of which were easily attributed to differences in locomotor behaviour and the associated differences in stress. However, differences in DJD were not limited to primates of different locomotor adaptations. Further variability of DJD was found among species within locomotor groups due to further variability in locomotor behaviour.

The study of different locomotor strategies suggested that a good number of the differences spotted within each locomotor group were likely to respond to differences in locomotor speed, or habitat and support use, as factors that modulate the intensity of the SRF. However, the relationship SRF-DJD was not always straightforward.

The null hypothesis of the question concerning locomotor strategy, SRF and DJD (Q2, chapter 1) could be confidently rejected, as primates performing different locomotor strategies exhibited different patterns of DJD expression. However, depending on the strategy considered either of the alternative hypotheses was supported but only partially. In the case of speed the slow-moving species exhibited higher average ranks of DJD expression than the fast-moving species, suggesting that the former were more likely to exhibit greater severity levels of DJD than the latter. Thus in this case the species experiencing lower SRF were prone to more severe DJD, leading to the acceptance of the second alternative hypothesis.

However, in the case of quadrupeds, that show different habitat and support use, the arboreal primates exhibited the lowest average DJD ranks, whereas terrestrial and semi-arboreal species showed higher average ranks. This way, the terrestrial and semi-arboreal species, subject to greater SRF, were more prone to severe development of DJD, therefore supporting the first alternative hypothesis by which primates experiencing greater SRF would exhibit higher levels of DJD.

One possible reason for slow-moving primates to develop higher levels of DJD was the difference in the composition and physical characteristics of the synovial fluid of the joints of fast and slow moving species, which could entail higher efficiency in dealing with intense forces during fast movements of joints (Jay et al., 2007). In the case of habitat and support use the highest average ranks were often observed for the semi-arboreal species. This was probably a result of positioning during terrestrial locomotion (experiencing greater loads than the terrestrial species) and a lack of morphological adaptation to terrestrial exploitation (Gebo and Sargis, 1994; Nakatsukasa, 1994). This could lead to a reduction of the efficiency to deal with strong reaction forces, inducing faster DJD development. Consequently, the hypotheses supported were only partially true, as the effect of morphology was not considered and seemed to be closely related to DJD development.

Different locomotor strategies could only explain part of the variability of DJD expression among species of each locomotor group. Differences in speed only seemed to explain differences in some synovial joints, whereas differences in support use in quadrupeds explained most of the variability of DJD in the earlier stages of its expression but failed to do so in more advanced stages. Consequently, not all the variability observed in DJD across primates could be explained by differences related to locomotion and other factors appeared to play an important role, as suggested by the descriptive analyses (chapter 6).

10.2 Effect of body mass in DJD expression

Body mass was treated as a further mechanical factor that was not directly related to locomotion. The association between body mass and DJD was tested only at the level of the limbs and significant positive correlations were observed between the two variables at the forelimb and hindlimb. The null hypothesis of question 3 (Q3, chapter 1) was thus rejected, supporting the alternative hypothesis that larger primates would exhibit higher expressions of DJD.

The correlation coefficients were not very high and they were different for the two sets of limbs, showing stronger correlations at the forelimb than at the hindlimb. This was initially unexpected, as primates generally rely more on the hindlimb than on the forelimb for locomotor purposes (Reynolds, 1985a, 1985b; Demes et al., 1994; Larson, 1998; Schmitt, 1998), but supported the limb ratios (chapter 6), tested in order to relate the hindlimb drive of primates and DJD. The ratios obtained were likely to be influenced by better adaptations for weight-bearing purposes present at the hindlimb, in contrast with the forelimb, which would greatly reduce DJD prevalence.

The greater adaptation of the hindlimb for weight support was reinforced by the analyses of pressure experienced at the knee and shoulder joints. The knee scaled better with body mass, exhibiting a much smaller range of pressures supported at this joint, in comparison with the shoulder. When pressure was correlated with DJD stronger correlations were observed at the knee than at the shoulder joint. Despite the knee's adaptations to weight-bearing functions, a small increase in the amount of pressure could entail a great increase in DJD development. These results suggested that the use of pressure in relation to DJD could be more accurate than the use of body mass. However, these data were only available for the shoulder and knee joints and were calculated using approximations of weight distribution between limbs, challenging their use for further analyses.

The lack of adaptation to a weight-bearing role was likely to be the reason that made the forelimb more susceptible to changes in body mass, compared to the hindlimb. The stronger correlations observed at the forelimb were related to the earlier stages of the disease, but this pattern was not necessarily true for the more severe expressions of DJD, suggesting that other factors would play a determinant role in the increase of DJD severity. The rather low coefficients obtained in these correlations suggested that body mass would only have a partial effect in DJD development.

Very few significant differences were observed in DJD expression between males and females, suggesting that sexual dimorphism that could lead to differences in body mass was not reflected in DJD expression for these taxa, contrary to what had been suggested for other primate species (DeRousseau, 1988).

10.3 Effect of age in DJD expression

Age has often been considered a very important factor in DJD (Rogers et al., 1987; Ethier and Simmons, 2008; Waldron, 2008; Aufderheide and Rodríguez-Martín, 2011). Degenerative processes involve an effect over time in their development and non-human primates were no exception. Significant positive correlations were found between relative age and DJD for the whole sample of primates considered in this thesis, supporting the first alternative hypothesis of question 4 (Q4, chapter 1), connecting DJD and age.

The correlation coefficients concerning DJD and relative age were not particularly high. In fact, the increase of DJD severity along a primate's life was not gradual and for some groups of primates the correlation between age and DJD did not even reach significance levels. The effect of relative age was particularly important at the later stages of an individual's life, generally producing an increased in severity of DJD. However, for this to happen, some levels of basal DJD had to be already present. Early signs of DJD were found in the early stages of adulthood, suggesting that DJD could develop even before reaching adulthood. Therefore, age on its own was unlikely to lead to great severities of DJD and, even less, be the only cause of its appearance.

10.4 Combined effect of all the factors in DJD expression

The role of locomotor behaviour, body mass and age were assessed independently in chapters 7 and 8, which provided information on how well these variables explained variability of DJD expression in different groups of primates and what stages of the disease these factors are more closely related to. All of these variables played an important but partial role in DJD expression, with the exception of sex that did not seem to result in differences in DJD expression.

The statistical models obtained in chapter 9 permitted a combined assessment of these factors in order to see how they contributed to DJD expression at the level of the limbs of two groups of primates: the quadrupeds and suspensory primates. These models showed the main effects in DJD development, as well as the relevance of the interactions between body mass and the locomotor strategy performed. The results confirmed the multivariate nature of DJD and evidenced the important contribution of both mechanically and non-mechanically related factors. This led to the acceptance of the third alternative hypothesis of question 5 (Q5, chapter 1), which conceived a mixed effect of mechanical and non-mechanical factors on DJD development.

One of the most important findings of these models was that the effect of the different factors could vary depending on the group of primates considered as well as on the body compartment analysed. Consequently, primates of different locomotor adaptations should be considered independently in order to accurately assess the effect of different factors on DJD expression. The same applied for the different body compartments, as the effects of the factors considered were slightly different for the forelimb and the hindlimb, according to the mechanical challenges faced by each of the limbs.

There was a consistently relevant role of mechanically related factors in the development of DJD. Most of the variability of DJD expression, both in quadrupeds and suspensory primates, was strongly related to differences in locomotor strategy, often showing interactions between locomotor strategy and body mass, with varying effects on DJD expression. For the quadrupeds, support deformability and age were the main factors contributing to DJD expression. These two factors were complementary as DJD drivers, for the effect of support use as a modulator of SRF explained well the first stages of DJD expression, whereas age contributed significantly towards the later stages of the individual’s life by increasing DJD severity.

The effect of body mass on DJD expression was especially relevant in conjunction with support use. It had been previously established that body mass correlated significantly with DJD but exhibited low coefficients, reflecting its weak contribution as an isolated factor but making possible its relevant role when it was considered in combination with support use. The correlations between body mass and DJD were stronger for the forelimb, similarly to the interaction between the effect of support compliance and body mass in quadrupeds. Even though present for both limbs, this interaction only contributed significantly to DJD at the forelimb level, probably resulting from postural differences between the limbs.

The interaction between locomotor strategy and body mass, and their significant combined effect on DJD development confirmed the importance of the system of forces acting on a moving primate concerning joint degeneration. DJD was partially dependent on an action force (i.e. weight, determined by body mass), a reaction force (SRF, determined by support deformability), and the corresponding loads, which can vary as a result of differences in posture (mainly degree of flexion) during locomotion. Differences in the level of limb yield (and thus of flexion at a joint) experienced in the forelimb and the hindlimb was reflected in the difference in contribution of the interaction on DJD development for quadrupeds.

Suspensory primates showed some effect of locomotor strategy in the development of DJD, especially at the forelimb. This was the only significant contributing factor at the forelimb level, while at the hindlimb age played the most significant role. There seemed to be some association between body mass and locomotor strategy, but it was not sufficiently strong to determine DJD expression variability across these species.

The main difference between the forelimb and hindlimb of suspensory primates was likely to be the amount of compressive stress exerted. The forelimb of suspensory primates experiences tensile stress almost exclusively, whereas the hindlimb is loaded with compressive forces more often than the forelimb. The great reduction of compression at the forelimb involved that DJD development was probably only a consequence of the load derived from the SRF. The levels of compression-related DJD would be virtually non-existent, which greatly reduced DJD altogether. This led to a lesser effect of age, as there would be lower basal levels of DJD and, ultimately, less differentiation of DJD at later stages of life. At the hindlimb joints, however, suspensory primates experience more compression and more compression-related DJD was displayed. Consequently, age played a greater role in joint degeneration and differentiation. These results evidenced a great advantage of suspensory behaviour in terms of DJD expression, suggesting that the differentiation between tensile and compressive stress was key to joint health maintenance in this group of primates.

The models obtained are informative but incomplete. In order to fully understand how DJD is developed in non-human primates, other variables should also be considered. The inclusion of the relevant variables in this kind of analyses would lead to robust models fit for predictions, which could have a great impact in the interpretation of skeletal remains of both extant and extinct primates.

10.5 Conclusions and further directions in the study of DJD

The main aims and objectives set out in chapter 1 have been met, and the research questions have been answered. As a result, more in-depth information on the nature of DJD was produced. In particular, new factors that were not commonly considered in previous research in DJD on non-human primates have been proved to be not only relevant, but also essential in the understanding of the diversity of DJD expression in primates.

One particularity of this study was that, contrary to what had previously been done in the study of DJD in non-human primates, no diagnose was given to the degeneration observed. Instead of documenting presence or absence of specific pathological expressions of DJD, the three indicators of DJD (osteophytosis, porosity and eburnation) were recorded separately. By doing this, greater insight was obtained on how DJD may develop, placing greater focus on the non-pathological or earlier expressions of DJD, which would have been overlooked if only the pathological stages had been recorded.

Locomotor behaviour was observed to be of great importance in DJD development, especially during the first stages of joint degeneration. Differences in DJD expression were observed across primates of different locomotor adaptations but also across species performing different locomotor strategies. A link was thus established between mechanical stress and DJD that was particularly important in the earlier stages of DJD development.

Other factors were likely to be more closely related to advanced expression of DJD. Of the variables studied in this research, age was closely associated to severe DJD expressions. It seemed likely that DJD would increase in severity over time as a result of ageing processes, but this was always preceded by low expressions of DJD during the earlier stages of an individual's life.

The results obtained point towards the early expressions of DJD being more closely related to locomotor behaviour, which then increased in severity as a result of ageing. This was evident in the multivariate models obtained for the quadrupeds, where the mechanical system of forces was very important in DJD development, together with age. The models obtained at the forelimb of the suspensory primates further supported this suggestion. They showed a significant contribution by locomotor strategy in DJD development but no significant effect of age, probably as a result of the lower overall levels of DJD coming from the reduction of compressive load on their limbs. Therefore, for age to have a significant effect on DJD development there was the need for DJD to be developed in the first place, even if this was for low severity stages, making age dependent on other factors.

Pathological stages of DJD would be rarely reached, were it not for the early, non-pathological DJD expression. Mechanical stress was paramount in the development of the early signs of DJD, in conjunction with morphological adaptations that determine the efficiency of the joints to deal with the system of forces they are subject to. The link between age and the high severity expressions of DJD at later stages of a primate's life implied that different factors that contribute to DJD development were likely to have different effects at different stages of expression of the disease.

The results obtained with this research greatly contribute to the fields of physical anthropology, ecomorphology and comparative anatomy of primates, giving the study of comparative DJD a newly attributed evolutionary value. First and foremost, it provides a much needed broad overview of the development of DJD in the primate order, as previous studies focussed on a much smaller samples, including fewer taxa and using unstandardized methodologies. It has cast new light on the process of DJD development and what factors are more important for each of the stages of DJD expression in our order, confirming the important role of locomotor behaviour in the variability of DJD expressions among primates, especially at the early stages of DJD. Moreover, the link between adaptation (either morphological or behavioural) and DJD is confirmed, suggesting that DJD can become an important tool in evolutionary studies of primates, including humans.

The findings obtained have great implications in the study of both for human and non-human primates. A connection was made between ecomorphological adaptations and how these could affect joint health in some primate taxa. This sort of knowledge could be applied to the archaeological and paleontological record, giving information on functional adaptation of extant and extinct primates. However, this research also has more contemporary applications. For instance, this knowledge could be implemented to improve the living conditions of primates in captivity. Captive primates live longer than their wild relatives (Uno, 1997), thus having greater chances of reaching extremely severe joint pathologies as a result of ageing (DeRousseau, 1985; O'Regan and Kitchener, 2005; Lewton, 2017). However, if efforts were placed on reducing mechanical stress by carefully designing their enclosures there is great potential that these pathologies could be reduced, thus improving the primates' quality of life by reducing pain. Similarly, this could have great impact on the field of medicine, where a change of paradigm in the way DJD is studied and treated could prove beneficial. Humans are exceptionally long-lived primates and develop high levels of DJD, greatly as a result of ageing. Therapies are being implemented for individuals of old age. However, this research suggests that it could be beneficial if greater efforts were placed in prevention therapies at earlier stages of life, rather than attenuation therapies once the disease has reached advanced stages.

Further research is still required to fully understand the role of the above-discussed factors in DJD expression. It would be extremely valuable if quantifications of the SRF and moment arms during locomotion could be obtained for a broader range of primates, ideally during interactions with their natural habitats and with specific types of support. Similarly, better approximations of the pressures experienced at weight-bearing joints would provide greater insight in order to have a better notion of exactly how body mass contributes to mechanical stress during locomotion. For this, specific quantifications of the amount of weight born by each limb would be necessary, as well as accurate quantifications of the area of each articular surface.

Many arguments in this thesis have been based on the amount of load that joints bear as a result of the moment arms experienced during locomotion. However, the role of musculature and associated structures that reduce load and impact was impossible to assess with the given resources. Data on musculature moment arms and mechanical quantifications of the damping effect of associate joint structures would provide further information that could help refine the actual amount of load supported by a joint, which could subsequently be more accurately related with DJD development.

Other factors that have not been considered in this thesis could also play a relevant role in DJD development, as suggested by the generalised linear models obtained. Some of these factors could include differences in bone density and trabecular bone arrangements, differences in metabolic rates and even genetics. The potential role of phylogeny should not be overlooked. Phylogeny did not seem to play a significant role in the comparisons of DJD expression between Old World and New World monkeys carried out in this study. However, the only monophyletic group considered in this thesis was the knuckle-walkers, which consisted of the non-human African great apes and these were very distinct to the other locomotor groups considered in terms of DJD expression. Even though their distinction could be due to locomotor and postural behaviour as well as their longevity, there is the possibility that some of the differences were at east partially due to phylogeny.

Recent technological advances are increasing the wealth of knowledge on primate morphology and locomotor mechanics. Some studies are starting to test biomechanics of primate locomotion in their natural habitats, obtaining preliminary quantifications of different interactions with different types of natural supports (Dunham et al., 2018a, 2018b). Moreover, non-invasive imaging techniques are being implemented to study the internal bone structure, producing invaluable data that may help understand the skeletal efficiency of joints (e.g., Schilling et al., 2013; Stephens et al., 2016; Tsegai et al., 2017). In conclusion, exciting times are ahead in the fields of morphology and biomechanics of locomotion of primates, which could be the platform for better approaches to DJD development in our order, hopefully leading to better prevention of the disease.

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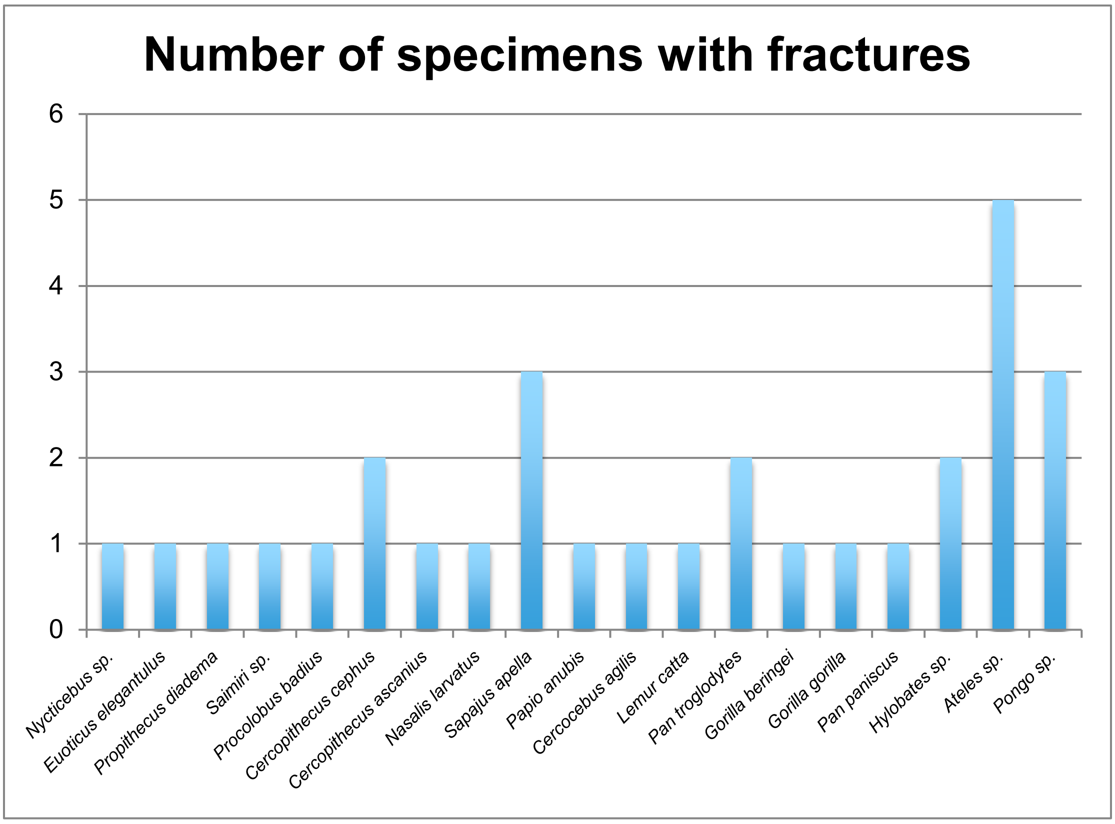
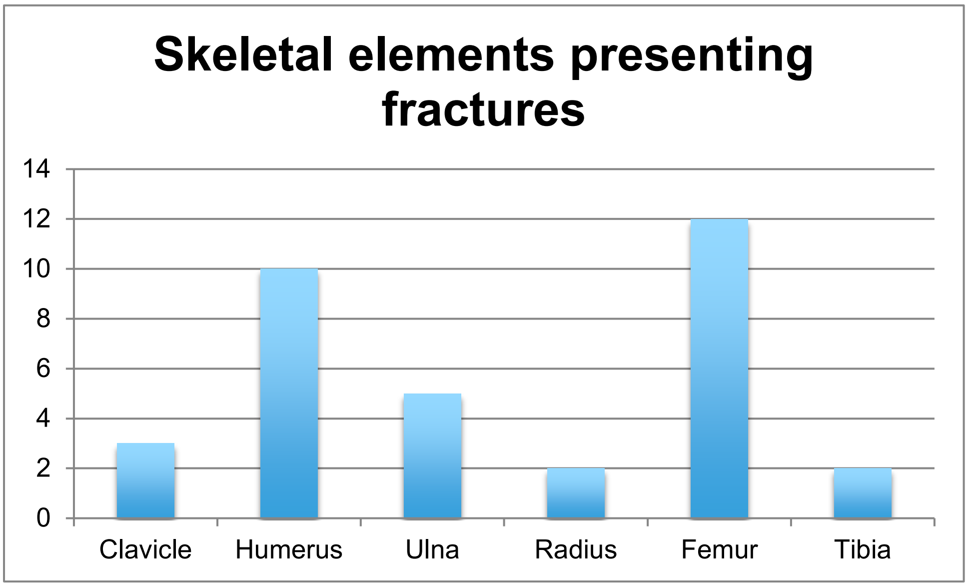
APPENDIX I. TRAUMA IN NON-HUMAN PRIMATES



Appendix 1.1. Bar chart representing the number of specimens with fractures across the sample and their taxa



Appendix 1.2. Bar chart representing the number of fractures across skeletal elements

Appendix 1.3. Examples of the types of fractures recorded as well as other cases of trauma. Top left: example of an aligned and fused fracture on a tibia in Propithecus diadema. *Bottom left: example of a non-aligned fused fracture on femur on* Gorilla beringei. *Middle top and bottom: modified acetabulum and proximal femur resulting from a hip dislocation in* Cercopithecus nictitans. *Right top and bottom: modified proximal ulna resulting from an elbow dislocation in* Cercocebus torquatus. *Note in the cases of the dislocations (middle and right four photographs) the presence of a secondary articular surface*

APPENDIX 2. COMPUTED ESTIMATES OF GENERALISED LINEAR MODELS (GLMS)

*Appendix 2.1. Summary table of the parameter estimates obtained for the GLM of the quadruped forelimb. Response variable=transformed combined DJD of the forelimb; model=(intercept), age, support deformability, body mass and support deformability*body mass*

Parameter Estimates GLM of forelimb of quadrupeds							
Parameter	B	Std. Error	95% Wald Confidence Interval		Hypothesis Test		
			Lower	Upper	Wald Chi-Square	df	Sig. (p-value)
(Intercept)	2.361	0.509	1.364	3.357	21.546	1	<0.001
[Age=1]	1.287	0.266	0.767	1.807	23.503	1	<0.001
[Age=2]	0.587	0.152	0.289	0.885	14.868	1	<0.001
[Age=3]	0.320	0.132	0.061	0.579	5.844	1	0.016
[Age=4]	0.118	0.116	-0.109	0.345	1.043	1	0.307
[Age=5]	0						
[Support deformability=1]	-2.356	0.590	-3.513	-1.199	15.925	1	<0.001
[Support deformability=2]	-1.276	0.593	-2.438	-0.114	4.632	1	0.031
[Support deformability=3]	-1.146	0.828	-2.769	0.477	1.916	1	0.166
[Support deformability=4]	-1.333	0.617	-2.542	-0.125	4.675	1	0.031
[Support deformability=5]	-3.124	2.599	-8.218	1.971	1.444	1	0.229
[Support deformability=6]	0						
Body mass inferred	-0.746	0.203	-1.144	-0.348	13.526	1	<0.001
[Support deformability=1] * Body mass	-0.766	0.203	0.368	1.163	14.257	1	<0.001
[Support deformability=2] * Body mass	0.671	0.205	0.270	1.072	10.752	1	0.001
[Support deformability=3] * Body mass	0.657	0.222	0.221	1.094	8.707	1	0.003
[Support deformability=4] * Body mass	0.606	0.238	0.140	1.071	6.509	1	0.011
[Support deformability=5] * Body mass	1.929	1.098	-0.222	4.081	3.089	1	0.079
[Support deformability=6] * Body mass	0						

*Appendix 2.2. Summary table of the parameter estimates obtained for the GLM of the quadruped hindlimb. Response variable=transformed combined DJD of the forelimb; model=(intercept), age, support deformability, body mass and support deformability*body mass*

Parameter Estimates GLM of hindlimb of quadrupeds							
Parameter	**B**	**Std. Error**	**95% Wald Confidence Interval**		**Hypothesis Test**		**Sig.(p-value)**
			Lower	**Upper**	**Wald Chi-Square**	**df**	
(Intercept)	1.056	0.618	-0.156	2.267	2.914	1	0.088
[Age=1]	1.047	0.283	0.493	1.602	13.713	1	<0.001
[Age=2]	0.662	0.200	0.270	1.055	10.935	1	0.001
[Age=3]	0.190	0.164	-0.132	0.512	1.342	1	0.247
[Age=4]	0.064	0.159	-0.247	0.375	0.165	1	0.685
[Age=5]	0						
[Support deformability=1]	-0.796	0.778	-2.322	0.729	1.046	1	0.306
[Support deformability=2]	0.558	0.803	-1.016	2.132	0.483	1	0.487
[Support deformability=3]	-0.508	1.089	-2.642	1.627	0.217	1	0.641
[Support deformability=4]	-1.537	0.784	-3.074	0.001	3.838	1	0.050
[Support deformability=5]	2.858	1.950	-0.964	6.681	2.148	1	0.143
[Support deformability=6]	0						
Body mass inferred	-0.096	0.285	-0.656	0.463	0.114	1	0.735
[Support deformability=1] * Body mass	0.112	0.286	-0.448	0.672	0.154	1	0.695
[Support deformability=2] * Body mass	-0.010	0.293	-0.583	0.563	0.001	1	0.972
[Support deformability=3] * Body mass	0.158	0.318	-0.465	0.782	0.248	1	0.619
[Support deformability=4] * Body mass	0.548	0.342	-0.122	1.218	2.567	1	0.109
[Support deformability=5] * Body mass	-0.784	0.679	-2.114	0.545	1.336	1	0.248
[Support deformability=6] * Body mass	0						

*Appendix 2.3. Summary table of the parameter estimates obtained for the GLM of the suspensory forelimb. Response variable=transformed combined DJD of the forelimb; model=(intercept), age, speed, body mass and speed*body mass*

Parameter Estimates GLM of forelimb of suspensory primates							
Parameter	**B**	**Std. Error**	**95% Wald Confidence Interval**		**Hypothesis Test**		**Sig. (p-value)**
			Lower	**Upper**	**Wald Chi-Square**	**df**	
(Intercept)	2.516	0.919	0.714	4.318	7.491	1	0.006
[Age=1]	0.360	0.356	-0.338	1.058	1.022	1	0.312
[Age=2]	0.746	0.294	0.170	1.322	6.451	1	0.011
[Age=3]	0.505	0.276	-0.035	1.046	3.358	1	0.067
[Age=4]	0.465	0.304	-0.131	1.061	2.340	1	0.126
[Age=5]	0						
[Speed of locomotion=1]	-1.907	0.295	-3.720	-0.094	4.249	1	0.039
[Speed of locomotion=2]	0						
Body mass inferred	-0.168	0.118	-0.399	0.062	2.053	1	0.152
[Speed of locomotion=1] * Body mass	0.166	0.118	-0.065	-0.397	1.995	1	0.039
[Speed of locomotion=2] * Body mass	0						

*Appendix 2.4. Summary table of the parameter estimates obtained for the GLM of the suspensory hindlimb. Response variable=transformed combined DJD of the forelimb; model=(intercept), age, speed, body mass and speed*body mass*

Parameter Estimates GLM of hindlimb of suspensory primates							
Parameter	**B**	**Std. Error**	**95% Wald Confidence Interval**		**Hypothesis Test**		**Sig. (p-value)**
			Lower	**Upper**	**Wald Chi-Square**	**df**	
(Intercept)	2.126	0.895	0.372	3.880	5.642	1	0.018
[Age=1]	0.988	0.521	-0.032	2.008	3.604	1	0.058
[Age=2]	1.071	0.309	0.465	1.678	11.981	1	0.001
[Age=3]	0.257	0.230	-0.194	0.708	1.251	1	0.263
[Age=4]	0.611	0.305	0.013	1.209	4.011	1	0.045
[Age=5]	0						
[Speed of locomotion=1]	-1.618	0.897	-3.376	0.139	3.259	1	0.071
[Speed of locomotion=2]	0						
Body mass inferred	-0.141	0.117	-0.369	0.088	1.459	1	0.227
[Speed of locomotion=1] * Body mass	0.141	0.117	-0.087	0.370	1.466	1	0.226
[Speed of locomotion=2] * Body mass	0						