Dragonfly locomotion: Ecology, form and function

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Submitted in accordance with the requirements for the degree of
Doctor of philosophy

The University of Leeds
Faculty of Biological Sciences
School of Biology

June 2018

Intellectual property statements

Acknowledgements

First and foremost I would like to thank my supervisor Dr. Christopher Hassall and co-supervisor Dr. Graham Askew, for endless encouragement, advice and assistance, in addition to giving me the opportunity to study in their laboratories. Without them and their guidance this work would not have been possible.

Secondly I would like to thank my family for supporting me and all of my endeavours throughout my entire life, even though my brother is the only one that knows what most of the words in this document mean.

Thank you to Julia Humes. Without her love and support this thesis would probably never have been finished, and my time at Leeds would have been nowhere near as amazing as it was.

I would like to thank all the great people I have met in Leeds University, past and present, for keeping me sane the last four years and providing a fantastic atmosphere to work in. In particular thank you to Dr. Giovanna Villalobos for sharing the load of trying to keep thousands of dragonfly larvae alive – despite their efforts to the contrary.

I would also like to thank all my friends in or out of Leeds, for putting up with me prattling on about dragonflies and lasers, countless hours of games and for telling me to get a real job no more once or twice a month. In particular thanks to Mr. William Farmer because he asked to be mentioned here (the reason for which I still don’t know).

Finally thank you the Natural Environment Research Council (NERC) for funding this work.

Abstract

The Odonata is a charismatic insect order remarked for their flight ability. They are a useful model system for ecological and evolutionary processes, but in particular their strong and unique flight abilities make them a model taxon to study the biomechanics of flight. Movement is fundamental to a range of processes in biology, including population spatial dynamics. With increasingly urgent demands to understand and predict the impacts of climate change, uncovering the processes driving the movement of populations is paramount. Currently the macroecological patterns caused by climate change are reasonably well documented – particularly for the Odonata. However the mechanisms driving population movements are less clear. Despite considerable advances in our knowledge of the biomechanics of insect flight, little of this has been applied in an ecological context. This thesis aims to identify the gaps in our knowledge of macroecological processes and how biomechanical techniques can advance the field. I have set out a number of methods demonstrating how the biomechanics of flight in Odonata impacts ecological patterns.

Range shifts are perhaps one of the best detailed impacts of climate change. At some level they must be driven by the movements of individuals, yet many studies have found little evidence to correlate flight ability and dispersal in insects. Using laboratory measures of flight performance I show that climate induced range shifts in the Odonata are limited by flight efficiency. This has important implications for conservation, as knowing how flight ability is able to restrict a species' range shift will aid reserve design and future ecosystem predictions.

The possible reason behind the lack of evidence linking flight ability and dispersal is the use of proxies for flight performance, and the assumptions of the relationship between these measures and actual flight performance. Indeed, in the literature there are a host of different often mutually exclusive assumptions regarding the role of morphology in shaping flight ability. I provide empirical evidence of how wing morphology affects flight performance, showing that a large proportion of assumptions made within the literature are not supported, or are only weakly supported. This calls into question how prevalent the effects of flight performance on dispersal are, given the use of misleading assumptions.

In many systems the state of adult organisms is strongly dependent on the experience of juveniles. For the Odonata, a number of mass and size carry-over effects exist between larva and adult forms, but whether locomotory performance is linked in this way is as of yet unknown. Here I show that there is no correlation between larval and adult locomotory performance, suggesting that muscle development mechanisms are different for larvae and adults. Except for existing mass and size effects, flight performance should not be strongly affected by larval conditions.

Finally, various behaviours have the capacity to affect dispersal in a species. One of the behaviours recently empirically confirmed in the Odonata is that of reversible polarotaxis: initial repulsion from polarised light sources as immature adults and the attraction back to polarised light as mature adults. I predicted that reversible polarotaxis would help aid dispersal, repelling insects from natal habitats and encouraging them to find new ones. However, the individual-based model of dispersal that I developed shows that reversible polarotaxis is more important in speeding up the progression through life stages, reducing the time taken to reach feeding habitats and to return to breeding sites. Individuals without polarotaxis would experience higher mortality and lower rates of energy uptake (taking longer to find food) and also higher mortality rates taking longer to return to breeding sites (including lower reproductive success from potentially spending less time at breeding sites).

All the work here is then synthesised to create a comprehensive description of Odonata flight morphology (form), its effects on flight performance (function) and the ecological patterns it generates (ecology). I demonstrate that biomechanics can provide important insights into ecological processes – in this case, that flight performance is an important limiting factor for range expansions, where other limitations are perhaps not present. In addition flight morphology is strongly linked with flight performance, suggesting that up to 74% of studies have used incorrect assumptions regarding the links between morphology and performance.

Table of Contents

Dragonfly locomotion: Ecology, form and function i

Intellectual property statements ii

Acknowledgements iii

Abstract iv

List of Tables x

List of Figures xii

List of abbreviations xviii

Chapter 1 – Introduction: A review of dragonfly flight ecology 1

- 1.1 Abstract 1
- 1.2 Introduction 2
- 1.3 Flight Biomechanics 5
  - *1.3.1 Insect flight* *5*
  - *1.3.2 Odonata muscle physiology* *9*
  - *1.3.3 Odonata flight biomechanics* *10*
- 1.4 The ecology of Odonata flight 13
- 1.5 Linking flight performance and dispersal 17
- 1.6 Thesis Outline 19
  - *1.6.1 – Chapter 2* *20*
  - *1.6.2 – Chapter 3* *20*
  - *1.6.3 – Chapter 4* *20*
  - *1.6.4 – Chapter 5* *21*
  - *1.6.5 – Chapter 6* *21*
- 1.7 Conclusion 21

Chapter 2 – Comparative analysis of Odonata flight performance and associations with climate-induced range shifts 23

- 2.1 Abstract 23
- 2.2 Introduction 24
  - *2.2.1 Climate-induced range shifts* *24*
  - *2.2.2 Flight biomechanics* *27*

2.2.3 The Odonata 28

2.2.4 Flight ecology 29

2.2.5 Linking biomechanics and ecology..30

2.3 Materials and Methods..30

2.3.1 Time and location...30

2.3.2 Animal capture and husbandry...30

2.3.3 Flight arena kinematics..33

2.3.4 Image processing 35

2.3.5 Range shift calculations 37

2.3.6 Statistical Analysis...38

2.3.7 Phylogenetic correction 40

2.4 Results...41

2.4.1 Interspecific flight performance..41

2.4.2 Range shifts...42

2.4.3 Range shifts and flight ability 43

2.5 Discussion...47

2.5.1 Linking flight performance and macroecology 47

2.5.2 Variation in flight performance 47

2.5.3 Coenagrion mercuriale flight performance 48

2.5.4 Implications of the work 49

2.5.5 Conclusion 49

Chapter 3 – Functional ecology of Odonata wing morphometrics 51

3.1 Abstract...51

3.2 Introduction 51

3.2.1 Wing shape and flight at different scales 52

3.2.2 Wing shape and ecology 54

3.2.3 Odonata wing morphometrics - Biomechanics......................................55

3.2.4 Odonata wing morphometrics – Ecology and behaviour 56

3.2.5 Flight related morphology 57

3.2.6 Linking wing morphometrics and flight performance 58

3.3 Methods...61

3.3.1 Wing dissection and preparation...61

3.3.2 Wing shape analysis...62

3.3.3 Statistics 64

3.3.4 – Phylogenetic corrections 64

3.4 Results 65
3.4.1 Wing descriptive statistics (SPCA) *65*
3.4.2 Wing shape (GPCA) *66*
3.4.3 Links between wing morphometrics and flight performance *67*
3.5 Discussion 76
3.5.1 The effect of wing morphometrics on flight ability *76*
3.5.2 Comparative wing morphometrics *79*
3.5.3 Future directions *80*
3.5.4 Conclusions *81*
Chapter 4 – Ontogenetic changes in locomotion: no correlation between larval and adult locomotory performance 82
4.1 Abstract 82
4.2 Introduction 82
4.2.1 Biomechanics and hemimetabolous development *82*
4.2.2 Odonata locomotion *84*
4.2.3 Odonata locomotor performance *87*
4.2.4 Locomotor carry-over effects *87*
4.3 Methods 88
4.3.1 Time and location *88*
4.3.2 Animal capture and husbandry *88*
4.3.3 Swimming kinematics *89*
4.3.4 & 4.3.5 Flight kinematics and image processing *91*
4.3.6 Image Processing: Swimming *91*
4.3.7 Statistical Analysis *91*
4.4 Results 92
4.4.1 – Swimming performance *92*
4.4.2 – Flight performance *92*
4.4.3 – Ontogenetic correlation *93*
4.5 Discussion 94
4.5.1 Ontological correlation *94*
4.5.2 Larval muscle development *95*
4.5.3 Swimming performance *96*
4.5.4 Flight performance *97*
4.5.5 Conclusion *97*
Chapter 5 – Modelling the effects of reversible polarotaxis on Odonata dispersal 99

5.1 Abstract 99
5.2 Introduction 100
5.2.1 Dispersal modelling 100
5.2.2 Animal movement 101
5.2.3 Polarotaxis 102
5.2.4 An IBM for reversible polarotaxis 103
5.3 Methods 103
5.3.1 Model construction 103
5.3.2 Model parameterisation 106
5.3.3 Statistical analysis 107
5.4 Results 108
5.4.1 The effect of reversible polarotaxis on dispersal 112
5.5 Discussion 114
5.5.1 Polarotaxis and dispersal 114
5.5.2 Polarotaxis and foraging ecology 116
5.5.3 Ecological traps 117
5.5.4 Model performance 118
5.5.5 Conclusions 119
Chapter 6 – General Discussion 120

6.1 Key findings 120
6.1.1 Chapter 2 120
6.1.2 Chapter 3 121
6.1.3 Chapter 4 122
6.1.4 Chapter 5 122
6.2 Synthesis *123*
6.2.1 Flight Ecology 124
6.2.2 Flight biomechanics 126
6.2.3 Biomechanics and ecology 127
6.3 Future directions 128
6.3.1 Real world dispersal 128
6.3.2 Flight efficiency 128
6.3.3 Comparative studies 129
6.3.4 Validation of laboratory experiments 131
6.4 Conclusion 132
References 133

List of Tables

Table 2.1 – Insect capture locations, dates accessed and species collected (see Table 2.2 for species abbreviations 32

Table 2.2 – Number of insects of 14 odonate species for which some flight data has been collected, and the number of separate flight sequences recorded 34

Table 2.3 – Chapter 2 minimum adequate model parameters with and without phylogenetic correction. Values to 3dp. 43

Table 2.4 – Table of correlation coefficients between the principal components (percentage of variance explained by each component in brackets) of the PCA and the original variables used in the analysis (all coefficients to 3 decimal places). Correlation coefficients over 0.5 are highlighted. 45

Table 3.1 – List of assumptions made about the links between wing morphology and flight performance. *^{1}These assumptions are supported by my data (dark grey, see section 3.5). *^{2}These assumptions are partially supported by my data, i.e. some aspect of flight performance is correlated to the wing metric but not all aspects (light grey, see section 3.5). *^{3}This particular geometric morphometric is similar to 2nd moment of area 59

Table 3.2 – Abbreviations of principal component analyses used in this chapter .. 61

Table 3.3 – Table of correlation coefficients between the principal components (percentage of variance explained by each component in brackets rounded to the nearest 1%) of the PCAs on wing statistics (SPCAs) and the original variables used (all coefficients to 3 decimal places). Only principal components with eigenvalues of 1 or higher or components above the elbow of the scree plot of the analysis are shown. Correlation coefficients over 0.5 are highlighted. 69

Table 3.4 – Explanation of separate principal components 71

Table 3.5 – AICc tables for mixed effects models (only includes the 3 minimum AICc models of 167 total models for each response variable). Data for the combined models (including forewing and hindwing data). 73

Table 3.6 – Minimum adequate mixed model parameters for combined forewing and hindwing data. All figures to 3dp, significant p values denoted with *. 74

Table 3.7 – Chapter 3 minimum adequate mixed model parameters with and without phylogenetic correction. Values to 3dp. 75

Table 3.8 – Statistically significant relationships between flight performance data and wing morphology. C: combined forewing and hindwing analysis. F: separate forewing analysis. H: Separate hindwing analysis. *Significant interaction term. . 79

Table 5.1 – AICc tables for all generalised linear models constructed. Habitat availability refers to the percentage freshwater habitat available. 111

Table 5.2 – Minimum adequate model parameters. Habitat availability refers to the percentage freshwater habitat available. *Indicates a Wald’s test has been carried out, otherwise t tests were performed. 113

List of Figures

Figure 1.1 – Photos of *Anax imperator* (Anisoptera) in flight and ovipositing. Photos by Alandmanson and Ken Billington respectively, both under a creative commons license CC-BY-SA.. 3

Figure 1.2 – Anatomical drawings of the diversity of UK Odonata forms from Lucas (1900). Not to scale – but relative scales are maintained. Males are on the left females on the right A) *Anax imperator* (Anisoptera), B) *Libellula quadrimaculata* (Anisoptera), C) *Sympetrum striolatum* (Anisoptera), D) *Ischnura elegans* (Zygoptera), E) *Pyrrhosoma nymphula* (Zygoptera), F) *Calopteryx splendens* (Zygoptera). 4

Figure 1.3 – Cross section of a theoretical aerofoil showing typical forces involved during flight 7

Figure 1.4 – Phylogenetic relationships of insect taxa and flight muscle characteristics. Dashed lines represent lineages with tenuous support. Figure from Trautwein et al. (2012) and Dudley (2000).. 8

Figure 1.5 – Diagrams showing horizontal and inclined stroke plane hovering. A) Horizontal hovering seen in hummingbirds and most insects. Adapted from Stolpe and Zimmer (1939). B) Inclined stroke plane hovering seen in Odonata. Adapted from Alexander (2004). 13

Figure 2.1 – Experimental setup for 'mirror corner-cube' flight arena.................. 35

Equation 2.1 – 4th Difference smoothing:.. 36

Equation 2.2 – 4th Difference smoothing, 1st point edge case:.............................. 36

Equation 2.3 – 4th Difference smoothing, 2nd point edge case:............................. 36

Equation 2.4 – 4th Difference smoothing, penultimate point edge case: 37

Equation 2.5 – 4th Difference smoothing, last point edge case: 37

Equation 2.6 – Velocity (and acceleration): 38

Equation 2.7 – Velocity (and acceleration), 1st point edge case: 38

Equation 2.8 – Velocity (and acceleration), 2nd point edge case: 38

Equation 2.9 – Velocity (and acceleration), last point edge case: 38

Equation 2.10 – Velocity (and acceleration), penultimate point edge case: 38

Equation 2.11 – Curvature: 38

Figure 2.2 – UK temperature from 1990 to 2015. Solid line represents average annual temperatures, and the dashed line is the statistically significant trend. 39

Figure 2.3 – Phylogenetic tree showing the relationships of the Odonata species studied in chapter two and three. 41

Figure 2.4 – Means of FPC1 (flight speed) and FPC2 (efficient flight behaviour) plotted with standard errors for each of the 13 species studied. Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. See Table 2.1 for species abbreviations. 42

Figure 2.5 – Calculated northward shift of the northern range margin for 13 UK species, grouped by taxonomy, shaded by status and labelled by species abbreviation (see Table 2.1). Range shifts are movements from the period of 1990-2000 to the period of 2005-2015 44

Figure 2.6 – Common squares method (CSM) calculated range shifts against A) flight speed (FPC1) and B) efficient flight behaviour (FPC2), labelled by species abbreviation (See Table 2.1). Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. Note that *Coenagrion mercuriale* (*Cm*) was excluded from the analysis and as such that point above is not included in the model best fit line. 46

Figure 3.1 – A) Diagram showing wing length and wing chord (average chord is the average of the chord across the entire length of the wing). B) Example of a high aspect ratio wing. C) Example of a low aspect ratio wing. D) Example of low wing loading. E) Example of high wing loading. 62

Figure 3.2 – Anisoptera (*Aeshna grandis*) forewing (A), hindwing (B) and landmarks used in the GPCA. Zygoptera (*Erythromma najas*) hindwing (C) and landmarks used in the GPCA. Zygoptera fore and hindwings have very similar structure so only one wing is shown here. 63

Figure 3.3 – Scatter graphs of species' average hindwing statistic vs. forewing statistic (left and right wings). A) Wing length, B) wing chord, C) wing area, D) wing loading. Error bars represent standard error and the line on each graph corresponds to 1:1. Where error bars are absent n=1. Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. For species abbreviations see Table 2.2. 67

Fig. 3.3 cont. – Scatter graphs of species' average hindwing statistic vs. forewing statistic (left and right wings). E) Aspect ratio, F) 2nd moment of area, G) 3rd moment of area, H) log total insect mass vs. femur length. Error bars represent standard error and the line on each graph corresponds to 1:1. Where error bars are absent n=1. Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. For species abbreviations see Table 2.2. 68

Figure 3.4 – Back-transform morphospace (Olsen, 2017) of the left forewings (-F) and hindwings (-H). Points are average principal component values for species. Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. See table 2.2 for species abbreviations. Landmarks are labelled on the back-transform morphospace as follows: Arculus (Ar), Nodus (N), Pterostigma (P), R1, R2, R3, R4, CuP, Anal cell (A).. 70

Figure 3.5 – See caption on next page (p73). 72

Figure 3.5 - Scatter graphs showing the relationships between FPC1, 2 and 3 (flight speed, efficiency of flight behaviour and flight path curvature respectively) and statistically associated wing statistics (SPCs and GPCs). Percentage variance explained by each PC is in brackets, error bars are standard errors. Relevant model fits (averaged across all species) are added with solid lines except: A) Model fits are added for GPC1-H = 0.2 (solid line – broad, non-petiolate wing), 0.1 (dashed line), 0 (dotted line) and -0.1 (finely dotted line – slim, petiolate wing). B) Model fits are added for SPC1-H = 1 (solid line – small, slender wing), -2 (dashed line) and -5 (dotted line – large, broad wing). C) Colour surface plot showing predicted flight speed (FPC1) from model fit of SPC1 and GPC1. Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. See table 2.2 for species abbreviations. 73

Figure 4.1 – See next page for full caption (p86). 85

Figure 4.1 cont. – Figures adapted from Maloeuf (Maloeuf, 1935), showing differences between adult and larval muscle structure. Right half of an adult and larval *Plathemis lydia* thorax. The muscles in the adult (B) are considerably fewer and larger, running mostly vertically, whereas in the larva (A), the vertical flight muscles are mostly reduced and horizontal muscles are larger, allowing longitudinal contractions for jet propulsion in this species. To aid interpretation, I have coloured the image to highlight different muscle groups: flight muscles are coloured in blue and muscles and features absent in the adult are coloured in red. Muscle 66 is coloured in yellow as it may have abdominal function – but Maloeuf's description is unclear. 86

Figure 4.2 – Experimental setup (not to scale) 90

Figure 4.3 – Model II regression graphs. A) Average horizontal swimming speed vs. horizontal average flight speed. B) Average horizontal swimming acceleration vs. average horizontal flight acceleration. C) Maximum horizontal swimming speed vs. horizontal maximum flight speed. D) Maximum horizontal swimming acceleration vs. maximum horizontal flight acceleration. 93

Figure 4.4 – Time from egg laid to time of recording of swimming data vs. A) average swimming speed and B) average swimming acceleration. The time is representative of growth speed up until the larvae grows a head width of 3mm.. 94

Figure 5.1 – Dispersal kernel used in trial movements 105

Figure 5.2 – Diagram of model process. Green represents foraging (immature) habitat and blue represents breeding habitat (mature). The process pictured here is initiated if a random number between zero and 100 generated at each time step is less than the percentage chance of moving based on the current habitat. The left panel shows an immature insect (green habitat is suitable habitat), the right panel shows a mature insect (blue habitat is suitable habitat). 107

Figure 5.3 – A comparison of paths taken by 50 individuals for 10 years (left) without and (right) with reversible polarotaxis, showing greater dispersal in the non-polarotactic run. Line colour is related to the year of the model run with bright red being year 10 and dark red being year 1. 109

Figure 5.4 – Scatter graphs of freshwater habitat area against average dependent variables. Points are mean values for each year within each grid, averaged across all 50 individuals. Filled circles represent non-polarotactic simulations, open circles represent simulations with reversible polarotaxis. Lines are minimum adequate glm fits of non-averaged data, with dashed lines for reversible polarotaxis and solid lines for non-polarotactic. A) Distance travelled, B) Potential area covered, C) Distance dispersed (displacement), D) Proportion of individuals ending lifespans in reproductive habitat, E) Time taken to reach feeding habitat and F) Time spent in feeding habitat. 110

Figure 6.1 – A) Vector field produced during a swimming (jet propulsion) trial of a *Sympetrum striolatum* larva, showing a single jet produced by the larva. B) Vorticity calculated from 6.1 A 130

List of abbreviations

p = position or dimensional co-ordinate

u = velocity

a = Acceleration

K = Curvature

AR = Aspect ratio

LEV = Leading edge vortex

PIV = Particle image velocimetry

PCA = Principle components analysis

Ai = *Anax imperator* (Emperor dragonfly)

Ag = *Aeshna grandis* (Brown hawker)

Aj = *Aeshna juncea* (Common hawker)

Cm = *Coenagrion mercuriale* (Southern damselfly)

Cp = *Coenagrion puella* (Azure damselfly)

Cs = *Calopteryx splendens* (Banded demoiselle)

Ec = *Enallagma cyathigerum* (Common damselfly)

En = *Erythromma najas* (Red-eyed damselfly)

Ev = *Erythromma viridulum* (Small red-eyed damselfly)

Ie = *Ischnura elegans* (Blue-tailed damselfly)

Ip = *Ischnura pumilio* (Scarce blue-tailed damselfly)

Lq = *Libellula quadrimaculata* (Four-spotted chaser)

Oc = *Orthetrum cancellatum* (Black-tailed skimmer)

Pn = *Pyrrhosoma nymphula* (Large red damselfly)

Ss = *Sympetrum striolatum* (Common darter)

Chapter 1 – Introduction: A review of dragonfly flight ecology

1.1 Abstract

As the most successful animal taxon on earth, insects and insect flight have received considerable attention. Research into dragonfly and damselfly (Odonata) flight first appeared in 1921, and then developed quickly to detailed analyses of flapping flight and the unsteady forces involved. The discovery of a range of unsteady flight mechanisms and advanced techniques for flow visualisation has greatly enhanced our understanding of insect flight. The Odonata also display a few unique aspects of flight performance among insects, such as direct muscle attachment to the wings/wing hinges, which allows out of phase wing strokes and they employ an unusual mode of hovering. The Odonata are important model systems for studying ecological and evolutionary processes, but they are particularly suited as a model system for flight, due to their relatively large size compared to other insects and that much of their adult life revolves around flight. Much work has been carried out attempting to understand how flight performance influences dispersal in insects, however we lack a mechanistic and empirically evidenced understanding of how proxies for flight performance (i.e. wing size and shape) are linked to quantitative measures of performance. Because of this lack of evidence, flight performance is often dismissed as an important driver of macroecological processes. Here I review the biomechanics of Odonata flight and Odonata ecology, highlighting the importance of dispersal and the current lack of biomechanical input and support to Odonata ecology. I then outline the steps I have taken to address the lack of biomechanical input and provide an understanding of the processes driving variation in flight performance and its effect in the field. I found that biomechanical input to ecological study exists but is sparse at best. Biomechanics could provide much needed insight into ecological processes, namely, the biomechanics of dispersal movements should help us to understand climate induced range expansions. In addition it is not yet clear how morphology drives variation in dispersal movements.

1.2 Introduction

The Odonata (dragonflies, Anisoptera and damselflies, Zygoptera) are a charismatic insect order remarked for their flight ability (see Figure 1.1 and 1.2). The order is ancient and considered to be relatively primitive due to its similarity to the Protodonata, an extinct order known from some of the earliest insect fossils (May, 1982). All members of the group are hemimetabolous, with an aquatic larval stage developing into a winged adult form. The Odonata are an important taxon in ecology, particularly as they live in freshwater – one of the most threatened habitats globally (Nel et al., 2009). For example, Odonata are used as indicator species for water and habitat quality (Oertli, 2008), and they play a significant role in investigating responses to climate change, particularly range shifts (Harabiš and Dolný, 2012; Hassall and Thompson, 2008; Hassall et al., 2007; Hassall et al., 2014; Hickling et al., 2005; Zeuss et al., 2014).

Adult Odonata rely on flight performance for territory defence, copulation, defence of ovipositing females, and are one of few invertebrates to capture prey on the wing (Corbet, 1999). Odonata flight musculature is also attached directly (direct flight musculature, see Section 1.3.2) to the wings using a hinge system for elevation and depression (Büsse, 2013; Büsse and Hörnschemeyer, 2013; Büsse et al., 2013; Thomas et al., 2004). Direct flight musculature is not seen in other more derived insect groups and allows the Odonata to control each wing separately (Thomas et al., 2004). As such, they are an attractive group for investigating flight performance – displaying the highest flight muscle ratios (FMR, ratio of flight muscle mass to total organismal mass) known among animals: up to 56% of adult body mass in Anisoptera (Córdoba-Aguilar, 2008; Marden, 1987; Marden, 1989).

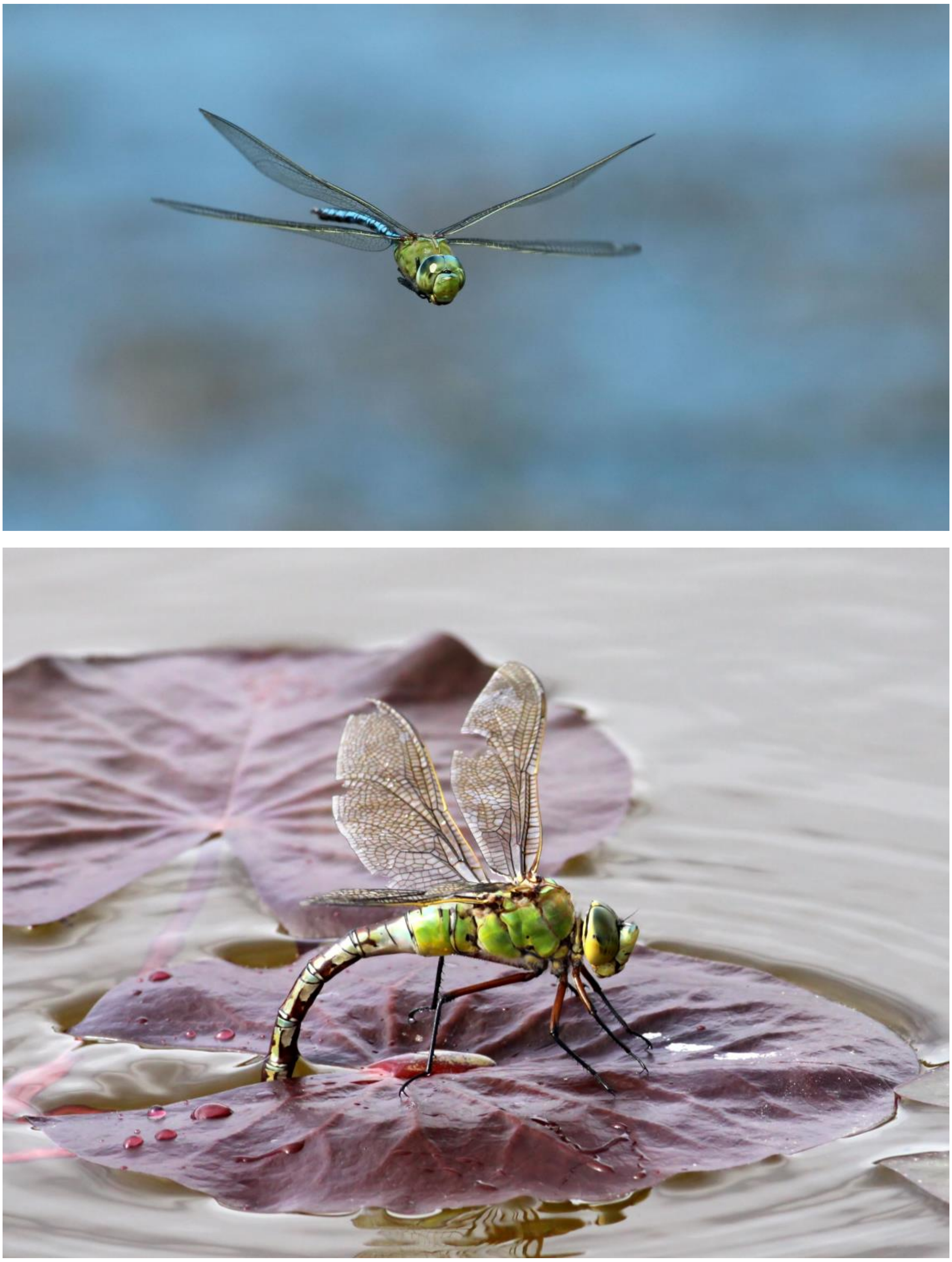


Figure 1.1 – Photos of *Anax imperator* (Anisoptera) in flight and ovipositing. Photos by Alandmanson and Ken Billington respectively, both under a creative commons license CC-BY-SA.

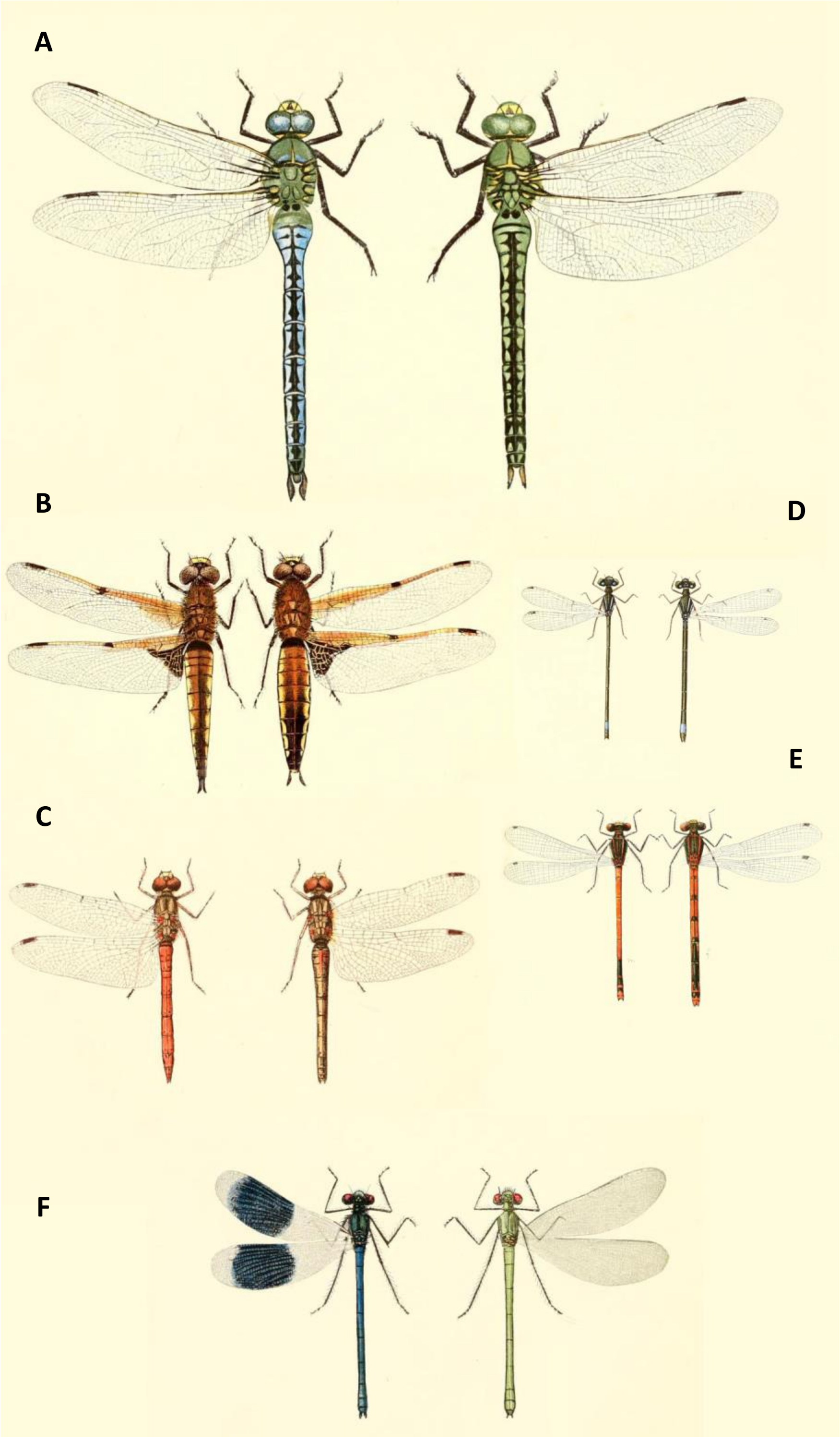


Figure 1.2 – Anatomical drawings of the diversity of UK Odonata forms from Lucas (1900). Not to scale – but relative scales are maintained. Males are on the left females on the right A) *Anax imperator* (Anisoptera), B) *Libellula quadrimaculata* (Anisoptera), C) *Sympetrum striolatum* (Anisoptera), D) *Ischnura elegans* (Zygoptera), E) *Pyrrhosoma nymphula* (Zygoptera), F) *Calopteryx splendens* (Zygoptera).

1.3 Flight Biomechanics

1.3.1 Insect flight

General animal flight involves the cyclic elevation and depression of aerofoils (wings), each of which is known as a ‘stroke’, with supination (up-turning motion) of the wing at the end of the downstroke and pronation (down-turning motion) at the end of the upstroke. As the wing travels through the air it creates two forces, lift and thrust, which allow the animal to stay aloft and move forward respectively (see Figure 1.3). In general lift is generated by the circulation of air around the wing, which creates pressure inequalities due to the differing flow speeds above and below the wing. Fixed wing (i.e. a wing which remains stationary relative to the body) flight had received considerable attention by the time the first insect flight studies were being carried out, due to its use in aviation, and the relative ease of describing steady aerodynamic conditions (Alexander, 2004). Steady flows are movements of air in which the velocity of airflow at any one point remains constant over time (but each point may have different velocities). The closest insects come to fixed wing flight is gliding, which only a few insect species do, and it is not their primary method of locomotion (Weis-Fogh and Jensen, 1956). Several early studies of insect flight suggested that unknown aerodynamic effects were responsible for empirical lift and drag measures higher than those theoretically predicted (Dudley, 2000; Osborne, 1951). Numerous studies have alternatively tried to show that steady aerodynamics can explain insect flight, using quasi-steady analyses of aerodynamics (Azuma and Watanabe, 1988; Azuma et al., 1985; Jensen, 1956; Weis-Fogh, 1956). Quasi steady analyses were developed form theory borrowed from helicopter flight known as blade element analysis. The wing is split into sections (or ‘blade elements’) and local angle of attack and airspeed are analysed for each section, allowing the calculation of lift and drag coefficients. Summing the values for each section provides an approximation for the total lift and drag of the entire wing at a given instant. Treating each instant as a short period of steady motion (hence ‘quasi-steady’), researchers then applied the method across a large number of instants for the entire wing stroke.

Whilst steady flows have been able to explain some insect flight, unsteady flows have been discovered to be an important part of flapping flight. Unsteady flows are flows of air in which the velocity of airflow of any one point does change over time. The inappropriate application of aerodynamic theory can be misleading, for example, the popular misconception that bumblebee flight does not obey the laws of physics (Altshuler et al., 2005). The misconception was brought about when fixed wing aerodynamics were applied to an insect with flapping flight. The first unsteady mechanism to be described was the ‘clap and fling’ which was first discovered in chalcid wasps (Alexander, 2004; Weis-Fogh, 1973). The ‘clap and fling’ mechanism increases the amount of lift produced during the down stroke, by starting the circulation of air around the wing, and hence lift, earlier in the stroke. At the top of the stroke, the wings are clapped together and then flung apart, with the trailing edges of the wings forming a hinge. Since then, other unsteady mechanisms have been discovered within insect flight including the leading edge vortex (Ellington et al., 1996; Thomas et al., 2004), and wing-wake interactions (Thomas et al., 2004).

With advances in both technology and theory, detailed flow analysis is now available through computational fluid dynamics (the use of computers to model complex unsteady flows (Vargas et al., 2008)) and advanced flow visualisation techniques such as digital particle image velocimetry (DPIV). The most important discovery through these techniques has been the presence, structure and effect of the leading edge vortex (LEV), which increases the lift of the wing (Dickinson and Götz, 1993). The LEV is an area of circulating air (vortex) formed over the leading edge of the wing during flight, and was first discovered for insects in the moth *Manduca sexta* (Bomphrey et al., 2005; Ellington et al., 1996), following which a number of different LEV structures have been described (Bomphrey et al., 2009b).

For many more derived insects, wing-wake interactions are less important or non-existent – except perhaps when hovering – as they only have one functional pair of wings (either they only possess one pair of wings or their forewings and hindwings are fused or attached to form a single pair of wings). For insects with two pairs of wings, the hindwings must travel through the wake of the forewings for at least some part of the stroke. In the Odonata a number of theories as to the potential disadvantages (Hu and Deng, 2009; Sun and Huang, 2007; Usherwood and Lehmann, 2008; Wang and Sun, 2005) and advantages (Hu and Deng, 2009; Usherwood and Lehmann, 2008; Wang and Russell, 2007) have been put forward, suggesting that out of phase flapping is present to minimise interaction or that the hindwing is able to conserve energy by "capturing" the wake of the forewing (see Section 1.3.3). In general there appears to be no increase in lift or other aerodynamic forces through wing-wake interactions during normal out of phase flapping but the efficiency of flight is increased. On the other hand in phase flapping whilst energetically expensive does increase lift and power (Thomas et al., 2004; Wang and Russell, 2007).

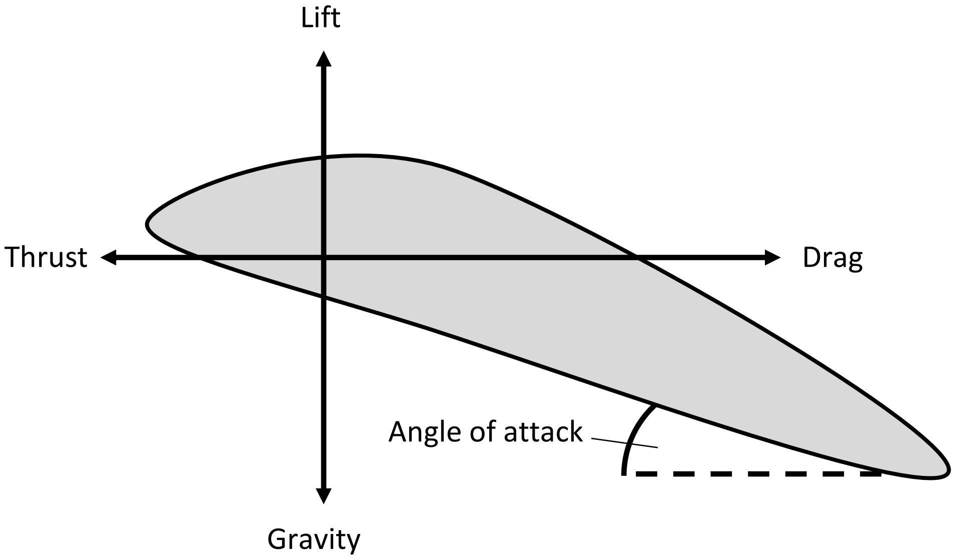


Figure 1.3 – Cross section of a theoretical aerofoil showing typical forces involved during flight

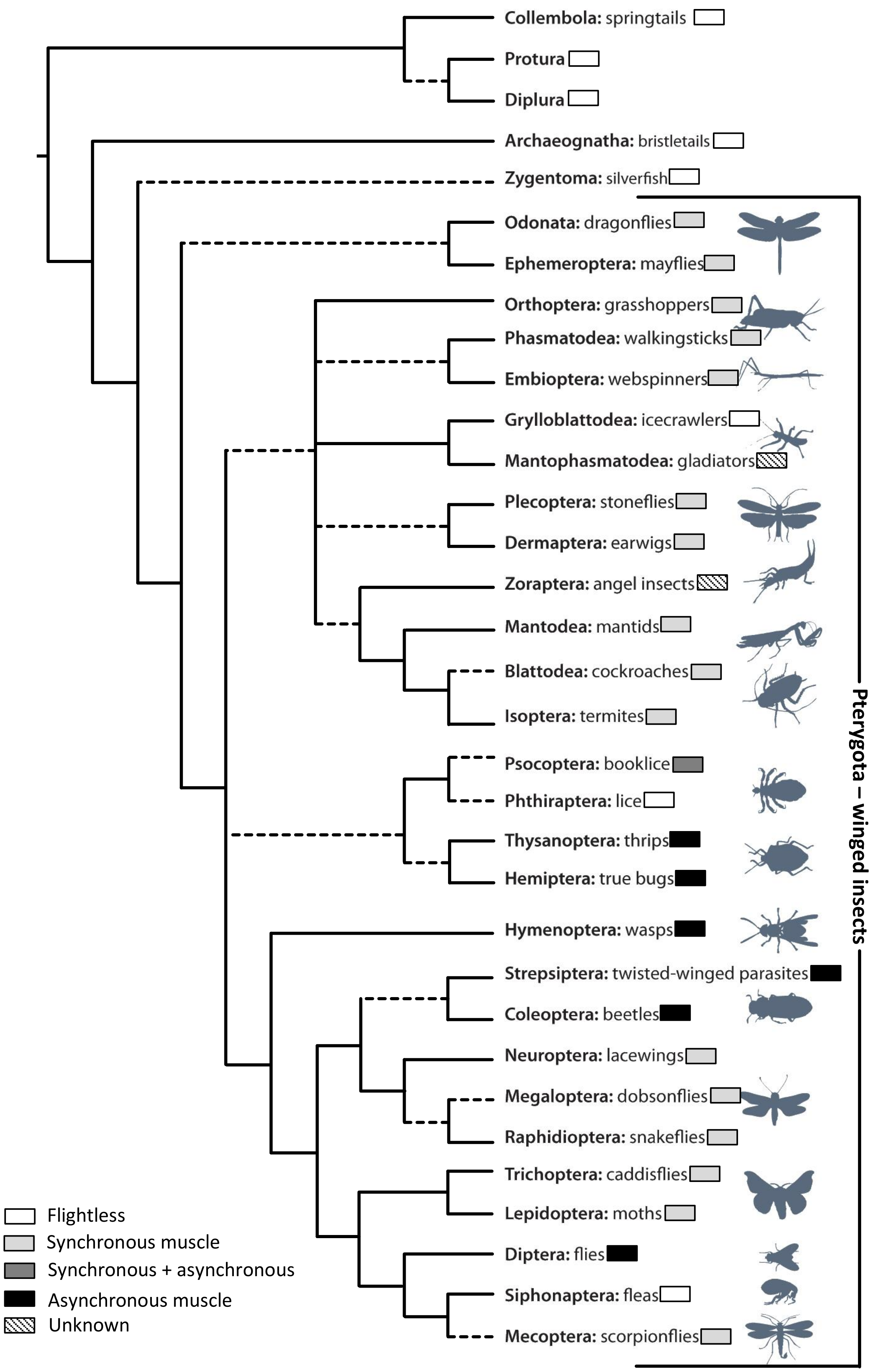


Figure 1.4 – Phylogenetic relationships of insect taxa and flight muscle characteristics. Dashed lines represent lineages with tenuous support. Figure from Trautwein et al. (2012) and Dudley (2000)

1.3.2 Odonata muscle physiology

Flight performance, particularly efficiency, is strongly affected by the physiology and energetics of flight muscles. The flight muscles, mediated by the physiology of wing hinges and other exoskeleton elements, affect the range of possible kinematics for the wingbeat, the efficiency of energy transfer to the surrounding air and the power with which this is done. The layout and function of muscles in the Odonata thorax has been known for some considerable time, but has only been covered in precise detail recently by Büsse (Büsse, 2013; Büsse et al., 2013). The muscle is synchronous (the rate of contraction is coupled to the rate of stimulation) as in some other primitive orders, most notably Orthoptera (see Figure 1.4). Orthoptera muscle properties are well described, but measures of efficiency and power output from Odonata muscles are relatively scarce (Ellington, 1985). Another important and evolutionarily primitive feature of the Odonata is that their flight muscles are connected directly to their wings or wing hinges (known as direct musculature or direct flight) allowing them control of each wing separately (Pfau, 1991). Other insects' musculature is indirect and deforms the exoskeleton of the thorax in order to transfer motion to the wings. Odonata have one of the highest ratios of flight muscle mass to total mass (FMR) known, up to 56% of body-weight (Córdoba-Aguilar, 2008; Marden, 1987; Marden, 1989). The effect of flight muscles on flight performance is reviewed by Marden (Córdoba-Aguilar, 2008), showing strong effects on aerodynamic power output and also on ecologically relevant measures of flight ability such as success in territorial disputes (Marden and Cobb, 2004).

An important aspect of flight muscle physiology is the scaling of forces produced by the muscles and those transferred from the wing to the surrounding air. Forces produced by muscles depend primarily on their cross-sectional area and will theoretically scale as the mass of the muscle$^{2/3}$ ($M^{0.67}$), however forces measured in various animal flight systems scale with a ratio close to M^1 (Marden et al., 2008). $M^{0.67}$ scaling means that usually the force output of a muscle increases close to unity with increasing mass at low masses, but the increase in force per unit mass decreases as mass increases. At M^1, force increases linearly with mass, which means that large muscles are not as inefficient (they can produce higher forces at the same mass value) as other systems where scaling remains at $M^{0.67}$. Schilder and Marden

(2004) used Odonata to show that $M^{0.67}$ was only relevant to isotonic muscle contractions (an isotonic contraction is one where the tension within the muscle remains constant) not typical of the oscillatory contractions (where muscles cycle between contraction and relaxation) seen *in vivo* during flight – measuring a scaling factor of $M^{0.83}$ for oscillatory work loops in odonate flight muscle. Further, they demonstrated that when considered *in vivo*, the scaling of mechanical levers in the dragonfly flight system also departed from the norm, allowing overall scaling ratios of roughly M^1 ($M^{1.036}$, not significantly different from M^1).

Temperature affects muscle efficiency, and thus flight performance. There are thermal minimum and maximum temperatures at which flight can occur (May, 1976a), and within these ranges temperature affects the wingbeat frequency in Odonata (May, 1981). In addition Odonata change their behaviour to help regulate their temperature (Mason, 2017). As flight occurs, excess heat is produced by the muscles, and in larger Odonata temporary endothermy is seen during prolonged flight with heat production from flight muscles balanced by pumping of haemolymph from the thorax to the abdomen (May, 1995; May, 2017). At high ambient temperatures in larval environments, for example those caused by climate change, adult Odonata morphology is altered, reducing flight performance through lower muscle masses, and apparently smaller wings (McCauley et al., 2018; Tüzün et al., 2018, but see Chapter 3).

1.3.3 Odonata flight biomechanics

The Odonata have four wings, each of which can be controlled separately, giving them greater control during flight. The precise kinematics and the muscular movements responsible for them were first described by Neville (1960), describing the movements of the elements of the wing hinges, basic kinematics of the wing motion and demonstrating experimentally that several muscles are involved in subtle changes to the wing motion, but notably the coxolar muscle is involved in elevation, supination and remotion (backwards motion) of the wing. The kinematics described here were however relatively basic, including just angles of elevation and depression, stroke plane angle (the 2-dimensional plane through which the wings cycle up and down), and the timing of stroke reversal. Another important observation, unique to the Odonata, is the difference in timing between the hind and forewings. Neville showed that the cycle of forewing movements is slightly behind that of the hindwings, i.e. as the hindwings are beginning the upstroke, the forewings are still part way through the downstroke. This style of flight is known as counter-stroking or “out of phase flight”, where the phases of the two separate wings differ.

One of the most detailed analyses of Odonata flight to date is a series of papers by Wakeling and Ellington, which describe steady gliding flight (1997c) and the precise flight kinematics and quasi-steady aerodynamics for two species of Odonata, one Anisoptera and one Zygoptera (1997a; 1997b; 1997c). There are significant differences in flight between Zygoptera and Anisoptera, with Anisoptera flying faster, with greater acceleration, higher wingbeat frequencies and smaller wingbeat amplitudes (Rüppell, 1989; Wakeling and Ellington, 1997b). It has also been suggested that Zygoptera flight performance is relatively invariant, as they have to produce close to maximum performance to stay aloft (Rüppell, 1989). Interestingly, although the different flight abilities between the two groups has been confirmed, the performance of the Zygoptera wing appears to actually be relatively more efficient (when correcting for mass, Zygoptera wings produce more thrust) than the Anisoptera, suggesting a more effective wingbeat in Zygoptera (Rüppell, 1989; Wakeling and Ellington, 1997b). The main limitation of Wakeling and Ellington’s work is the treatment of both wings as one, ignoring flow interactions between the fore and hindwings, and that some lift is generated through unsteady mechanisms, first suggested by Somps and Luttges (Somps and Luttges, 1985). They show that in Zygoptera the ‘clap and fling’ mechanism is used (Wakeling and Ellington, 1997b), whereas they cite unsteady lift generation in the Anisoptera as an avenue for further study when more detailed flow analysis is available (Wakeling and Ellington, 1997c).

As detailed flow analysis became available, the assumption that interactions between fore and hindwings in Odonata generated lift through unsteady mechanisms was partially confirmed for Odonata. The LEV structure for the forewing in Odonata is U-shaped, forming over the forewing during the downstroke, usually during pronation of the forewing (Thomas et al., 2004). When shed, the forewing LEV appears to be “captured” by the hindwing in normal counter-stroking flight, i.e.

the vortex (and hence energy) left behind by the forewing is intersected with the hindwing generating lift and recapturing a portion of that energy, making interaction between the fore and hindwing beneficial (Hu and Deng, 2009; Sun and Huang, 2007; Thomas et al., 2004; Usherwood and Lehmann, 2008; Wang and Russell, 2007; Xie and Huang, 2015). The direct musculature of the Odonata means they are able to vary the phase difference between their fore and hindwings during flight, which allow them to control LEV formation and prevent stalling by altering angle of attack (Thomas et al., 2004). Varying phase differences allow the Odonata to switch between different modes of flight to trade between power and efficiency (Alexander, 1984; Rüppell, 1989), or increase oscillation damping for more stable flight (Wang and Russell, 2007), presumably useful for vision and predation. Control of flight must be precise as whilst certain ranges of phase differences are beneficial, providing vibration stabilisation or reduced energy required for flight, others have can have detrimental effects such as decreasing the overall lift produced (Sun and Huang, 2007; Wang and Russell, 2007; Wang and Sun, 2005).

A unique aspect of Odonata flight is the mechanism of hovering flight employed. Hovering flight differs substantially from normal forward flight as whilst travelling forward, there is air flowing over the wings and thus some lift is generated, whether the animal is flapping the wings or not. In hovering flight it is only the movement of the wings that generates air flow over the wings. Insects are among the only fliers that regularly hover as they are among the only fliers powerful enough to do so, and those insects that do are generally relatively small in comparison to the Odonata and have indirect musculature. To hover they are able to sweep their wings back and forth in a horizontal stroke plane, generating lift on both the upstroke and down stroke (see Figure 1.5). The Odonata hover using an inclined stroke plane, up to 60° from the horizontal (Alexander, 2004; Ellington, 1984a).

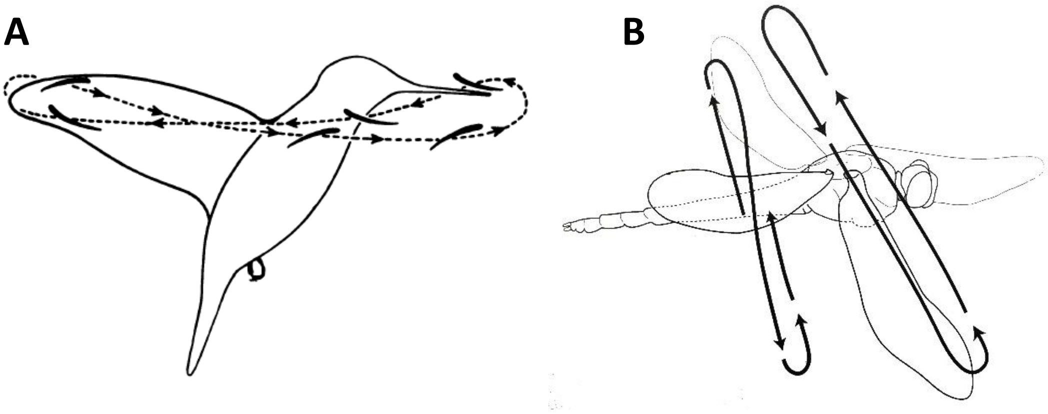


Figure 1.5 – Diagrams showing horizontal and inclined stroke plane hovering. A) Horizontal hovering seen in hummingbirds and most insects. Adapted from Stolpe and Zimmer (1939). B) Inclined stroke plane hovering seen in Odonata. Adapted from Alexander (2004).

At first, this style of hovering seems counterintuitive as the majority of the lift required must be provided during the down stroke, whereas other insects are able to provide significant quantities of lift on the upstroke. Hypothesised advantages for inclined stroke plane hovering include the ability to remain horizontal (note the body angle of the hummingbird in Figure 1.5 is close to vertical, whereas the Odonata is horizontal) whilst hovering, allowing better vision for prey detection and predator evasion, and/or possibly allowing faster or more efficient starts to forward flight than in insects that hover normally (Alexander, 2004). On closer inspection, birds seen using inclined stroke plane hovering are usually flying into a headwind rather than truly hovering, and this could be the case for dragonflies too (Wakeling and Ellington, 1997c). Given that inclined stroke plane hovering requires more power than normal hovering (the upstroke does less useful work), it may explain why Odonata do not hover for significant periods of time.

1.4 The ecology of Odonata flight

Where animals have evolved the means to fly, it is usually the primary if not only means of locomotion, as flight is energetically very costly (Dudley, 2000; Schmidt-Nielsen, 1972). The benefits of flight and their energetic cost mean that variation in flight ability should play an important role determining an individual animals' fitness. However, our knowledge of effects of flight performance on individual fitness are largely confined to predation or mating success as measuring dispersal for individual insects is challenging (Kissling et al., 2014). Several attempts with varying degrees of success have been made through radio telemetry to track the movements of Odonata but have not looked to relate these movements to flight performance (Hardersen, 2007; Wikelski et al., 2006). By far the greatest portion of work on Odonata dispersal is through mark release recapture studies, detailing how far from a natal water source recaptured individuals have been found (Allen and Thompson, 2010; Angelibert and Giani, 2003; Anholt, 1990; Conrad et al., 1999; Rouquette and Thompson, 2007; Thompson, 1991; Thompson and Purse, 1999). Empirically, Zygoptera that dispersed were found to be heavier (remembering that Odonata have very high flight muscle ratios) at emergence, suggesting that better fliers were better dispersers or more likely to disperse (Anholt et al., 1991), although conflicting evidence has been presented showing no relationship between flight performance related characters and dispersal. It has been argued that any relationship seen between mass and dispersal is likely an artefact of development time for mass and that Anholt et al. did not record maiden flights (Thompson, 1991).

The effects of flight performance on mating success have been demonstrated through correlations between muscle power and mating success (Marden and Cobb, 2004). Flight muscle gain in Odonata is rapid during maturation, with some sexual dimorphism seen, as females increase abdomen (ovaries) mass in addition to thorax (flight muscle) mass (Anholt et al., 1991; Marden, 1989). Increased FMRs have been correlated with mating success (Marden, 1989), suggesting that they do contribute to flight performance as both mating and territory defence in Odonata requires flight. However, there is an implied trade-off between FMR (proxy for flight ability) and gut content/fat reserves (nutritional state) (Marden and Waage, 1990). Odonata therefore have to balance short term competitive ability and long term mating success for competition or “energetic wars of attrition” (Gyulavári et al., 2017; Marden and Waage, 1990; Takeuchi et al., 2016). There can also be stabilising selection on body size and thus flight muscle mass in some species with scramble competition (Stoks, 2000), whereas others show no trend between mating performance and putative flight ability (Vilela et al., 2017), suggesting that there are different selection pressures on flight depending on mating system. It is interesting to note that in other species, such as butterflies, similar display behaviour is apparently attributable to ‘erroneous courtship’ rather than ‘wars of attrition’ (Takeuchi et al., 2016), but whether flight performance has a different role given the different mechanism remains to be seen.

Little previous work has examined prey capture in the Odonata in detail, due to the difficulty of observing the precise nature of the interaction – predation can be difficult to observe in the field and difficult to reproduce in the laboratory. The links between flight performance and high predation success (usually 80-90% for suitably sized prey) (Combes et al., 2013) of Odonata have been shown in some detail recently, using quantitative measures of flight performance, showing that wing damage reduced flight performance and hence the usually high predation success rates (Combes et al., 2010). Predatory pursuit flight has now been well described in Odonata, including the neurobiology of prey detection, predictive flight paths (Bomphrey et al., 2016; Combes, 2015; Combes et al., 2013; Mischiati et al., 2015) and the diets of wild individuals – showing that species and size of prey is generally consistent across species (Kaunisto et al., 2017), although no large Anisoptera were studied.

The previous studies have primarily considered patterns and processes regarding single individuals, and so here I describe the smaller body of work on species or populations. At the population level flight performance should logically be linked with dispersal: animals that can move with greater efficiency or performance should be better equipped to disperse further or negotiate potential dispersal barriers. For example, flying animals are often the first to colonise new terrain such as volcanic islands (Alexander, 2004). Dispersal can be defined as the movement of a species away from its natal habitat or origin, i.e. any movement that allows the flow of genes spatially (Ronce, 2007). Dispersal is an important factor in any population as it affects a multitude of processes, such as gene flow between populations, the ability of a population to respond to environmental changes and the persistence of metapopulation structures. For flying animals the speed at which they can move is usually higher than any terrestrial form of locomotion, and physical barriers are more easily overcome. Swarming (dispersive) locusts are known to exhibit changes in morphology enhancing flight performance, with two different morphs, a long winged dispersive morph and a short winged sedentary morph (Harrison, 1980; Holland et al., 2006). In the Odonata and many other insects discrete morphs are not present, but rather continuous variation in wing morphology can occur, sometimes across a geographical cline from the centre to the edge of a species' range (range front), particularly where a species is expanding its range (Hassall, 2015; Hassall et al., 2008; Hassall et al., 2009; Therry et al., 2014; also see Hill et al., 2011). The changes in morphology are rarely as extreme as in discrete morphs, but swarming behaviour can still be observed (Holland et al., 2006). Variation in wing size also occurs across latitudinal gradients, although both Bergmann (increasing body size with latitude due to decreasing temperature) and converse Bergmann clines (decreasing body size with latitude due to shorter growing seasons) are seen in arthropods with some species becoming larger at higher latitudes (for example, Diptera and Hymenoptera) and others smaller (for example, Lepidoptera and Odonata) (Blanckenhorn and Demont, 2004; Chown and Gaston, 1999). These changes in insect mass and wing size are very likely to have an impact on insect flight performance and are potentially direct evidence of an impacted flight performance due to climate, however the precise nature of the effect of wing morphology on flight performance is not clear (see Chapter 3).

With climate change affecting ecosystems on a global scale (Parmesan and Yohe, 2003), one of the primary population responses is poleward (or altitudinal) range shifts (Hassall and Thompson, 2008; Hickling et al., 2005; Hickling et al., 2006; Parmesan, 2006; Parmesan et al., 1999; Walther et al., 2002), highlighting the need for greater understanding of dispersal processes. Again flight performance should logically play a role in the dispersive movements required to establish new populations at higher latitude or altitude. The Odonata are a good candidate for dispersal studies in relation to climate change, as their development is directly proportional to temperature and they have shown considerable and immediate responses to climate change (Hassall, 2015b; Hassall and Thompson, 2008; Hickling et al., 2005; Hickling et al., 2006; Mason et al., 2015), shifting ranges polewards up to 10km a year in some species (Hickling et al., 2005). Attempts to discover the relationship between dispersal and flight performance have mostly relied on 'flight related' parameters as proxies for flight performance. The most common of these proxies are measures of the shape and size of the wings (aspect ratio, area, length etc.) and flight muscle mass or ratio. The latter has been shown empirically to correlate with greater aerodynamic power (Marden and Cobb, 2004), but the former is more complicated. Often mutually exclusive assumptions are made around the correlations between wing morphology and performance, based on relatively few empirical and theoretical studies (see Chapter 3). Several studies have shown that dispersal is related to flight performance proxies, but with opposing trends, e.g. Hassall et al. (2009), Hughes et al. (2007) and Swaegers et al. (2014) all found positive correlations between wing aspect ratio and dispersal, whereas Hill et al. (1999) and McCauley (2013) found negative correlations and Hill et al. (1998) and Therry et al. (2014; 2015) found no correlation between wing morphology and dispersal but did find correlations between flight muscle mass and dispersal. Within butterflies (Lepidoptera), qualitative estimates of flight performance are also often used which do not show any relationship to dispersal, but also are usually correlated with wing traits not necessarily actual ability and may have biases (Mair et al., 2014; Sekar, 2012; Stevens et al., 2010).

1.5 Linking flight performance and dispersal

Dispersal is a key component of a range of macroecological processes including the maintenance of metapopulations (dispersal is required to establish or re-establish population patches), speciation (the inability to disperse between two populations is required to initiate allopatric speciation) and range sizes and boundaries (as these are defined by the locations dispersing individuals can reach and establish populations). As outlined above, flight performance should play a role in prey capture, competitive ability, and dispersal – a key aspect for Odonata as adult dispersal is the only likely way populations can move between different water bodies as the larvae are relatively sedentary (Corbet, 1999). In particular, dispersal of the Odonata that are known to migrate long distances, particularly *Anax junius* north and south across the US and *Pantala flavescens* from India to Africa (Anderson, 2009; Hobson et al., 2012; Holland et al., 2006; Lack and Lack, 1951; Wikelski et al., 2006) should be influenced strongly by their flight performance. The effect that flight performance has on dispersal is currently unclear as quantitative measures of flight performance are rarely considered in an ecological context.

Dispersal itself is also difficult to quantify at the level of the individual and, despite its importance for the Odonata, most studies to date have only measured dispersal through the distances marked individuals have travelled in mark release recapture (MRR) studies (Allen and Thompson, 2010; Angelibert and Giani, 2003; Anholt, 1990; Conrad et al., 1999; Rouquette and Thompson, 2007; Thompson, 1991; Thompson and Purse, 1999). With the rise of genetic approaches to studying population structure, population genetics can be used to identify gene-flow and hence dispersal between populations (Watts et al., 2004) and also how gene polymorphisms can be correlated with spatial dynamics, for example in the Glanville fritillary (*Melitaea cinxia*) polymorphisms in the phosphoglucose isomerase gene are correlated with variation in flight metabolic rate and dispersal rate (Hanski, 2011). However, data from genetic population structures cannot necessarily provide information on the processes behind movements and as such cannot help predict future movements. More recently, with smaller tags available in radio telemetry, much more accurate data on dispersal ability and behaviour could be gathered (Kissling et al., 2014) both for short range movements (Levett and Walls, 2011), and even for long range migrations (Wikelski et al., 2006). For macroecological processes, however, population measures of dispersal, i.e. the magnitude of range shifts, are sufficient to describe dispersal.

With dispersal data we can help inform conservation efforts by giving rough estimates of how far apart protected areas can be before dispersal becomes impossible, or identifying potential new protected areas (Pryke et al., 2015; Venter et al., 2014; Watson et al., 2016). We can also look for patterns in the movement of species in relation to climate change (Kleisner et al., 2016; McGuire et al., 2016; Urban et al., 2016), how new assemblages are forming with different dispersal rates among species (Harris, 2015; Kleisner et al., 2016; Lord and Whitlatch, 2015) and we can gain insight into how far invasive species have spread, helping us target interventions (Ficetola et al., 2007; Gallien et al., 2010; Rocchini et al., 2015; Stewart-

Koster et al., 2015; Vander Zanden and Olden, 2008). However, so far we have a good understanding of the patterns of species movement but not the processes underlying them (Urban et al., 2016). As I've mentioned, flight performance should logically play a role in dispersal of flight capable species but there is little empirical evidence to support this. Further, there is a lack of mechanistic understanding of how wing morphology affects variation in flight performance, which itself is usually not described in a quantitative, biomechanically-sound fashion. Without understanding the processes driving dispersal, we cannot predict future movements, which are essential to helping conserve populations moving under climate change and to help prevent invasive species (Urban et al., 2016; Watson et al., 2016). To understand the mechanisms underlying dispersal we need to understand how animals move and then how their movement patterns apply in a real-world context, hence the need to link the biomechanics of flight and how it impacts ecology.

The lack of quantitative flight performance metrics used in dispersal studies highlights a key area for future research as these metrics become easier to obtain. Linking the currently rather disparate fields of ecology and biomechanics is an important new direction, which can have synergistic impacts if done correctly. A prime example of a study with synergistic impacts is seen in the Odonata, where an interdisciplinary approach was taken to Odonata predation behaviour and prey survival. Coombes et al. (2012) demonstrated that combining quantitative biomechanical data and ecology was able to provide a more comprehensive explanation of predator-prey interactions.

1.6 Thesis Outline

The purpose of this thesis is to provide a much-needed evidence base to link form, function, and ecology in a model insect taxon. In the following chapters I demonstrate methods to build this body of evidence and demonstrate how it advances our mechanistic understanding of species' movements:

1.6.1 – Chapter 2

In this chapter I measure quantitatively the flight mechanics of a range of UK Odonata species, comparing flight mechanics data to observed range shifts during a period of warming. This comparison will help to demonstrate that population level movements are affected by the flight ability of the species, and to ascertain what specific aspect of flight performance drives macroecological patterns. Alongside providing baseline descriptions of flight performance for several Odonata species, I demonstrate the function of flight performance in influencing ecological movements.

1.6.2 – Chapter 3

Our theoretical understanding of how wing morphology affects flight performance is good, but empirical evidence is lacking. Further, a host of often mutually exclusive assumptions regarding links between morphology and flight performance have been made in the literature. Here I demonstrate empirically the effect of different wing shapes across the same range of Odonata species as in chapter 2, on their flight performance. From describing the detailed form of wing morphology I can demonstrate its function in driving flight performance and following back up through chapter 2, driving ecological range shifts.

1.6.3 – Chapter 4

Odonata like many insects have a complex life cycle, so the adult is very much dependent on the larval stage. Several previous studies have found ‘carry-over’ effects from larva to adult, but few have looked for an effect in locomotory performance. In this chapter I look for ‘carry-over’ effects of locomotory performance in Odonata from larva to adult by measuring swimming performance and subsequent flight performance when the larva emerges. It is still not known exactly how the form of flight morphology is produced, so here I demonstrate the potential function of larval form in affecting adult flight morphology, and the ecological basis of larval variation in swimming performance.

1.6.4 – Chapter 5

The previous chapters aim to establish a mechanistic understanding of locomotory performance, relating form to function and understanding its effects on Odonata ecology. They do not take into account how behaviour might modulate this process. In this chapter I provide a spatially explicit individual based model of Odonata movement to investigate the potential impact of reversible polarotaxis, a behaviour seen in Odonata, on dispersal. Through my work, I aim to demonstrate the emergent macroecological effects from individual behaviours, informed in part from the dispersal mechanisms outlined in the previous chapters.

1.6.5 – Chapter 6

Here I describe how the preceding chapters link to form a comprehensive explanation of the form and function of Odonata biomechanics and its effects on individual and population level ecological patterns, starting from potential larval influences through to adult flight morphology. I then compare the work here to our current understanding of biomechanics and ecology and how it amends or adds to current theory. Finally I suggest the best direction for future work, looking to improve and expand on the work I have carried out here.

1.7 Conclusion

The flight biomechanics and ecological patterns in the Odonata are well described within those two respective fields. However, the underlying processes are still unclear in some cases and links between the two areas of work are few and often tenuous, due to conflicting evidence and potentially poor proxies of the properties involved being used. In the following chapters I attempt to bring together biomechanics and macroecology to explain underlying processes. I will first look at the links between quantitative flight performance data and climate induced range shifts across a range of Odonata species, followed by an empirical demonstration of the effects of wing morphology on flight performance in the Odonata. I will also look for ontogenetic carry-over effects of biomechanical performance across the odonate life cycle, to see if larval performance has an impact on macroecological patterns seen in the adults. Finally using an individual based dispersal model I test the effect that certain behaviours might have on odonate dispersal. I will give a brief discussion in each of these chapters on the results obtained, followed by an in depth discussion and synthesis in chapter 6.

Chapter 2 – Comparative analysis of Odonata flight performance and associations with climate-induced range shifts

2.1 Abstract

The Odonata (dragonflies and damselflies) is a charismatic insect order, in which the flight of winged adults is important for almost all aspects of their life, but particularly colonisation of new habitats. Some species have shown large range expansions in response to climate change, but it is not yet known why some species are shifting faster than others. Several potential factors responsible for variation in range shift speed have been discussed at length, such as habitat connectivity and biotic interactions, but the underlying mechanisms remain unclear. Logically, flight ability could have an important role to play in determining how far and fast a species can disperse, but estimates of flight ability in insects with respect to dispersal are rare and often qualitative. I quantified flight performance from laboratory recorded trajectories of 124 individual dragonflies from 13 UK species, using a mirror-corner-cube arena setup and high speed camera. The results showed a clear distinction between the flight performances of different species, but particularly between the four families studied, with Calopterygidae and Aeshnidae showing high maximum flight speeds and accelerations and Coenagrionidae showing slower maximum speeds and low acceleration. The Libellulidae showed considerable variation in performance with different species demonstrating almost the full range of flight performance measures shown in the other groups. Comparing this dataset to climate-induced range shifts derived from biological records, raw speed and acceleration showed no correlation to rate of range movement. However, efficient flight (characterised by relatively high average speeds and low accelerations) was positively and significantly correlated with range shifts. My findings demonstrate a subtle relationship between flight kinematics and macroecological patterns unlikely to be detected by more common indirect or qualitative data, such as expert opinion. My approach demonstrates the value of linking detailed kinematic data and

macroecological patterns to understand responses to global climatic change. Flight performance is an important limiting factor when considering range expansions, an example of how biomechanics can help us understand ecological processes. Knowing how flight performance can limit range expansion will help identify available habitat for range expansions, alongside identifying where other factors might be limiting current range expansions.

2.2 Introduction

2.2.1 Climate-induced range shifts

Climate change is impacting ecosystems on a global scale (Parmesan and Yohe, 2003). Recorded impacts include shifts in population ranges northward or to higher altitudes (Hickling et al., 2006; McCarty, 2001; Parmesan, 2006; Parmesan et al., 1999; Walther et al., 2002), shifts in phenology (McCarty, 2001; Parmesan, 2006; Parmesan and Yohe, 2003; Visser and Both, 2005; Walther et al., 2002), behavioural and genetic adaptation (Hill et al., 2011; Parmesan, 2006) and population reduction or loss (Parmesan, 2006). Among these, shifting population ranges is one of the more immediate and measureable responses and has the potential to cause dramatic changes in an ecosystem through changes in interspecific interactions. Of particular concern is the movement of pollinators, disease vectors, and invasive species due to their economic significance. A population's range is defined and affected by a multitude of biotic and abiotic factors, such as geography, environment, dispersal behaviour, survival, and interaction with other species (Brown et al., 1996; Lawton, 1996; Sexton et al., 2009).

Temperature is an overarching driver of most processes involved with range determination, as a species will not be able to survive outside its thermal limits (Addo-Bediako et al., 2000; Kellermann et al., 2012; Stuart-Smith et al., 2017) and temperature also often mediates behaviour and thus species interactions (Taniguchi and Nakano, 2000). As temperatures change, populations are having to either adapt to new thermal regimes or move to stay within their preferred thermal niche. For mobile species the most immediate response to temperature change is to colonise newly available habitat at higher latitudes or altitudes. Extinction in lower altitude or latitude populations may also occur, although evidence for this is scarcer (Franco et al., 2006; reviewed in Parmesan, 2006). One of two scenarios are usually considered when studying climate induced movements, latitudinal shifts poleward or shifts to higher altitudes. Both of these movements have already been detected in a number of species, for example, latitudinal shifts have been seen in arthropods (including arachnids and flying and non-flying insects), fish, reptiles birds and mammals (Hickling et al., 2006; Mason et al., 2015; Pounds et al., 1999).

In order to predict these movements the concept of a thermal niche or 'climate envelope' of a species was developed and it is still used extensively when attempting to predict the movement of populations in response to varying climate change scenarios (Pearson and Dawson, 2003). These models are the subject of considerable debate (Brooker et al., 2007; Davis et al., 1998; Pearson and Dawson, 2003) as they often do not take into account a number of relevant factors, and therefore may lack the complexity needed to predict actual changes in population ranges.

Contributing factors omitted from climate envelope models include landscape structure (for example barriers to movement or dispersal corridors) (Lövei et al., 1998; Mader et al., 1990; Öckinger and Smith, 2008), microclimates (Gillingham et al., 2012; Lawson et al., 2014; Suggitt et al., 2011), interspecific interactions (Brooker et al., 2007; Taniguchi and Nakano, 2000) and dispersal behaviour (Lindstrom et al., 2013; Phillips et al., 2010). Because of the number of different factors affecting range shifts, the movement of populations, or shifts in their range, in response to climate change is not necessarily uniform with respect to predicted temperature rises, with intraspecific and interspecific differences in magnitude or speed of range expansions or even contractions in similar areas (Brooker et al., 2007; Phillips et al., 2008). Across large scales, the rate of temperature change is also not uniform, potentially increasing the complexity of movement patterns. Further, although they are often studied separately, climate change will likely invoke both adaptive and behavioural responses (Simmons and Thomas, 2004), which operate at different time scales (Davis et al., 2005). Finally, although responses to climatic change have been detected in a number of species, the majority of responses are lagging behind the change in climate to differing degrees (Chen et al., 2011), making population movements yet harder to predict.

More recent and advanced models attempt to incorporate some of these missing factors, in particular, the interaction between species, although most will still include a degree of climate envelope modelling. For example, Clark et al. (2017) use a generalised joint attribute model, a complex model incorporating multiple types of input data and species, allowing for analysis of community structure and responses – whilst still assuming climate distribution correlations. Another possible missing factor is the speed at which a species can disperse to new areas, which is still not often included even in recent models. Dispersal can be defined as any movement of individuals or propagules, but in general refers to movements that have the potential to allow gene flow spatially (Ronce, 2007). Here I define dispersal as movement of an individual away from its natal habitat or area. Within the Odonata, this definition pertains to movement away from the body of water the insect emerged from. Dispersal ability can be divided into two major components: first, dispersal behaviour within a species, i.e. when and where individuals within a species or population choose to disperse, and second, the physical ability of an individual or species to disperse. Dispersal ability may not be included in models due to missing behavioural data that would help us define the regularity of dispersal events, but also the lack of biomechanical data explaining the physical limits to a species' dispersal. For large mammals and birds, assessment of dispersal ability may be easier (if costly) through the use of GPS tracking (Hebblewhite and Haydon, 2010; Nathan, 2001; Recio et al., 2011; Schofield et al., 2007; Weimerskirch et al., 2002), but for insects with larger populations, and fewer dispersal barriers, dispersal ability is harder to quantify. Where attempts at describing insect dispersal have been made, they have primarily been focussed on butterfly species. Stevens et al. have reviewed a number of methods of describing butterfly dispersal ability (Stevens et al., 2010), but concluded that life history traits may be more accurate for describing dispersal (Stevens et al., 2013).

A few insect studies have tried to include dispersal ability, but have concluded that it has no or little effect on population range changes (Mair et al., 2014), despite studies suggesting that expanding range front populations have dispersal-adapted morphology (Hill et al., 1999; Jenkins et al., 2007), generally thought to correlate with flight performance (Betts and Wootton, 1988; Norberg and Rayner, 1987, but see Chapter 3).

2.2.2 Flight biomechanics

Animals with the ability to fly almost always use flight as their primary method of locomotion, presumably due to its considerable advantages over terrestrial locomotion (Dudley, 2000; Hein et al., 2012; Weber, 2009) despite high energetic costs of flight (Harrison and Roberts, 2000; Hein et al., 2012; Nudds and Bryant, 2000; Schmidt-Nielsen, 1972; Weber, 2009). Our understanding of biological flight as one of the more costly but most effective dispersal mechanisms is now reasonably well established, particularly in larger organisms such as birds (Alexander, 2004; Bomphrey, 2012; Harrison and Roberts, 2000). As such we have comprehensive descriptions of wing morphology (Wootton, 1991; Wootton, 1992), and, more recently, wing hinge structure and microstructures within the wing (Appel et al., 2015; Guillermo-Ferreira et al., 2017; Rajabi et al., 2016a; Rajabi et al., 2016b; Walker et al., 2014). Flapping flight in small organisms, i.e. insects, is reasonably well understood now, after the discovery of lift enhancing mechanisms such as the 'clap-fling' (Weis-Fogh, 1973) and the increasingly advanced technologies to study detailed air flows, for example three dimensional particle image velocimetry (Kitzhofer et al., 2011). Some more recent work has started to look at flight 'performance envelopes' and suites of biomechanical data that correlate with certain flight behaviours (Bomphrey et al., 2009a), which could more readily be used to relate back to ecology.

Despite recent advances describing wing structure and flight kinematics and the forces involved, much of the energetics and behaviour of flight remains unknown and there are few comparative approaches looking beyond a single study species or group. In addition, how any of these underlying drivers of flight performance affect the ecology of the species in question is rarely considered and empirical data is scarce. Logically the dispersal of flying animals should be influenced by their flight performance. Flight performance refers to the speed, acceleration, agility and efficiency of an organism's flight and is influenced by numerous factors, including wing morphology (Berwaerts et al., 2002; Norberg and Rayner, 1987), muscle energetics (Ellington, 1985; Harrison and Roberts, 2000; Morris et al., 2010), the structure of the wing hinge and wing (Walker et al., 2014; Wootton, 1992) and to some extent behaviour too (Bomphrey et al., 2009a). Wing shape is measured by a number of traits, but wing loading and aspect ratio are generally the most informative for flight performance (but see chapter 3). Aspect ratio is the ratio of length to width of the wing, with high aspect ratio wings generally good for efficiency as they provide greater lift and lower amounts of drag but they are poor for agility as there are greater inertial power requirements to move the wing and they cannot be accommodated in smaller spaces (Norberg and Rayner, 1987). Wing loading is the amount of mass that a given area of wing is required to support to keep the animal aloft, and whilst higher values correlate with greater power and so higher speeds or agility in flight, they do so at the expense of efficiency as the wing as a whole must generate more lift to do so. For dispersal, efficiency in flight will likely be more advantageous than other aspects of flight performance as it minimises the energy expenditure required for travelling (during which time the organism is unlikely to be carrying out any other useful processes such as feeding or mating). Flight speed, acceleration and/or agility are likely to be more applicable to predation, mating or competition, as they require quicker movements within smaller confines. Speed and agility may however also have functions in dispersal as for example, if an organism must cross inhospitable habitat or avoid predation during dispersal, these aspects of flight performance will help with survivability by decreasing the chances of successful predation and increasing the chances of successfully navigating a physical dispersal barrier.

2.2.3 The Odonata

Much of the work on insect flight has been carried out on the Odonata (dragonflies and damselflies) as they make very useful model organisms for flight studies (Marden, 2008). The Odonata are an ancient group of insects that display remarkable flight, despite a more primitive musculature than most other insects. In fact, it is their more primitive musculature that may give them an advantage as they are able to control all four of their wings separately unlike most other insects. All

Odonata are successful hunters, all of which catch prey on the wing as adults (Combes et al., 2012; Corbet, 1999). A number of detailed analyses on the mechanisms through which the Odonata provide lift (Azuma et al., 1985; Hu and Deng, 2009; Russell, 2004; Thomas et al., 2004; Wakeling and Ellington, 1997a; Wakeling and Ellington, 1997b; Wakeling and Ellington, 1997c) have already been carried out, showing that unusually high lift coefficients are probably generated through the interaction of the two pairs of wings. There is some discussion as to how zygopterans might display greater agility as a trade-off for general flight performance, but this is currently unconfirmed (Bomphrey et al., 2016).

A larger body of work exists for Odonata ecology than for many other insects, as their colour and larger size makes them conspicuous in the field and relatively easy to identify and work with. They act as indicator species for already relatively fragile freshwater ecosystems (Bried and Samways, 2015; Briers and Biggs, 2003; Sahlén and Ekestubbe, 2001) and their development is directly related to temperature (Krishnaraj and Pritchard, 1995; Pickup and Thompson, 1990; Pritchard et al., 2000; Van Doorslaer and Stoks, 2005), so they are well suited to demonstrating climate change responses in fragmented and fragile habitats. As a group they are showing possibly some of the largest range shifts to warming temperatures in the UK (Hickling et al., 2006; Mason et al., 2015) with one *Sympetrum striolatum* shifting its range by over 300km from 1960-1970 to 1985-1995 (Hickling et al., 2005).

2.2.4 Flight ecology

In general, linking biomechanical data to ecological processes or vice versa is rare, although more recently researchers have begun to realise the greater potential of more interdisciplinary studies of this type (Combes et al., 2012). As such, quantitative measures of dispersal are rare, with a handful of radio tracking attempts with varying degrees of success (Cant et al., 2005; Hardersen, 2007; Wikelski et al., 2006). For the most part Odonata dispersal ability is described using mark-release-recapture (MRR) studies (Allen and Thompson, 2010; Angelibert and Giani, 2003; Bilton et al., 2001; Macagno et al., 2008; McCauley, 2013; Thompson and Purse, 1999) – which may have confounding factors depending on the spatial and temporal extent of the study, and the proportion of the population they manage to include (Hassall and Thompson, 2012). Some other studies use simply an ‘expert opinion’ to categorise dispersal ability (Cowley et al., 2001; Mair et al., 2014; Pöyry et al., 2009; Warren et al., 2001), which may have some merit, but aside from a correlation with wing size (Sekar, 2012) has not been tested against quantitative data. The practice of using expert opinion is also seen in several butterfly studies (Dennis and Shreeve, 1997; Sekar, 2012; Wood and Pullin, 2002).

2.2.5 Linking biomechanics and ecology

Here, I record quantitative flight performance measures and relevant morphological data for 14 UK species of Odonata (6 Anisoptera and 8 Zygoptera) using a biomechanical approach. I then test the hypothesis that flight performance is correlated with observed range shifts over a well recorded period of warming in the UK. I expect dragonfly species with higher flight speeds and poorer agility (lower turn frequencies, larger turning radii and lower accelerations) will show greater dispersal ability (larger range shifts), due to a general trade-off between agile flight and efficient long-distance flight.

2.3 Materials and Methods

2.3.1 Time and location

Experiments were carried out between the months of April and September in accordance with Odonata flight seasons, in 2015, 2016 and 2017. Insects were captured from the field around the peak of their flight season (differing times for different species) from the following locations in Table 2.1. Permission to collect insects from each site was sought from and granted by landowners and managers before any work commenced.

2.3.2 Animal capture and husbandry

Insects were captured using standard insect nets and stored in plastic Ziploc bags in a portable insulated container whilst transported to the University of Leeds. Once at the University of Leeds, they were transferred to either cube-shaped Bugdorms

(4S3030, 0.3m width x 0.3m length x 0.3m height, MegaView Science Co. Ltd., Taiwan) or cylindrical insect cages (0.25m diameter x 0.3m height, JoTech ltd. t/a Insectopia, UK) in a controlled temperature room kept at 15°C/25°C (2015/2016-2017). The temperature change was related to rearing odonate larvae in the same room and all insects in 2015 were allowed to warm up to 25°C before experiments. Each insect was provided with wooden sticks as perches and *Drosophila melanogaster* or other assorted insects caught on site. Each female insect was also provided with a petri dish of water with filter paper in, which were regularly checked for eggs. After use in flight experiments insects were killed by freezing and their wings removed and mounted on to translucent tape for morphometric studies (see chapter 3). The remains of the adult insects were preserved in 100% ethanol for future research.

Where possible, at least 10 adult insects of each study species were collected. Often greater numbers were collected as not all insects would fly under experimental conditions. Some insects also suffered wing damage or died before they could be used in experiments. Where possible only five or fewer insects of a particular species were captured in a given field visit. Taking only five insects reduces any potential impact on the local population, but more importantly, five insects is a manageable number in terms of carrying out kinematic recordings. *Coenagrion mercuriale* is a protected species in the UK under Schedule 5 of the 1981 Wildlife and Countryside Act (The Wildlife and Countryside Act 1981), is listed in Appendix II of the Bern Convention (The Convention on the Conservation of European Wildlife and Natural Habitats), in Annex II of the EC Habitat Directive (Council Directive 92/43/EEC) and is listed as a priority species in the UK Biodiversity Action Plan (BAP) in which it has its own species action plan (SAP). As such all work concerning *C. mercuriale* was carried out under a license from Natural England and all individuals were preserved in 100% ethanol for potential future work, regardless of whether kinematic data was collected from them. A habitats regulations assessment was completed and approved for all work in the New Forest National Park as the area is classified as a site of special scientific interest (SSSI), a special protection area (SPA), a special area of conservation (SAC) and is a RAMSAR site.

Table 2.1 – Insect capture locations, dates accessed and species collected (see Table 2.2 for species abbreviations

Site	**County**	**Latitude °N, longitude °E**	**Manager**	**Species collected**	**Dates of collection**
Letchmire Pastures Nature Reserve	West Yorkshire	53.741, -1.359	Yorkshire Wildlife Trust	*Cs*, *Ie*, *Lq*, *Oc*, *Ss*	2015 2016
St. Aidan's Nature Reserve	West Yorkshire	53.753, -1.396	Royal Society for the Protection of Birds	*Ai*, *Cs*, *Ie*, *Lq*, *Oc*, *Ss*	2015 2016
Paull Holme Strays	East Riding of Yorkshire	53.709, -0.214	Yorkshire Wildlife Trust, formerly Environment Agency	*Cs*, *Ie*, *Lq*, *Oc, Ss*	2016
Potteric Carr	South Yorkshire	53.499, -1.114	Yorkshire Wildlife Trust	*Cp*, *Ie, Pn*	2017
Sandiway Lakes	Cheshire	53.215, -2.593	Warrington Anglers Association	*En*	2017
Crockford Bottom	Hampshire	50.790, -1.505	Forestry Commission	*Cm*	2016
Latchmore Brook	Hampshire	50.915, -1.730	Forestry Commission	*Ip*	2017

2.3.3 Flight arena kinematics

Flight trajectories were recorded from the captured insects. These were filmed in a mirrored corner cube arena (Bomphrey et al., 2009, see Figure 1) using a high speed camera (FASTCAM SA3, Photron Ltd., Tokyo, Japan) fitted with a 24-70mm f1-2.8 zoom lens (Nikon Corporation, Tokyo, Japan). Two different sizes of arena were used, a larger version for Anisoptera species using 3 x 1.8m^2 metal frames with a reflective membrane stretched across and a smaller version for Zygoptera species using 3 x 0.8m^2 glass mirror panels mounted in wooden frame.

The camera was mounted on a tripod as close to the arena corner directly opposite the intersection of the 3 mirrors as possible, at around 0.8m high for the small arena setup, or 1.8m high for the large arena setup. It was aimed downwards at roughly 45° pointed at the intersection between all 3 mirrors (see Figure 2.1). The area was lit as evenly as possible with 3 or 4 lamps in varying configurations, due to changes in location and equipment throughout the 3 years of experiments. Sometimes standard room lighting and/or 20W LED lamps were incorporated into lighting setup. The volume in the arena was calibrated by filming a spinning fixed length of metal or wood. For the large arena a 0.32m long, 5mm diameter piece of wooden dowelling was used, whereas a 0.148m long, 0.64mm diameter metal rod was used for the small arena.

Each insect was released into the flight chamber and allowed to fly naturally until it landed or left the arena, at which point recording was stopped. This process was repeated 10 times, or sometimes more, to provide 10 different videos of flight (referred to as sequences), or until the insect stopped flying (see Table 2.2 for the total number of recordings). For each repeat the insect was initially allowed to take off of its own accord. If an insect did not take off after a few minutes it was gently encouraged to fly again by tapping the abdomen, or captured and re-released into the chamber. Almost all sequences were filmed at 250fps, with a shutter speed of 1/250ths of a second, a resolution of 1024x1024 and with varying lighting and F-stop configurations to allow even backlighting (10 sequences filming *Anax imperator* were shot at 1000fps, 1/1000 shutter speed). Each insect was weighed after kinematic recordings using a balance (Mettler Toledo AX26, Mettler Toledo, Leicester, UK, ±0.5µg, values rounded to nearest 0.1mg).

Table 2.2 – Number of insects of 14 odonate species for which some flight data has been collected, and the number of separate flight sequences recorded.

Taxonomic group	Species	No. of individuals (no. males, no. females)	Number of sequences
Anisoptera (Aeshnidae)	*Aeshna grandis* (Ag)	7 (6,1)	64
Anisoptera (Aeshnidae)	*Aeshna juncea* (Aj)	1 (1,0)	12
Anisoptera (Aeshnidae)	*Anax imperator* (Ai)	1 (0,1)	11
Anisoptera (Libellulidae)	*Libellula quadrimaculata* (Lq)	5 (5,0)	49
Anisoptera (Libellulidae)	*Orthetrum cancellatum* (Oc)	10 (8,2)	64
Anisoptera (Libellulidae)	*Sympetrum striolatum* (Ss)	17 (14,3)	149
Zygoptera (Calopterygidae)	*Calopteryx splendens* (Cs)	8 (5,3)	73
Zygoptera (Coenagrionidae)	*Coenagrion mercuriale* (Cm)	12 (10,2)	111
Zygoptera (Coenagrionidae)	*Coenagrion puella* (Cp)	13 (10,3)	118
Zygoptera (Coenagrionidae)	*Erythromma najas* (En)	10 (9,1)	100
Zygoptera (Coenagrionidae)	*Erythromma viridulum* (Ev)	8 (8,0)	73
Zygoptera (Coenagrionidae)	*Ischnura elegans* (Ie)	10 (9,1)	101
Zygoptera (Coenagrionidae)	*Ischnura pumilio* (Ip)	10 (10,0)	99
Zygoptera (Coenagrionidae)	*Pyrrhosoma nymphula* (Pn)	12 (8,4)	117

2.3.4 Image processing

Video footage from the flight arena was saved in a RAW format from the Fastcam camera and converted to AVI using Photron Fastcam Viewer (PFV version 3.3.4.1, Photron Limited 2006). The calibration video was analysed using custom written Python software (Python Software Foundation, http://www.python.org), in which the location of at least five reflections of the calibration object was specified.

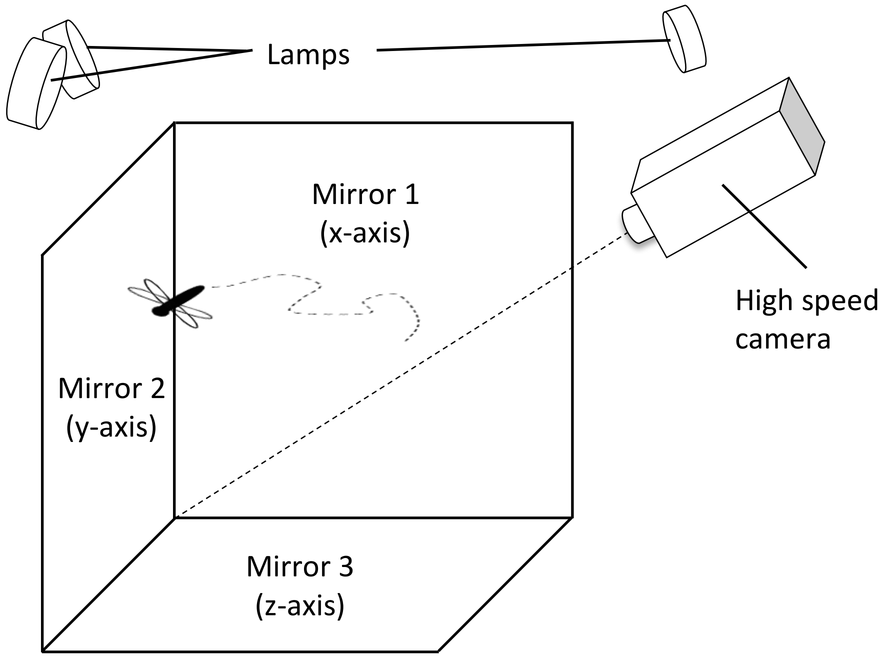


Figure 2.1 – Experimental setup for 'mirror corner-cube' flight arena. Lamp setup varied between experiments to attain most even lighting. Not to scale.

Knowing the length of the calibration object in multiple areas of the image, scaling values and how they change with respect to dimension are calculated. In addition, rotational corrections (ω, ψ and κ_r) for non-orthogonally positioned mirrors and radial (K_1, K_2 and K_3) and tangential distortion coefficients (P_1 and P_2) are calculated. Flight sequences were analysed using custom written Python software (Python Software Foundation, http://www.python.org) to extract 3D position data. The software first locates the 2-dimensional location (X and Y co-ordinates within the image) of the insect and its reflections by tracking high contrast areas of a certain size from a given start point. Using the calculated calibration values the software then iteratively solves the collinearity equations of the photogrammetric model outlined in Bomphrey et al. (2009) to generate 3D co-ordinates (x, y and z coordinates). Manual input was sometimes required to correct the automated tracking. Biomechanical data is often subject to high levels of noise (Rayner and Aldridge, 1985) so 4th difference smoothing was applied to the positional data series (x, y and z coordinate series) to remove any erroneous spikes in the 3D trajectory (see Equations 2.1-2.5). All velocities and accelerations (i.e. velocity and acceleration in the x, y and z direction separately) were calculated from the smoothed data along with path curvature following the techniques outlined in Rayner and Aldridge (1985), see Equations 2.6-2.11. Total velocities and accelerations in the horizontal plane (x and y directions) and overall (x, y and z directions) were calculated using Pythagoras' theorem. Both means and maximums per recorded flight were taken for all parameters to be used in analysis. Lastly all sequences were filtered to remove sections where total acceleration values exceeded 500ms^{-2} (and two frames either side), as these corresponded with collisions with objects in the arena.

Equation 2.1 – 4th Difference smoothing:

$$p'_i = p_i - \frac{3\Delta^4 p_i}{35}$$

Equation 2.2 – 4th Difference smoothing, 1st point edge case:

$$p'_1 = p_1 + \frac{\Delta^3 p_{5/2}}{5} + \frac{3\Delta^4 p_3}{35}$$

Equation 2.3 – 4th Difference smoothing, 2nd point edge case:

$$p'_2 = p_2 - \frac{2\Delta^3 p_{5/2}}{5} - \frac{\Delta^4 p_3}{7}$$

Equation 2.4 – 4th Difference smoothing, penultimate point edge case:

$$p'_{n-1} = p_{n-1} + \frac{2\Delta^3 p_{n-3/2}}{5} - \frac{\Delta^4 p_{n-2}}{7}$$

Equation 2.5 – 4th Difference smoothing, last point edge case:

$$p'_{n} = p_{n} - \frac{\Delta^3 p_{n-3/2}}{5} + \frac{3\Delta^4 p_{n-2}}{35}$$

2.3.5 Range shift calculations

Range shifts were calculated using UK Odonata records from the British Dragonfly Society (BDS Recording Scheme, previously Dragonfly Recording Network) from 1807 – 2012. Range margins were calculated for the periods of 1990 – 2000 and 2005 – 2015, as these periods represent 2 of the best recorded periods within the dataset and during the time between them, the UK has undergone significant warming (an increase in mean annual temperature of +0.05°C and a maximum increase of +1.79°C, see Figure 2.2) (Parker et al., 1992). The latitudinal difference in kilometres between the two margins was recorded as the range shift for that period. The common squares method (CSM) was used to account for recorder effort (Hassall and Thompson, 2010; Hickling et al., 2005). For the common squares method, only records in 10km grid squares that had records for both time periods were included. The range margin was calculated as the mean northing (measured in metres north of the origin of the British National Grid projected coordinate system) of the 10 most northerly records. The resulting range shifts were jackknifed, removing one of the 10 most northerly records from either or both time periods, but this did not significantly change the range shift values (a difference of 1.95km between the minimum and maximum range shifts for *Erythromma viridulum* after jackknifing). Range shifts were also calculated using an alternate method using resampling (records from the period with more records were sampled at random to the number of records in the other time period for each 100km grid square) and bootstrapped with 1000 repetitions, but this did not significantly change the those resulting calculated range shifts either, showing that the shifts are present and robust to both the removal of outliers and resampling of the data.

Equation 2.6 – Velocity (and acceleration):

$$u_i = (-2p'_{i-2} - p'_{i-1} + p'_{i+1} + 2p'_{i+2})/10\tau$$

Equation 2.7 – Velocity (and acceleration), 1st point edge case:

$$u_1 = (-21p'_1 + 13p'_2 + 17p'_3 - 9p'_4)/20\tau$$

Equation 2.8 – Velocity (and acceleration), 2nd point edge case:

$$u_2 = (-11p'_1 + 3p'_2 + 7p'_3 + p'_4)/20\tau$$

Equation 2.9 – Velocity (and acceleration), last point edge case:

$$u_{n-1} = -(-11p'_n + 3p'_{n-1} + 7p'_{n-2} + p'_{n-3})/20\tau$$

Equation 2.10 – Velocity (and acceleration), penultimate point edge case:

$$u_{n-2} = -(-21p'_n + 13p'_{n-1} + 17p'_{n-2} + 9p'_{n-3})/20\tau$$

Equation 2.11 – Curvature:

$$\kappa_c = (u_x a_y - u_y a_x)/({u_x}^2 + {u_y}^2)^{3/2}$$

2.3.6 Statistical Analysis

Statistical analysis was carried out in R (R Core Team, 2017). A Principal Components Analysis (PCA) was carried out on most flight metrics (x direction and y direction velocities and accelerations were excluded as they are not relevant measures of performance, and are included in the horizontal measures) to establish types of

flight. The data points for the PCA were the average flight metrics from each recorded sequence. *Anax imperator* was excluded from analyses as most sequences were recorded at different frame rates, and acceleration filtering removed all but 2 sequences. Correlations between principal components (PCs) and the original variables established what each PC represented in terms of flight performance.
A generalised linear model (GLM) was generated for the first two PCs (and their interaction) as explanatory variables and range shift data as the response variable using the “MASS” R package (Venables and Ripley, 2002). The data points for this analysis were the PCA values averaged per species (as the range shift data has only one observation per species). Only the first two PCs were used as they explained the majority of variation in the original variables, and the dataset was too small to build models with more variables. Model simplification was then used to find the minimum adequate model.

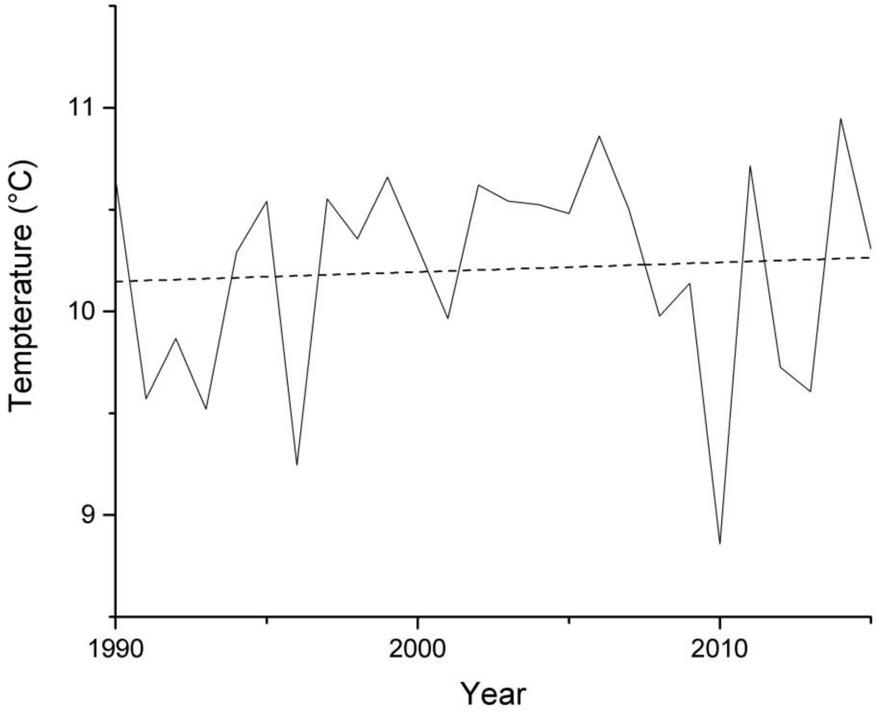


Figure 2.2 – UK temperature from 1990 to 2015. Solid line represents average annual temperatures, and the dashed line is the statistically significant trend.

2.3.7 Phylogenetic correction

The data from this chapter is based on several species with varying but often close evolutionary links. This evolutionary correlation between species may have influenced the results of the statistical analyses carried out. I re-analysed the data using the same methods as above whilst in addition considering the phylogenetic relationships involved. A phylogenetic tree from the Odonata was downloaded from the Open Tree of Life (Hinchliff et al., 2015), consisting of phylogenetic data supported by three studies (Letsch and Simon, 2013; Rota-Stabelli et al., 2013; Simon et al., 2009), shown in Figure 2.3. Note that the *Anax imperator* branch (in addition to all the other Odonata species not shown in Figure 2.3) was removed for analysis as this species was not included in the analyses in chapters two and three. Using R and the phytools (Revell, 2012), caper (Orme et al., 2018), geiger (Harmon et al., 2008) and picante (Kembel et al., 2010) packages, the minimum adequate models constructed in chapters two and three were reconstructed but accounting for the correlation structure brought about by phylogenetic relationships. This was done using the general least squares (GLS) method, and assuming a Brownian motion process for evolution. The Ornstein-Uhlenbeck (OU) process could not be used as there was insufficient data to generate the required correlation structure. The results remained the same after taking phylogenetic relationships into account (see Table 2.3).

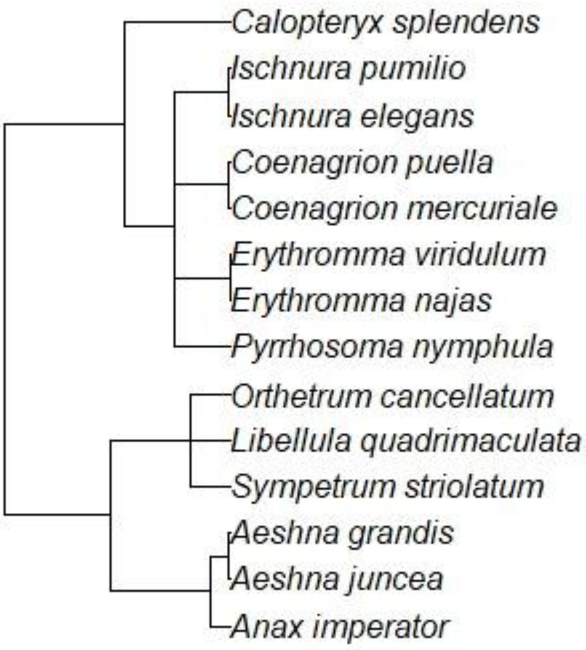


Figure 2.3 – Phylogenetic tree showing the relationships of the Odonata species studied in chapter two and three.

2.4 Results

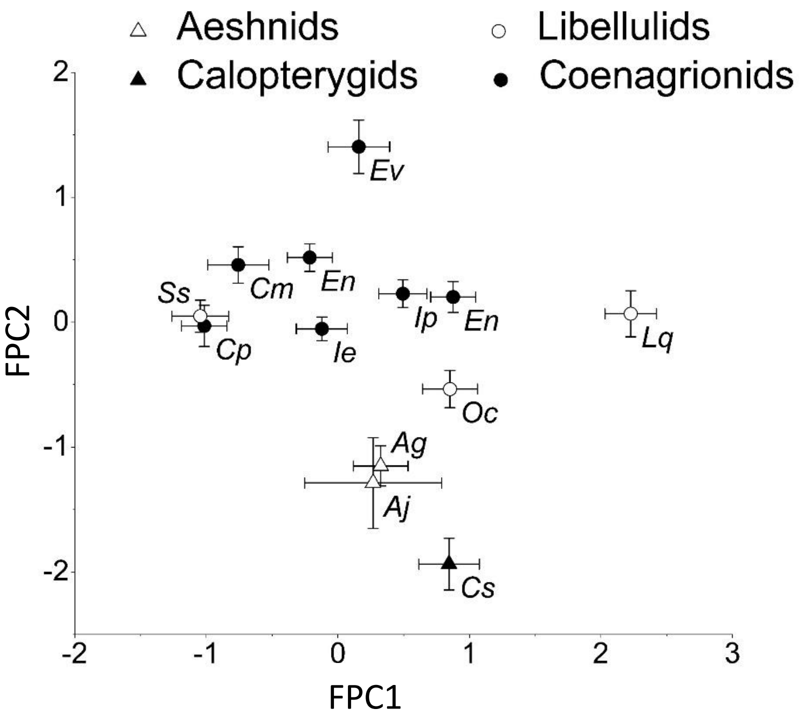
In total 1141 flights were recorded from 124 individual insects from 14 species. The maximum average speed per flight recorded was 38.92ms^{-1} (*Orthetrum cancellatum*) and the minimum was 1.75ms^{-1} (*Sympetrum striolatum*). Range shifts were all positive except for *Coenagrion mercuriale* which showed a small range contraction in the studied time period. The maximum observed range shift was from *Erythromma viridulum*, moving over 219km in up to 25 years.

2.4.1 Interspecific flight performance

Interspecific variation in flight performance was demonstrated across the 13 species studied (see Figure 2.4). The principal component analysis generated 16 principal components with the first 2 accounting for 44.85% of the variance of the original flight performance metrics. Back correlating the principal components to the original variables showed that principal component 1 (FPC1) was positively correlated with all measures of speed and acceleration (see Table 2.4) – and will be used as a measure of flight speed from now. Principal component 2 (FPC2) was positively correlated with horizontal velocity, but negatively correlated with acceleration, representing a measure of efficient flight behaviour so will be described as “flight efficiency” from now on (see Table 2.4 and Section 2.5.1).

2.4.2 Range shifts

Only the endangered *C. mercuriale* showed a negative range shift (contracting range, by 2.71km), with all other Odonata species showing range shifts between 4km to over 200km over up to 25 years (see Figure 2.5).



Fast, but steady or efficient flight behaviour (High average speed, low accelerations)

Slow, but agile flight (High accelerations, low average speed)

Slow flight (Low speed and acceleration)

Fast, agile flight (High speed and acceleration)

Figure 2.4 – Means of FPC1 (flight speed) and FPC2 (efficient flight behaviour) plotted with standard errors for each of the 13 species studied. Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. See Table 2.1 for species abbreviations.

2.4.3 Range shifts and flight ability

C. mercuriale was removed from the analysis as previous work has already shown that the species is limited by habitat rather than climate (Thompson et al., 2003; Watts et al., 2004). There is some evidence to suggest that *Ischnura pumilio* (the second greatest outlier) could be removed on the same grounds but this species has been observed to arrive quickly at newly available sites, suggesting a high dispersal capacity, and so has not been removed here (Allen and Thompson, 2010; Allen et al., 2010). After the removal of *C. mercuriale* and retaining *I. pumilio*, PC2 was significantly correlated with the observed range shifts across UK species (GLM, Chi(1,10), p = 0.0145, see Figure 2.6 B).

Table 2.3 – Chapter 2 minimum adequate model parameters with and without phylogenetic correction. Values to 3dp.

Response variable	**Parameter**	**Estimate (95% confidence intervals)**	**SE**	**t**	**p**
Without phylogenetic correction					
Range Shift	Intercept	82.000 (48.562, 115.435)	17.060	4.807	**< 0.001***
	PC2	45.300 (7.453, 83.156)	19.310	2.346	**0.041***
With phylogenetic correction					
Range Shift	Intercept	77.764 (69.977, 85.552)	3.973	19.572	**< 0.001***
	PC2	44.184 (29.221, 59.146)	7.634	5.788	**< 0.001***

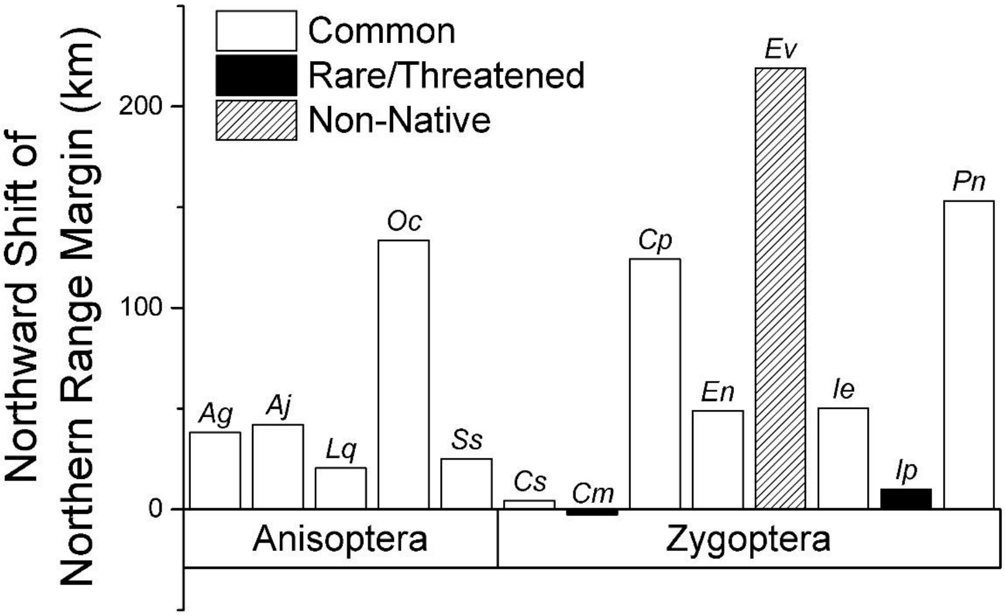
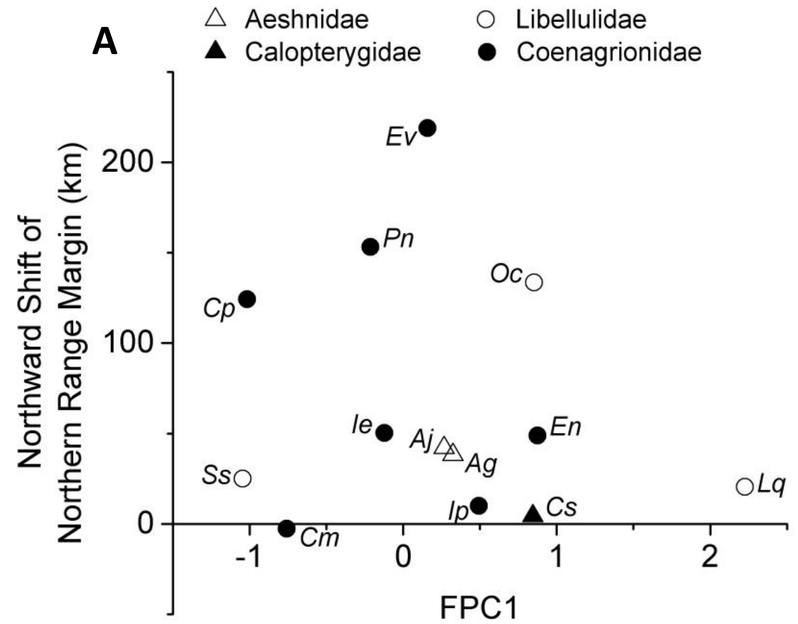


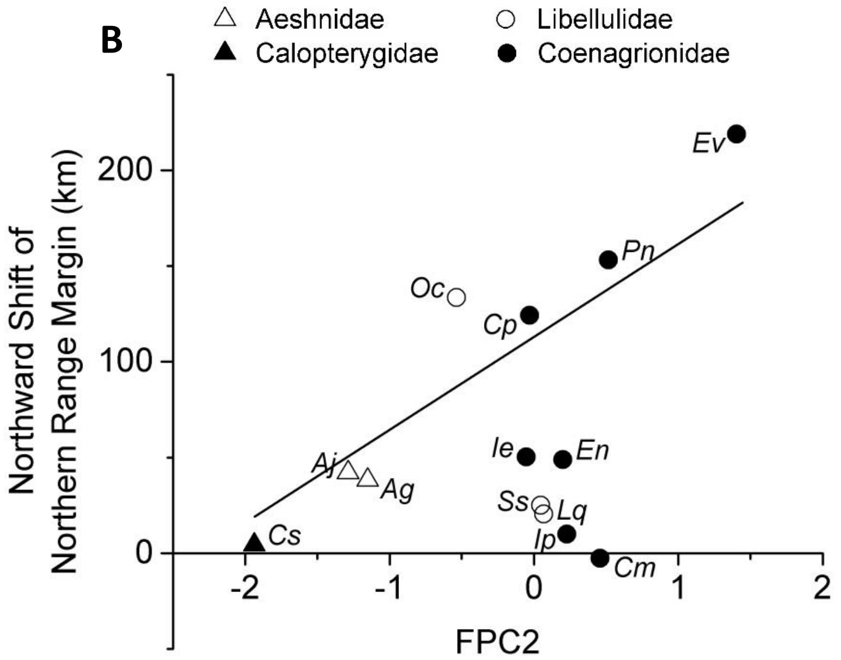
Figure 2.5 – Calculated northward shift of the northern range margin for 13 UK species, grouped by taxonomy, shaded by status and labelled by species abbreviation (see Table 2.1). Range shifts are movements from the period of 1990-2000 to the period of 2005-2015

Table 2.4 – Table of correlation coefficients between the principal components (percentage of variance explained by each component in brackets) of the PCA and the original variables used in the analysis (all coefficients to 3 decimal places). Correlation coefficients over 0.5 are highlighted.

	FPC1 (29.2%)	FPC2 (15.7%)	FPC3 (13.4%)	FPC4 (9.6%)	FPC5 (6.4%)	FPC6 (6.3%)
Mean Vertical Velocity	0.173	0.042	-0.076	**-0.839**	0.176	-0.094
Mean Horizontal Velocity	**0.753**	**0.522**	-0.210	0.192	-0.039	-0.015
Mean Total Speed	**0.770**	**0.520**	-0.211	0.099	-0.002	-0.005
Mean Vertical Acceleration	0.071	0.045	-0.027	-0.168	**-0.939**	0.029
Mean Horizontal Acceleration	**0.544**	**-0.627**	0.188	0.182	-0.002	-0.166
Mean Total Acceleration	**0.627**	**-0.564**	0.172	0.123	-0.056	-0.126
Horizontal Path Curvature	-0.108	-0.208	**-0.666**	0.019	-0.086	-0.076
Rate of Change of Curvature	0.024	-0.044	-0.071	0.052	0.059	**0.953**
Maximum Vertical Velocity	**0.500**	0.045	-0.105	**-0.739**	0.136	0.026
Maximum Horizontal Velocity	**0.842**	0.327	-0.209	0.201	0.019	-0.023
Maximum Total Speed	**0.867**	0.337	-0.214	0.080	0.054	-0.007
Maximum Vertical Acceleration	0.491	-0.318	0.051	-0.325	-0.260	0.164
Maximum Horizontal Acceleration	**0.599**	**-0.567**	0.060	0.112	0.096	0.058
Maximum Total Acceleration	**0.614**	**-0.586**	0.094	-0.004	0.064	0.093
Maximum Horizontal Path Curvature	-0.210	-0.331	**-0.893**	0.034	0.001	-0.068
Maximum Rate of Change of Curvature	-0.206	-0.321	**-0.785**	0.031	0.041	0.032



Slow flight (low accelerations, low speed) ⟷ Fast flight (High accelerations, high speed)



Slow, but agile flight (High accelerations, low average speed) ⟷ Fast, but steady flight (High average speed, low accelerations)

Figure 2.6 – Common squares method (CSM) calculated range shifts against A) flight speed (FPC1) and B) efficient flight behaviour (FPC2), labelled by species abbreviation (See Table 2.1). Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. Note that *Coenagrion mercuriale* (*Cm*) was excluded from the analysis and as such that point above is not included in the model best fit line.

2.5 Discussion

2.5.1 Linking flight performance and macroecology

The results here suggest that there is a link between flight performance and climate induced range shifts. Namely, that high speed, low acceleration flight is positively correlated with the magnitude of range shifts in the UK Odonata. PC2 in this experiment is likely to represent some measure of flight efficiency, as at higher PC2 values the insect is maintaining a high speed, but with low accelerations – suggesting that the insect is avoiding sharp turns, or changes in speed, which should help reduce the energy expended. The link demonstrated here contradicts studies that have considered dispersal ability (categorised by expert opinion) as an unimportant factor for determining range shifts (Mair et al., 2014) and there may be grounds for them to re-consider whether it genuinely is unimportant, or whether the metric used to represent it needs more refinement or quantification.

Ideally phylogenetic correction would be applied to the data here, but a highly resolved and certain phylogeny does not yet exist for the Odonata (Carle et al., 2015; Dumont et al., 2010).

2.5.2 Variation in flight performance

A strong degree of interspecific variation in flight performance was to be expected as the species studied here are very different in size and shape. However, it was expected that in general the Anisoptera and Zygoptera would be split by showing fast but not agile flight and slow but agile flight, respectively, based on previous field observations (Corbet, 1999). Instead no agile vs. not-agile dichotomy was found but instead most Anisoptera grouped as relatively slow fliers with average to low 'efficiency'. The exception being *Sympetrum striolatum* which showed flight performance remarkably similar to *Coenagrion puella*, despite *S. striolatum* on average weighing 0.13g and having a wingspan of 5.8cm whereas *C. mercuriale* on average weighs 0.02g and has a wingspan of 3.5cm. As expected, *Calopteryx splendens* was considerably separated from other species – presumably its intermediate wing morphology between Anisoptera and Zygoptera species gives it its intermediate flight speed and acceleration. On the other hand its flight efficiency as measured by PC2 was the lowest of any of the species studied, suggesting that intermediate modes of flight performance, or intermediate morphology are perhaps poorly optimised, requiring unusual and inefficient styles of flight to support their weight. Another possibility is that as *C. splendens* uses wing colouration for courtship, adaptations brought about by sexual selection might have reduced the effectiveness of their wings for dispersal. If this is the case, the flight mode may also be deliberately inefficient as costly displays are an important aspect of territoriality – particularly in *C. splendens* (Suhonen et al., 2008).

2.5.3 Coenagrion mercuriale flight performance

Coenagrion mercuriale (Southern Damselfly) is a rare and habitat restricted species, with small and generally isolated habitats in the south of the UK and Wales (Thompson et al., 2003). Despite no quantitative data published on the flight ability of the species, it is generally considered to be a poor flyer (Thompson and Purse, 1999; Watts et al., 2004). The data collected here suggests otherwise, as *C. mercuriale* performance is generally towards the middle of the range of performance variables (See Figure 2.4). Whilst it is not necessarily a strong flyer, it has significantly stronger flight abilities along the PC2 axis and shows statistically no difference along the PC1 axis, than its closest relative studied here *Coenagrion puella*. As such its physical dispersal capability is unlikely to be the reason for any decline in the species. It is possible that although *C. mercuriale* has a faster, more efficient and/or more agile flight, its endurance could be lower than that of other Odonata species, causing poorer dispersal ability, but this seems unlikely as *C. mercuriale* individuals did not tire from flight trials any faster or slower than the other species here (pers. obs.). It is more likely that as a habitat specialist species, *C. mercuriale* is in a more fragmented landscape than *C. puella* and other Odonata, so even with greater flight ability it would be unable to disperse until suitable habitat (in an appropriate climate) is available within range (Watts et al., 2004).

2.5.4 Implications of the work

Assuming these results apply outside the studied taxon and variation in flight ability has a causal link with range expansions (as opposed to just being correlated), we must start to take this into account when predicting population movements. Whilst generally only geographical barriers have been considered in the past, invisible barriers are likely to exist where suitable habitat exists outside of a species dispersal range due to poorer flight performance. The habitat could still be colonisable, but may require 'stopover' rests or even generations to reach. These stepping stone habitats could be provided by conservation efforts and have already been considered in some cases (Ignatieva et al., 2011; Pereira et al., 2011; Saura et al., 2014). This emphasis on functional ecology (i.e. the interpretation of landscape configurations in light of the behaviour and physiology of species) must feed into conservation planning, where species with limited dispersal capacity could be identified, so conservation can focus on the provision of dispersal corridors, not just restoration of current habitat for example. High dispersal ability, with small northward range shift may be an indicator that the species is facing other, more important threats.

Further studies should certainly try to examine whether efficient flight measured more accurately through respirometry also correlates with these range shifts. This result is not unexpected as more efficient flyers will be able to fly for longer, which might increase the chances of longer distance dispersal, but does not help us elucidate whether a trade-off between agile flight and overall flight speed exists. We also don't yet know the behavioural mechanisms that facilitate range expansion – at least not in the Odonata. What conditions encourage long distance dispersal? Or are Odonata continually dispersing as far as possible – but only rising temperatures allow them to survive in the new environments? The Odonata data used here to calculate range shifts look at the presence of adult insects – so presence does not necessarily indicate a suitable habitat or breeding population.

2.5.5 Conclusion

I used modern biomechanical techniques to collect flight performance data for UK Odonata species. The data provides a quantitative description of UK Odonata flight performance and its intra- and interspecific variation, allowing comparative measurements of mobility. Little evidence was found to support the idea that Anisoptera are generally fast but non-agile fliers and the Zygoptera are the opposite. Instead the evidence supports flight efficiency as the leading difference between the two groups' flight performance.

Flight efficiency also correlated to recent range shift magnitudes, suggesting that some aspect of dispersal ability is important when considering population movements. Without considering both biomechanics and ecology, it is unlikely that the impact of mobility on macroecological patterns could have been detected, supporting the use of interdisciplinary approaches. Future modelling work should consider the inclusion of quantitative locomotory performance, when considering the movement of populations. In addition, future work will hopefully advance this area of research by analysing flight efficiency with respect to population movements, using more direct techniques, such as respirometry.

Chapter 3 – Functional ecology of Odonata wing morphometrics

3.1 Abstract

Wing morphometrics play an important role in determining the flight performance of insects. This is particularly true for species that undergo costly long distance migrations, but also when considering the dispersal of insect populations in relation to climate change, or the spread of invasive species. Whilst many features of wing shape and size have been studied, the variation across insect taxa is remarkable and links between form and function are rarely tested. Here I record wing morphometrics for 124 individuals of 14 Odonata species alongside biomechanical flight performance measures. The insects involved ranged from 0.02g to 1.01g and wing aspect ratios ranged from 5.6 to 8.9. The results showed a strong correlation between several measures of wing size and shape and flight performance with speed, acceleration and agility positively correlated with wing shape (aspect ratio, 2nd and 3rd moments of area) and negatively correlated with size characters (insect mass, wing loading, wing length, wing chord and wing area). A measure of flight efficiency was positively correlated with the same size characters and negatively correlated with wing shape. The fine details of wing shape measured through geometric morphometrics were only correlated with speed and acceleration of flight, with faster flight characterised by broader less petiolate wings. Using these novel findings, I evaluate 35 prior assumptions from the published literature regarding wing morphology and flight performance, of which only about 25% are supported with any certainty and at least 42% are inconsistent with the new data. I show that the size and shape of a wing can predict the efficiency of flight behaviour and path curvature in Odonata, with large, broad wings being linked with tighter turns in flight but less efficient behaviour and small slender wings linked with efficient flight behaviour, but wider turns in flight. Given the lack of consistency with assumptions regarding morphology and flight performance, considerable re-evaluation of these links is required.3.2 Introduction

3.2.1 Wing shape and flight at different scales

All flying animals and even some plant seeds have wings, which act to provide lift and/or motion control during flight. The diversity of shapes and sizes of wings produced by the natural world is staggering, from the 3.7m wingspan of a wandering albatross, to the 0.4mm wingspan of fairyflies in the *Kikiki* genus (Huber and Beardsley, 2000). With flight as such an advantageous yet expensive evolutionary trait, the shape and size of any wing is important, and should be adapted to the locomotion needs of an individual. However, animal wings usually represent a compromise between multiple adaptive functions, flight being primary, but also several secondary functions, for example, sensing, signalling, courtship or the ability to fold wings away, which may limit their aerodynamic efficiency (Wootton, 1992). Flight performance of any animal is influenced by a large number of traits, making it difficult to separate out the effects of any individual trait (Outomuro et al., 2013a). To further complicate wing morphometrics, animal flight occurs at a range of different scales (Reynolds numbers) changing the physics involved in flight and often the impact of certain morphologies (Wootton, 1992). Reynolds number is a non-dimensional quantity representative of the ratio of inertial to viscous forces present in a fluid. It is a common feature of fluid dynamics, and changes with the size of the object moving through a fluid and the speed at which it is moving among others. Insects operate at comparatively low Reynolds numbers around 10 to 10^5 (Dudley, 2000; Sane, 2003).

Ellington (1984) separates flight related parameters into two distinct categories, gross and shape parameters, gross parameters being quantitative descriptions of the size and mass of insect morphology, for wings these are length, chord, area and wing loading. Wing chord is the width of the wing and is usually expressed as average or normalised chord (as this parameter varies along the length of the wing). Wing loading is the amount of mass that a given area of wing has to support in flight, i.e. the average amount of pressure exerted by the wings on the surrounding air (see Equation 3.1). Shape parameters are defined as being the distribution of these gross parameters i.e. the shape of the wings, including aspect ratio (AR), and the 2nd and 3rd moments of wing area. AR is the ratio between the squared wingspan and the area of the wing or the wingspan and the mean chord of the wing, see Equation 3.2).

These flight parameters will all affect flight performance of an individual but flight performance is itself a complex quantity, comprised of multiple possible features, that needs to be explained.

Here I try to separate flight performance into the ideas of efficiency, straight line speed, and manoeuvrability and agility. Efficiency is the measure of energy used to perform a certain task, so in this case efficiency is the distance travelled given a certain amount of energy input. Efficiency is important for gliding and long distance migration. Wing morphology is important in determining flight efficiency, as it dictates the surface used to provide lift for weight support and thrust for movement in the air. AR is positively correlated with low induced power requirements and high lift to drag ratios (Betts and Wootton, 1988; Wootton, 1992). However at lower Reynolds numbers, higher AR wings' relatively increased profile drag cause them to become less efficient, so a compromise must often be met in smaller insects (Ennos, 1989). At higher ARs in insects not only is relatively higher profile drag a problem, but they also start becoming too thin to support the outer portion of the leading edge vortex that forms over the wing (Luo and Sun, 2005; Phillips et al., 2015). Wing loading is also important for efficiency as wings with a high wing loading generally require greater power in order to provide enough lift to allow for flight, as they must be moved through the air at greater speed to provide sufficient lift, possibly reducing their efficiency (Wakeling, 1997). Weis-Fogh (1973) showed that the 2nd moment of area is proportional to the average lift produced by the wing, so will have an influence on efficiency by providing greater lift for certain shapes.

Straight line speed or steady flight is an important aspect of flight performance as it reflects the speed at which an animal can move from A to B and also the chance of an animal catching up to prey or a mate etc. It is also the easiest of the three aspects of flight performance to quantify and measure. In general, the larger the area of an animal's wings the greater the downwash and thrust that can be produced, and thus the faster straight line speed. AR does not have an impact on steady flight speed (except where gliding is concerned) (Norberg and Rayner, 1987). The square root of wing loading has been shown to be proportional to flight speed, although this only applies under fairly rigorous assumptions (wing shape and size vary isometrically with body mass and wing lift coefficients remain constant) and is not the sole influence on straight line speed (Betts and Wootton, 1988; Norberg and Rayner, 1987). In general it is gross parameters that are responsible for generating straight line speed, as the larger the animal the larger the forces that can be produced for flight. One exception is the 3rd moment of area, which Weis-Fogh showed to be proportional to the average power profile of the wing, suggesting that some aspects of wing shape still remain important for thrust production.

Manoeuvrability and agility are separate yet similar parameters which can often be used interchangeably. Here I use Norberg and Rayner's definitions of the two quantities (Norberg and Rayner, 1987). Manoeuvrability is a measure of turning circle, the minimum space in which an animal can turn in flight and represents the minimum sized spaces an animal can fly in. Agility is a measure of how quickly a turn can be initiated, i.e. the reflexive speed of an animal in flight. Both rely on gross and shape parameters. Wing length increases the inertial forces required to turn the wings and can also prevent the animal entering small spaces due to potential collisions (Betts and Wootton, 1988; Norberg and Rayner, 1987).

3.2.2 Wing shape and ecology

Unlike the links between wing morphology and flight performance, the link between wing morphology and ecology or behaviour has received considerable attention. Of particular interest is the relationship between wing morphology and dispersal, although many studies have found no evidence for wing morphology affecting ecology or behaviour, often finding that flight muscle mass is a more important driver (Hill et al., 1998; Therry et al., 2014; Therry et al., 2015). However, some studies have found correlations with AR, although these are not consistent even within the same genus, with some studies finding high AR associated with dispersal (Hassall et al., 2009; Hughes et al., 2007; Swaegers et al., 2014), and others finding low AR associated with dispersal (Hill et al., 1999; McCauley, 2013). Another interesting aspect, particularly given the use of wings for courtship or signalling in some species is the difference in wing morphology between sexes. A number of studies have described morphological differences between male and female wings (Bots et al., 2009; DeVries et al., 2010; Gallesi et al., 2016; Grabow and Rüppell, 1995; Wickman, 1992), and gone on to test whether the mechanisms behind these differences are due to sexual selection, or natural selection (Breuker et al., 2007; Outomuro and Johansson, 2011).

Geometric morphometrics as used in many of the studies mentioned here are increasingly used to analyse morphological characteristics in relation to identification (Francoy et al., 2008; Tofilski, 2008), ecology (Bots et al., 2012; Gómez et al., 2014; Olsen, 2017; Outomuro and Johansson, 2011; Outomuro and Johansson, 2015; Outomuro et al., 2014) and evolution (Debat et al., 2003; Johansson et al., 2009; Outomuro et al., 2012; Outomuro et al., 2013b; Outomuro et al., 2013c). The advantage of geometric morphometrics is that they incorporate all aspects of the shape in question independently of size, position and orientation, however few biomechanical studies have used geomorphometrics, still using features like 2nd moment of area to define wing shape instead, so the influence of exact shape is still uncertain in regards to flight biomechanics.

3.2.3 Odonata wing morphometrics - Biomechanics

In terms of flight performance, many of the specifics of Odonata flight have been known for a considerable period of time, covered in detail by Wakeling and Ellington (1997a; 1997b; 1997c), and Wakeling and Wootton both cover odonate wing morphologies in relation to flight (Wakeling, 1997; Wootton, 1991). The two major odonate groups (Anisoptera and Zygoptera) differ considerably in wing shapes, with the Zygoptera having similar fore and hindwings and the majority of their wing mass distributed distally (67% of wing mass in the distal half of the wing) (Wakeling, 1997). In contrast the fore and hindwings of the Anisoptera are considerably different and only 45-53% of the wing mass is located in the distal half of the wing (Wakeling, 1997). More recent studies using geometric morphometrics have started to find significant differences between the shapes of the fore and hindwings in Zygoptera, even though their gross parameters might be similar (Outomuro and Johansson, 2011; Outomuro et al., 2012), although the differences between Anisoptera and Zygoptera remain. The difference seen between anisopteran and zygopteran wings is thought to reflect different flight styles, with slow flight in the Zygoptera and fast flight in the Anisoptera (Wakeling, 1997). The relative airflow over flapping wings is much higher towards the tip of the wing, so at the low flight speeds of the

Zygoptera, wing area towards the body will not be moving at fast enough speeds to provide enough lift – hence the increased area distally (Wakeling, 1997). Higher wing loadings (Grabow and Rüppell, 1995) in the Anisoptera likely contribute to higher flight speeds (Norberg and Rayner, 1987).

A further consideration that is rarely incorporated into functional analysis is the microstructure of odonate wings. The wings of dragonflies are not flat as they may appear to be from a distance, but rather corrugated, with multiple peaks and troughs, when viewed in cross section. Rotating vortices develop in these troughs during flight which are thought to help provide lift whilst not producing more drag than would be expected of a flat surface (Kesel, 2000). Like other insect wings, Odonata wings passively deform during flight to change twist, camber and other aerodynamically useful features (Wootton, 1992). A complex system of spikes, and vein joints often involving a rubbery substance known as resilin is responsible for passive deformations of the wing (Rajabi et al., 2015; 2016a; 2016b; 2016c; 2016d). The location of resilin placement differs between Zygoptera and Anisoptera, perhaps explaining some of the aerodynamic differences between the two clades (Donoughe et al., 2011).

3.2.4 Odonata wing morphometrics – Ecology and behaviour

Work on odonate wing shapes and its effect on ecology and behaviour have mostly been conducted on Zygoptera species, with considerable focus on the *Calopteryx* genus, perhaps due to the larger size (for zygopterans) and conspicuous nature of these species and thus ease of field study.

Many Odonata species are territorial, and defend territories through aerial contests, so logically flight performance should be important for determining the outcome of such contests. In contrast, competition studies show wing shape as unimportant in determining the winner of male-male competition (Bots et al., 2012; Outomuro et al., 2014). It is possible though that these studies may not have properly captured relevant statistics involved in territorial disputes (Bots et al., 2012). A difference in wing shape based on geometric morphometrics has been shown between territorial and non-territorial tactics of *Calopteryx* sp. (Outomuro et al., 2014).

Several studies consider the implications of flight morphology and dispersal, particularly given the importance of climate change induced range shifts, and increasingly fragmented freshwater habitats. At local levels, wing chord was shown to vary with landscape (Outomuro et al., 2013c). Studies with wider geographical scope showed variations in aspect ratio of *Calopteryx maculata* wings across temperature gradients (Hassall, 2015a), *Coenagrion puella* showed a negative correlation between latitude and wing loading (Hassall et al., 2008) and that the shape of front wings in *Calopteryx virgo* correlates with latitude, although no explanation for how these different shapes suited different latitudes was given (Outomuro and Johansson, 2011).

Anisopteran studies are fewer than those for Zygoptera although some ecologically relevant trends in wing morphology have been found. In libellulids, larger species have greater wing loadings and aspect ratios and are found at higher perches (Worthen and Jones, 2007). It is not clear if perch height is due to larger species preferring higher airspeeds for flight or competitive interactions. Migration and also possibly mate guarding was found to correlate with geometric morphometrics of wing shape in 26 Anisoptera species (Johansson et al., 2009)

3.2.5 Flight related morphology

To date, few studies have looked for direct impacts of wing morphology on flight performance, though several have taken the next step and compared wing morphology to ecology or behaviour. Even fewer haver attempted to determine the general effect of wing morphology on flight, looking at species from different groups and scales. Those that have attempted to synthesise the mechanisms through which wing shape translates to flight performance are often relatively old, acknowledge the limited knowledge we have, the general lack of data available and the difficulty of synthesising material that is linked with such complexity (Betts and Wootton, 1988; Ellington, 1984b; Norberg and Rayner, 1987; Wootton, 1991; Wootton, 1992). Some newer attempts have been made but with unhelpful or vague measures of flight performance being used (Berwaerts et al., 2002). Within the Odonata, behavioural studies dealing with wing shape and behaviour have also been primarily focussed on the *Calopteryx* genus and have generally not tested the suitability of flight relevant morphological measures. Here I test the following set of assumptions regarding wing morphology and flight in Odonata.

3.2.6 Linking wing morphometrics and flight performance

There is no unanimous agreement on the influence of wing morphometrics on flight performance. A number of assumptions with varying levels of support from the literature are set out in Table 3.1. From these I set out to test the validity of the assumptions by comparing quantitative flight data collected in chapter 2 to the wing morphometrics of the individuals involved, covering a range of different Odonata species. The exact nature of the relationship between wing morphometrics and flight performance is likely to change between different sized insects, and between those that effectively only have one pair of wings (for example Diptera with only one pair of wings or Lepidoptera with attached forewings and hindwings) rather than two pairs. Here, I predict that gross parameters such as length, chord and area will be more important for steady flight/speed of flight, whereas aspect ratio, and shape factors will be more important for efficiency, manoeuvrability and agility.

Table 3.1 – List of assumptions made about the links between wing morphology and flight performance. *[1]These assumptions are supported by my data (dark grey, see section 3.5). *[2]These assumptions are partially supported by my data, i.e. some aspect of flight performance is correlated to the wing metric but not all aspects (light grey, see section 3.5). *[3]This particular geometric morphometric is similar to 2nd moment of area

Wing morphometric	Aspect of flight performance affected	Trend (+/-)	Study group	Source
1 – Length	1.1 -Agility & Manoeuvrability	+	Odonata (639 species)	[1]
		- *[1]	**Odonata (26 species)**	**[2]**
			Odonata (3 *Libellula sp.*)	**[3]**
	1.2 - Efficiency	+	Odonata (639 species)	[1]
			Odonata (26 species)	[2]
			Odonata (3 *Libellula sp.*)	[3]
	1.3 - General performance	+ *[2]	Odonata (*Calopteryx maculata*)	[4]
2 – Chord	2.1 - Agility & Manoeuvrability	+	Odonata (*Enallagma cyathigerum*)	[5]
			Odonata (*Calopteryx virgo*)	[6]
		- *[1]	**Odonata (3 *Libellula sp.*)**	**[3]**
	2.2 - Efficiency	+	Odonata (3 *Libellula sp.*)	[3]
	2.3 - Speed	+ *[2]	Odonata (26 species)	[2]
	2.4 - General performance	+ *[2]	Odonata (*Calopteryx maculata*)	[4]
3 – Area	3.1 - General performance	+ *[2]	Lepidoptera (*Parage aegeria*)	[7]
	3.2 - Speed	+ *[2]	Lepidoptera (*Hesperia comma*)	[8]
			Lepidoptera (*Parage aegeria*)	[9]
4 – AR	4.1 - Efficiency	+ *[1]	**Lepidoptera (*Melitaea cinxia*)**	**[10]**
			Lepidoptera (21 *Morpho sp.*)	**[11]**
			Odonata (*Calopteryx splendens*)	**[12]**
			Odonata (3 species)	**[13]**
			Odonata (*Calopteryx virgo*)	**[14]**
			Odonata (37 Calopterygidae species)	**[15]**
			Odonata (16 *Coenagrion sp.*)	**[16]**
		-	Odonata (*Calopteryx maculata*)	[17]
		0	Odonata (3 *Libellula sp.*)	[3]
	4.2 - General performance	+ *[2]	Lepidoptera (*Parage aegeria*)	[7]
			Odonata (*Coenagrion scitulum*)	[18]
	4.3 - Agility & Manoeuvrability	+ *[1]	**Odonata (*Calopteryx maculata*)**	**[17]**
		-	Odonata (*Enallagma cyathigerum*)	[5]
			Odonata (*Calopteryx virgo*)	[6]
			Lepidoptera (21 *Morpho sp.*)	[11]
			Odonata (*Calopteryx splendens*)	[12]

			Odonata (*Calopteryx virgo*)	[14]
			Odonata (37 Calopterygidae species)	[15]
			Odonata (*Calopteryx splendens*)	[19]
			Odonata (32 *Trithemis sp.*)	[20]
			Odonata (3 *Calopteryx sp.*)	[21]
	4.4 - Speed	+ *^{2}	Lepidoptera (*Melitaea cinxia*)	[10]
			Lepidoptera (44 species)	[22]
5 - Wing Loading	5.1 - Efficiency	+	Lepidoptera (*Melitaea cinxia*)	[10]
		- *^{1}	**Odonata (16 *Coenagrion sp.*)**	**[16]**
			Lepidoptera (44 species)	**[22]**
	5.2 - General performance	+ *^{2}	Lepidoptera (*Parage aegeria*)	[7]
		-	Odonata (*Coenagrion scitulum*)	[18]
	5.3 - Agility & Manoeuvrability	**- *^{1}**	**Odonata (*Enallagma cyathigerum*)**	**[5]**
	5.4 - Speed	**+ *^{1}**	**Lepidoptera (*Melitaea cinxia*)**	**[10]**
			Lepidoptera (44 species)	**[22]**
6 - 2nd Moment of Area	6.1 - Efficiency	**+ *^{1}**	**Lepidoptera (21 *Morpho sp.*)**	**[11]**
		-	Odonata (37 Calopterygidae species)	[15]
	6.2 - Speed	- *^{2}	Odonata (37 Calopterygidae species)	[15]
	6.3 – Agility and Manoeuvrability	**+ *^{1}**	**Odonata (*Epipleoneura williamsoni*)**	**[23]**
7 - 3rd Moment of Area	7 - Speed	+ *^{2}	Lepidoptera (21 *Morpho sp.*)	[11]
8 - Geometric morphometrics (wing ‘roundness’)	8.1 - Efficiency	-	Odonata (*Calopteryx splendens*)	[12]
	8.2 - Agility & Manoeuvrability	+	Odonata (*Calopteryx splendens*)	[12]
9 - Geometric morphometrics (wing tip ‘pointedness’)	9 - Efficiency	+	Odonata (26 species)	[2]
10 - Geometric morphometrics (wing base breadth)*^{3}	10.1 - Agility and Manoeuvrability	-	Odonata (26 species)	[2]
	10.2 - General performance	+ *^{2}	Odonata (32 *Trithemis sp.*)	[20]
11 - Geometric morphometrics (concave leading edge – through indented nodus)	11 - Agility & Manoeuvrability	+	Odonata (*Calopteryx splendens*)	[19]

References used in Table 3.1

1. (Sacchi and Hardersen, 2013)
2. (Johansson et al., 2009)
3. (McCauley, 2013)
4. (Taylor and Merriam, 1995)
5. (Bots et al., 2009)
6. (Bots et al., 2012)
7. (Hughes et al., 2007)
8. (Hill et al., 1998)
9. (Hill et al., 1999)
10. (Breuker et al., 2007)
11. (DeVries et al., 2010)
12. (Gallesi et al., 2016)
13. (Hassall et al., 2009)
14. (Outomuro and Johansson, 2011)
15. (Outomuro et al., 2013a)
16. (Swaegers et al., 2014)
17. (Hassall, 2015a)
18. (Therry et al., 2014)
19. (Outomuro and Johansson, 2015)
20. (Outomuro et al., 2013c)
21. (Outomuro et al., 2014)
22. (Wickman, 1992)
23. (Vilela et al., 2017)

3.3 Methods

See Section 2.3.1-2.3.4 for methodology for collecting flight performance data and the insects involved. The principal components analysis (PCA) carried out in chapter 2 will be referred to as flight principal components, for example, ‘FPC1’ is the first principal component of the PCA on biomechanical flight performance values, representing flight speed (see Table 3.2 for PCA abbreviations).

Table 3.2 – Abbreviations of principal component analyses used in this chapter

Abbreviation	Name	Description
FPC (FPC1, FPC2 and FPC3)	Flight principal component	Values pertaining to the biomechanical flight performance measured in the laboratory. See Section 2.4 and Table 2.3 for interpretations.
SPC (SPC1-F and SPC1-H)	Shape principal component	Values pertaining to morphometric variation in wing size and area (including 3 size independent measures – see Table 3.3 and Section 3.3.2)
GPC (GPC1-F and GPC1-H)	Geometric morphometric principal component	Values pertaining only to shape variation of the wing independent of size (see Figure 3.4 and Section 3.3.2)

3.3.1 Wing dissection and preparation

Wings from insects for which flight performance had been recorded (see chapter 2) were dissected off the insect after death using a scalpel. They were then mounted on transparent tape and scanned using a Canon (LiDE 25) scanner. Images were then cropped and manually cleaned of dust spots etc. before analysis.

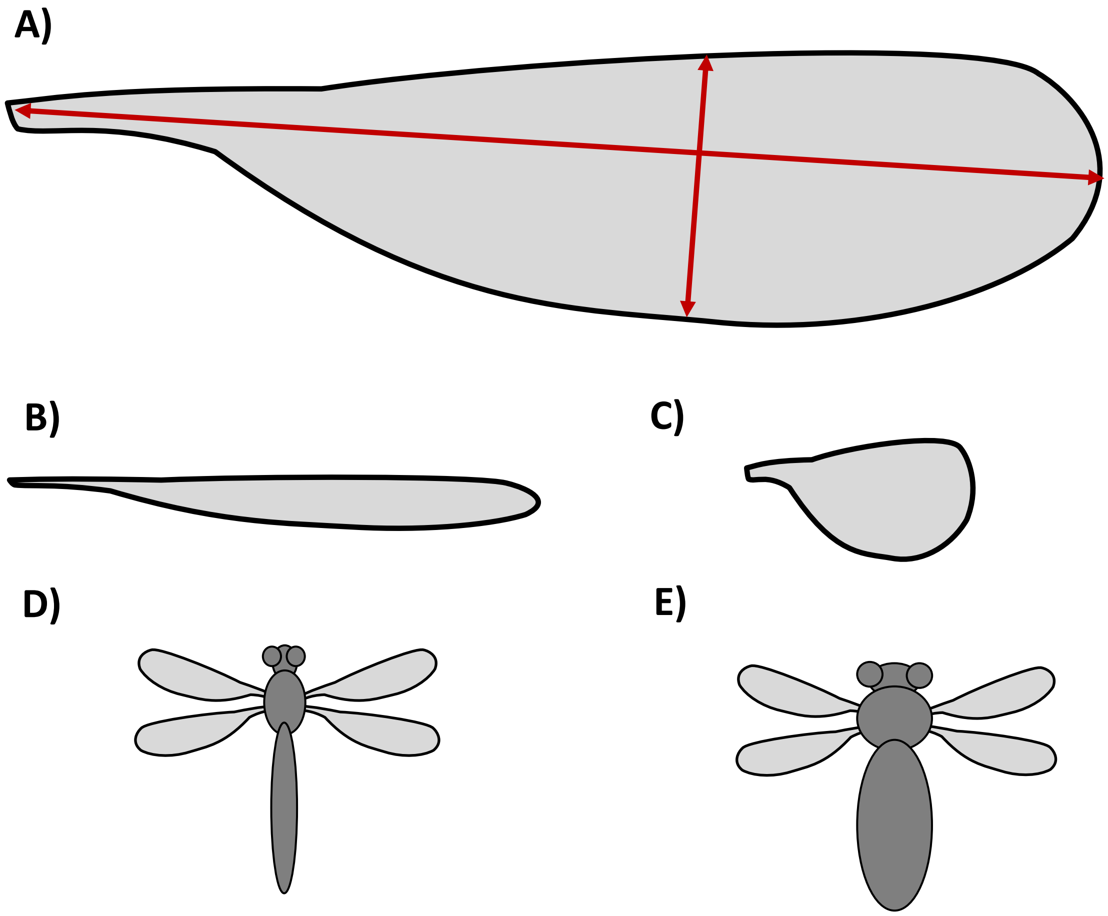


Figure 3.1 – A) Diagram showing wing length and wing chord (average chord is the average of the chord across the entire length of the wing). B) Example of a high aspect ratio wing. C) Example of a low aspect ratio wing. D) Example of low wing loading. E) Example of high wing loading.

3.3.2 Wing shape analysis

WingImageProcessor (custom written Matlab software written by Hedrick Lab, http://www.unc.edu/~thedrick/) was used to calculate basic wing shape statistics (length, average chord, area, AR, 2nd moment of area, see Figure 3.1). Simple (univariate) morphometric properties of the wings (insect mass, wing length, wing chord, wing area, wing loading, aspect ratio, 2nd moment of area and 3rd moment of area, hereafter referred to as wing statistics) were recorded for each insect and combined using two separate PCA analyses, one for the forewings and one for the hindwings. Only the left forewings were used in the analyses to avoid issues of asymmetry and the left wing dataset was slightly more complete than the right (fewer damaged wings). Note that here AR is taken for each wing separately. The principal components of these analyses will be referred to as shape (SPCs) as opposed to the FPCs or GPCs. For example, ‘SPC1-F’ is the first principal component of the forewing PCA analysis of the wing statistics. If the wing letter is left off at the end (e.g. SPC1), the principal components from both analyses are being referred to.

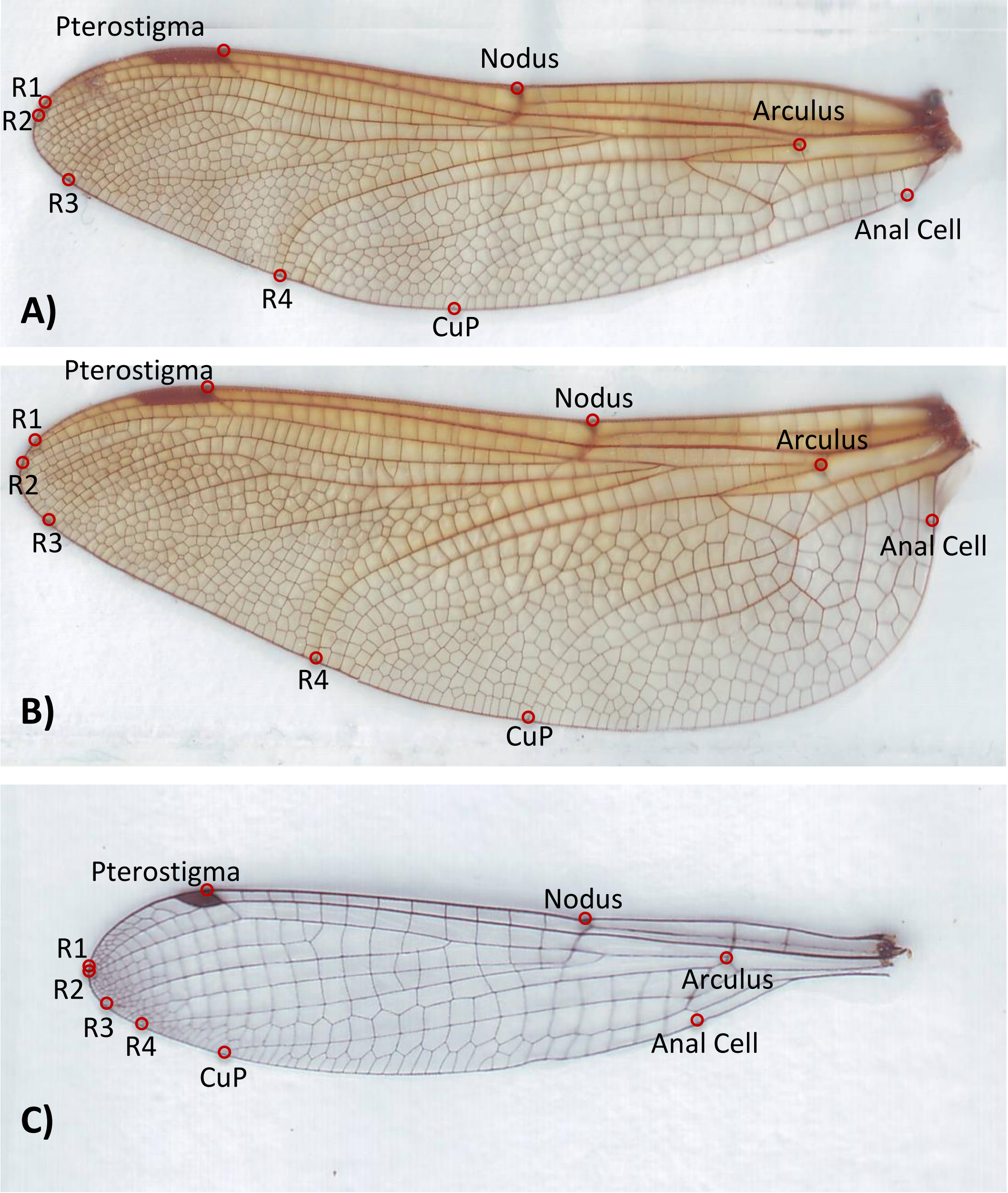


Figure 3.2 – Anisoptera (*Aeshna grandis*) forewing (A), hindwing (B) and landmarks used in the GPCA. Zygoptera (*Erythromma najas*) hindwing (C) and landmarks used in the GPCA. Zygoptera fore and hindwings have very similar structure so only one wing is shown here.

Afterwards, the software tpsDIG2 (Rohlf, 2005) was used to digitise nine landmarks (See Figure 3.2) on all wing images. Where wing damage had removed or obscured landmarks they were marked as missing. R (R Core Team, 2017) was used to carry out a generalised Procrustes analysis (GPA) on the landmarks (Adams et al., 2017; Dryden, 2017). The GPA acts to superimpose the shapes created by the landmarks onto an arbitrary reference landmark by uniformly scaling, translating or rotating the array of landmarks. If the reference shape then lies outside a threshold value from the mean of all the superimposed shapes, the mean is then used instead as a reference (and the process is repeated). The new co-ordinates of the landmarks (with size and rotation data effectively removed) can then be used to represent shape alone. Only the data for wings on one side of the body was carried forward to avoid pseudoreplication. The left wings were chosen as fewer of them had sustained damage. The principal components produced by the GPA were termed GPCs (see Table 3.2).

3.3.3 Statistics

Flight data was analysed as in chapter 2. All statistics were carried out in R (R Core Team, 2017). Separate PCAs were carried out for both forewings and hindwings on the wing statistics (SPCA) and the Procrustes analysed landmark data (GPCA). The principal components of the latter of which will be referred to as GPCs. For example 'GPC1-H' is the first principal component of the geometric morphometrics PCA on the hindwing landmark data (See Figure 3.4 for the shape that GPC1 represents). A mixed effects model was then built using the "lme4" R package (Bates et al., 2015), with flight performance (represented by the principal components from chapter 2, FPCs) as the dependent variable, the first principal components of the SPCAs and GPCAs as the fixed effects (those that explained the majority of variation in the dataset and were above the elbow of the PCA scree plots) and species as a random effect. AIC was minimised to select the model that best fit the data using the "MuMIn" R package (Barton, 2008), and variance inflation factors were calculated using the "car" R package (Fox and Weisberg, 2011) to check for collinearity in the predictor variables.

3.3.4 – Phylogenetic corrections

The data from this chapter is based on several species with varying but often close evolutionary links. This evolutionary correlation between species may have influenced the results of the statistical analyses carried out. I re-analysed the data using the same methods as above whilst in addition considering the phylogenetic relationships involved. A phylogenetic tree from the Odonata was downloaded from the Open Tree of Life (Hinchliff et al., 2015), consisting of phylogenetic data supported by three studies (Letsch and Simon, 2013; Rota-Stabelli et al., 2013; Simon et al., 2009), shown in Figure 2.3. Note that the *Anax imperator* branch (in addition to all the other Odonata species not shown in Figure 2.3) was removed for analysis as this species was not included in the analyses in chapters two and three. Using R and the phytools (Revell, 2012), caper (Orme et al., 2018), geiger (Harmon et al., 2008) and picante (Kembel et al., 2010) packages, the minimum adequate models constructed in chapters two and three were reconstructed but accounting for the correlation structure brought about by phylogenetic relationships. This was done using the general least squares (GLS) method, and assuming a Brownian motion process for evolution. The Ornstein-Uhlenbeck (OU) process could not be used as there was insufficient data to generate the required correlation structure. The results remained the same after taking phylogenetic relationships into account, except that agility and manoeuvrability (FPC3) is no longer significantly correlated with forewing size (SPC1-F), but only marginally so (see Table 3.7).

3.4 Results

3.4.1 Wing descriptive statistics (SPCA)

The wing statistics measured here were similar to previously published values and continue to support the difference between Anisoptera and Zygoptera, where Zygoptera hind and forewings are similar and Anisoptera forewings differ from their hindwings, shown by the deviation of Anisoptera from the 1:1 lines in Figure 3.3. Wings ranged in size from $0.16cm^2$ to $7cm^2$, with loadings of $0.035g\cdot cm^{-2}$ to $0.43\ g\cdot cm^{-2}$ and aspect ratios between 5.6 and 8.9.

Wing statistics (SPCA) was well described by a single principal component with 75-76% of the variance explained by the first principal component (SPC1, see Table 3.3), which was correlated negatively with mass, wing loading, wing area, length and average chord (gross parameters) and positively correlated with AR, dimensionless 2nd and 3rd moment of area (shape parameters). These correlations suggest that SPC1 is a measure of how small and slender a wing is.

3.4.2 Wing shape (GPCA)

The Anisoptera and Zygoptera are shown to have significantly different wing shapes (this trend is not disrupted when including the intermediate *Calopteryx splendens*), although the variation in GPCs seems relatively small. The variation in wing geometric morphometrics between species of the same group (Anisoptera or Zygoptera) also seems relatively small as shown by Figure 3.4, with a maximum difference of 0.24 between Zygoptera in the first principal component (90-94% of the variance in the dataset). *Calopteryx splendens* is immediately set apart from all other species having an intermediary wing shape between the Anisoptera and other Zygoptera on GPC1, and the only species showing considerable differences to the others along the 2nd principal component axis.

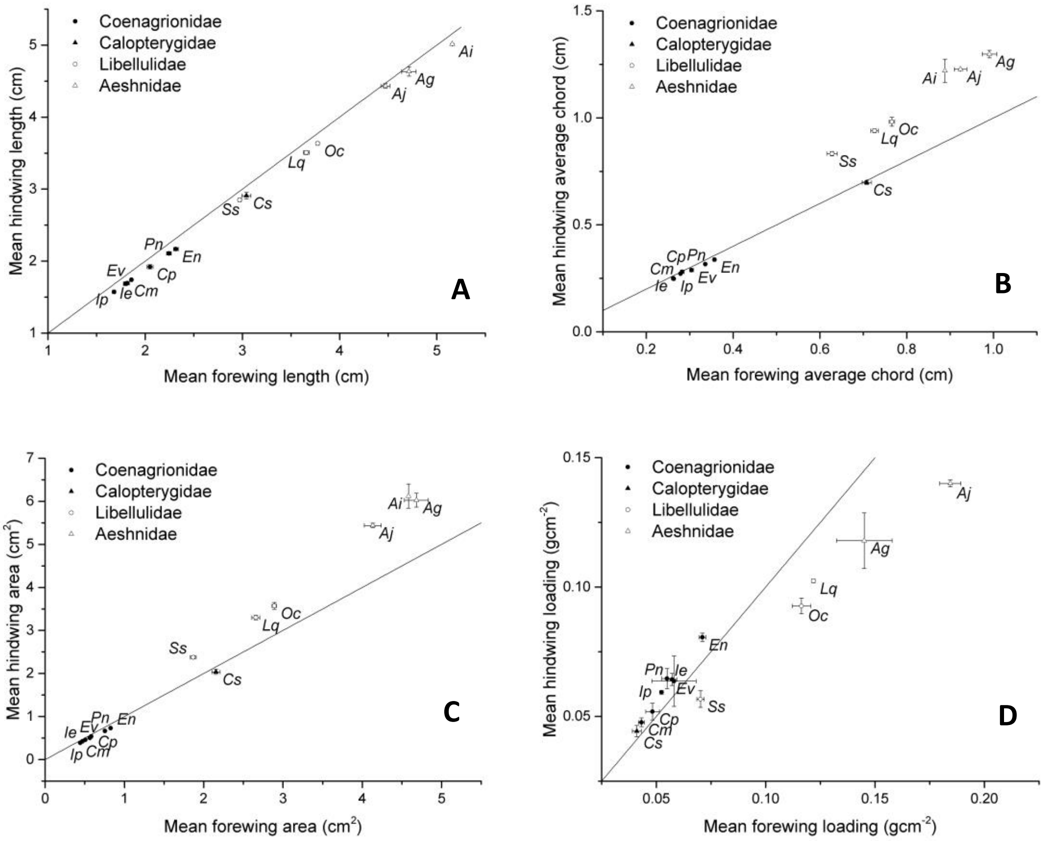


Figure 3.3 – Scatter graphs of species' average hindwing statistic vs. forewing statistic (left and right wings). A) Wing length, B) wing chord, C) wing area, D) wing loading. Error bars represent standard error and the line on each graph corresponds to 1:1. Where error bars are absent n=1. Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. For species abbreviations see Table 2.2.

3.4.3 Links between wing morphometrics and flight performance

Here I describe the principal components involved in statistical analysis, followed by the relationships seen in the mixed affects models constructed for both fore and hindwings together. The dependent variables, the FPCs (see Table 2.3, chapter 2) are, FPC1 positively correlated with speed and acceleration (flight speed), FPC2 positively correlated with flight efficiency (high speed, low acceleration – efficient flight behaviour) and FPC3 negatively correlated with flight path curvature (flight manoevrability) (see Table 3.4). The independent variables used are SPC1 and GPC1. SPC1 is positively correlated with AR, 2nd and 3rd moment of area and negatively correlated with insect mass, wing loading, wing area, wing length and wing chord (see Table 3.5 and 3.6). GPC1 represents a generally broad and less petiolate wing at higher values (see Figure 3.4).

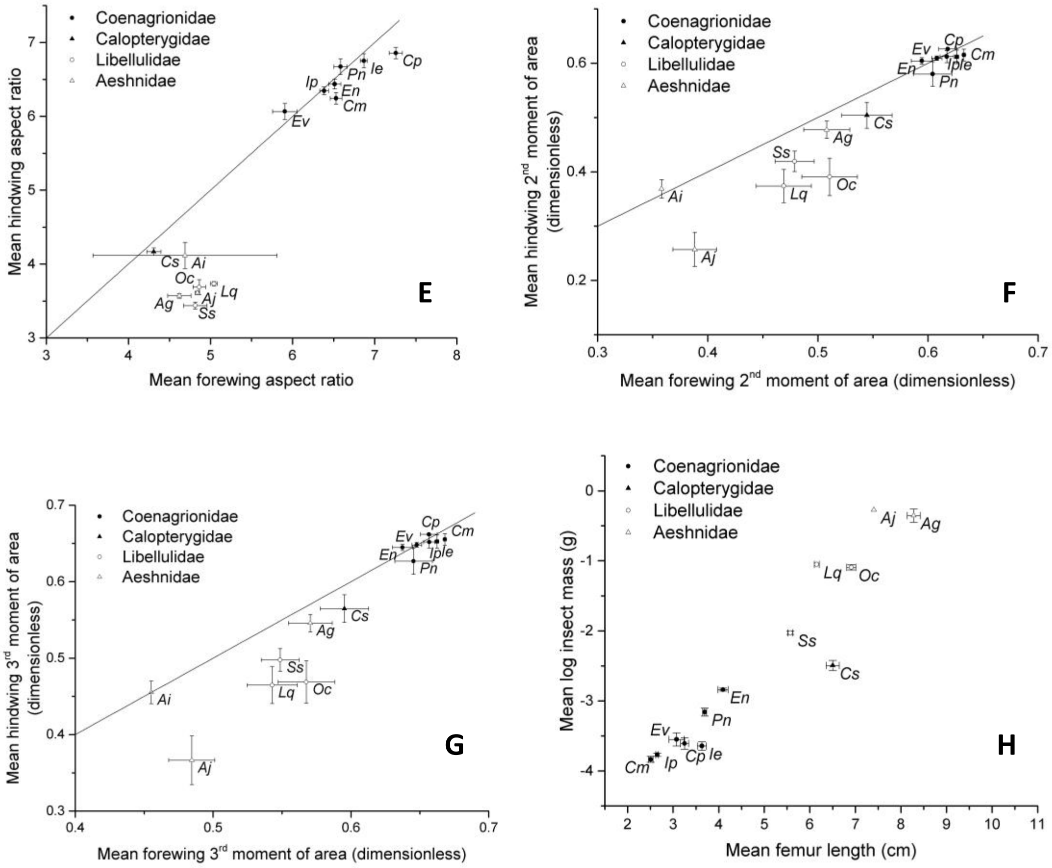


Fig. 3.3 cont. – Scatter graphs of species' average hindwing statistic vs. forewing statistic (left and right wings). E) Aspect ratio, F) 2nd moment of area, G) 3rd moment of area, H) log total insect mass vs. femur length. Error bars represent standard error and the line on each graph corresponds to 1:1. Where error bars are absent n=1. Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. For species abbreviations see Table 2.2.

Table 3.3 – Table of correlation coefficients between the principal components (percentage of variance explained by each component in brackets rounded to the nearest 1%) of the PCAs on wing statistics (SPCAs) and the original variables used (all coefficients to 3 decimal places). Only principal components with eigenvalues of 1 or higher or components above the elbow of the scree plot of the analysis are shown. Correlation coefficients over 0.5 are highlighted.

	Forewing		**Hindwing**	
	SPC1-F (76%)	SPC2-F (13%)	SPC1-H (75%)	SPC2-H (14 %)
Insect Mass	**-0.908**	-0.322	**-0.902**	0.368
Wing Loading	**-0.820**	-0.314	**-0.635**	**0.527**
Area	**-0.967**	-0.198	**-0.962**	0.181
Length	**-0.966**	-0.160	**-0.966**	0.144
Average Chord	**-0.968**	-0.117	**-0.975**	0.049
Aspect Ratio	**0.784**	-0.068	**0.863**	0.191
Dimensionless 2nd Moment of Area	**0.768**	**-0.622**	**0.787**	**0.549**
Dimensionless 3rd Moment of Area	**0.767**	**-0.623**	**0.791**	**0.546**

The mixed effects models showed that FPC1 is significantly positively correlated with SPC1-H at higher levels of GPC1-H, but negatively correlated with SPC1-H at low levels of GPC1-H. Flight PC2 is significantly positively correlated with only SPC1-F and Flight PC3 is significantly negatively correlated with only SPC1-H (see Table 3.5 and 3.6 for AICc and p values). In other words, higher flight speeds and accelerations are accompanied by small but high AR hindwings but with as broad and less petiolate shape as possible or large, low AR wings with a more petiolate shape. Flight speed and acceleration decreases in large, low AR wings with a broad non petiolate shape and also with small high AR wings with a petiolate shape. Higher flight efficiency is accompanied by smaller but higher AR forewings and tighter turning performance is accompanied by large low AR hindwings.

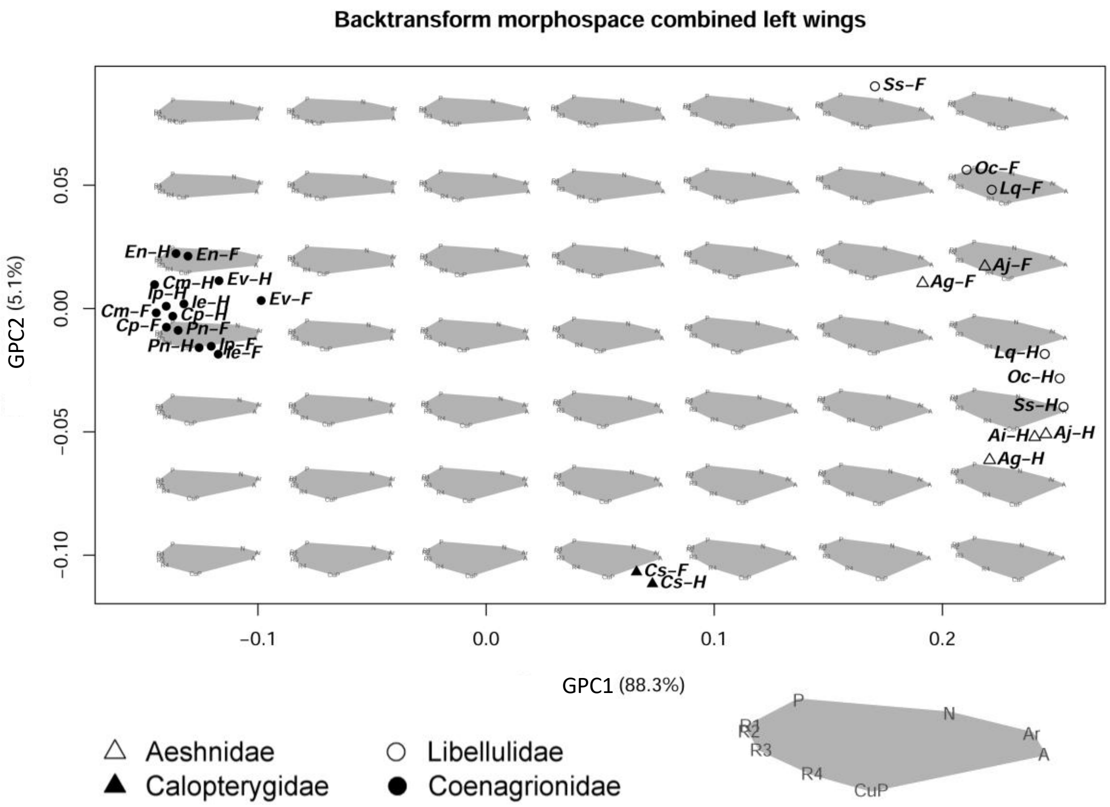


Figure 3.4 – Back-transform morphospace (Olsen, 2017) of the left forewings (-F) and hindwings (-H). Points are average principal component values for species. Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. See table 2.2 for species abbreviations. Landmarks are labelled on the back-transform morphospace as follows: Arculus (Ar), Nodus (N), Pterostigma (P), R1, R2, R3, R4, CuP, Anal cell (A).

The models constructed separately for forewings and hindwings showed the same patterns as the combined models above, except that FPC1 was only positively correlated with GPC1-F in the forewing analysis, and in the hindwing analysis similar significant correlations were found for SPC1-H, FPC2 and FPC3 as seen in the forewing and combined analysis (see Table 3.5 and 3.6 and Figure 3.5). Further flight principal components were not significantly correlated with any measures of wing morphology.

These results support only 9 of 35 prior assumptions found in the literature with partial support for a further 11. Overall the majority of assumptions are not supported or uncertain.

Table 3.4 – Explanation of separate principal components

Variable type	**PC name**	**Interpretation**
Flight	FPC1	A measure of flight speed and acceleration (positively correlated with both)
	FPC2	A measure of efficient flight behaviour (positively correlated with speed, negatively correlated with acceleration)
	FPC3	A measure of agility and manoeuvrability (negatively correlated with flight path curvature)
Shape	SPC1	A measure of wing size and broadness (negatively correlated with, insect mass, wing length, wing chord, wing area, and wing loading. Positively correlated with aspect ratio and 2nd and 3rd moments of area)
Geometric morphometrics	GPC1	A measure of wing broadness and petiolate-ness (positively correlated with broad shapes and negatively correlated with how petiolate the wing is – see Figure 3.5)

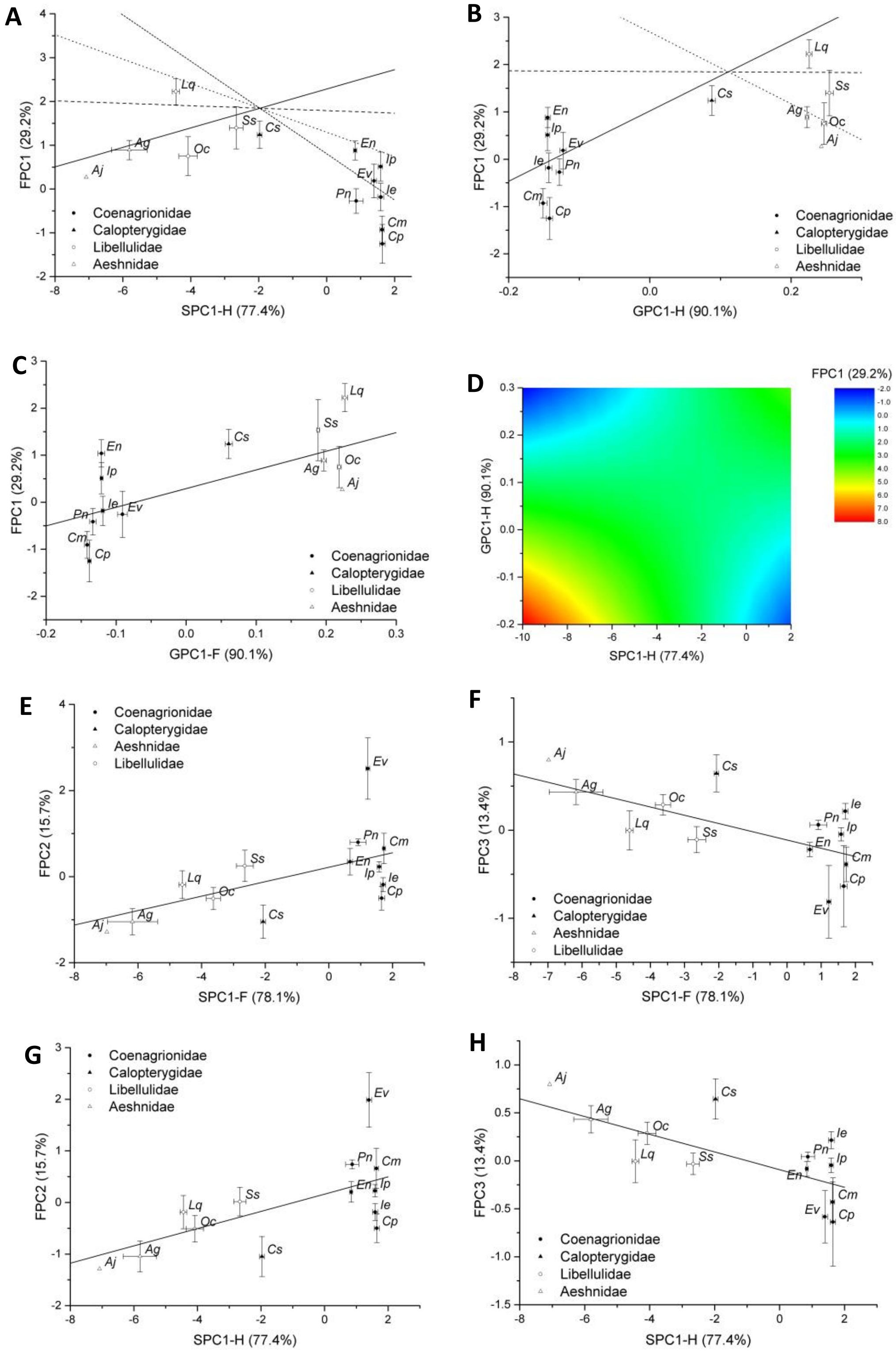


Figure 3.5 – See caption on next page (p73).

Figure 3.5 - Scatter graphs showing the relationships between FPC1, 2 and 3 (flight speed, efficiency of flight behaviour and flight path curvature respectively) and statistically associated wing statistics (SPCs and GPCs). Percentage variance explained by each PC is in brackets, error bars are standard errors. Relevant model fits (averaged across all species) are added with solid lines except: A) Model fits are added for GPC1-H = 0.2 (solid line – broad, non-petiolate wing), 0.1 (dashed line), 0 (dotted line) and -0.1 (finely dotted line – slim, petiolate wing). B) Model fits are added for SPC1-H = 1 (solid line – small, slender wing), -2 (dashed line) and -5 (dotted line – large, broad wing). C) Colour surface plot showing predicted flight speed (FPC1) from model fit of SPC1 and GPC1. Open symbols represent Anisoptera species, closed symbols represent Zygoptera species. See table 2.2 for species abbreviations.

Table 3.5 – AICc tables for mixed effects models (only includes the 3 minimum AICc models of 167 total models for each response variable). Data for the combined models (including forewing and hindwing data).

Response variable	**Model terms**	**df**	**AICc**	**ΔAICc**	**Weight**
FPC1 (flight speed and acceleration)	SPC1-H + GPC1-H + SPC1-H : GPC1-H	6	210.9	0.00	0.075
	SPC1-F + GPC1-H + SPC1-F : GPC1-H	6	210.9	0.07	0.073
	GPC1-H	4	211.3	0.45	0.060
FPC2 (flight efficiency)	SPC1-F	4	187.6	0.00	0.145
	SPC1-H	4	187.8	0.19	0.132
	GPC1-H	4	188.6	1.08	0.085
FPC3 (flight path curvature)	SPC1-F	4	134.4	0.00	0.149
	SPC1-H	4	134.6	0.13	0.139
	SPC1-H + GPC1-F	5	136.2	1.72	0.063

Table 3.6 – Minimum adequate mixed model parameters for combined forewing and hindwing data. All figures to 3dp, significant p values denoted with *.

Response variable	**Parameter**	**Estimate**	**SE**	**t**	**p**
FPC1	Intercept	1.297	0.487	2.662	**0.010***
	SPC1-H	-0.278	0.248	-1.121	0.267
	GPC1-H	4.924	2.682	1.836	0.072
	GPC1-H : SPC1-H	2.501	1.158	2.159	**0.035***
FPC2	Intercept	0.218	0.211	1.036	0.305
	SPC1-F	0.168	0.067	2.497	**0.016***
FPC3	Intercept	-0.112	0.087	-1.293	0.201
	SPC1-F	-0.094	0.032	-2.932	**0.005***

Table 3.7 – Chapter 3 minimum adequate mixed model parameters with and without phylogenetic correction. Values to 3dp.

Response variable	Parameter	Estimate	SE	t	p
Without phylogenetic correction					
FPC1	Intercept	1.297 (0.346, 2.242)	0.487	2.662	**0.010***
	SPC1-H	-0.278 (-0.759, 0.223)	0.248	-1.121	0.267
	GPC1-H	4.924 (-0.267, 10.529)	2.682	1.836	0.072
	GPC1-H : SPC1-H	2.501 (0.221, 4.735)	1.158	2.159	**0.035***
FPC2	Intercept	0.218 (-0.226, 0.668)	0.211	1.036	0.305
	SPC1-F	0.168 (0.029, 0.305)	0.067	2.497	**0.016***
FPC3	Intercept	-0.112 (-0.301, 0.069)	0.087	-1.293	0.201
	SPC1-F	-0.094 (-0.160, -0.030)	0.032	-2.932	**0.005***
With phylogenetic correction					
FPC1	Intercept	1.578 (-0.357, 3.513)	0.987	1.599	0.144
	SPC1-H	-0.922 (-1.622, -0.222)	0.357	-2.583	**0.030***
	GPC1-H	-4.493 (-14.562, 5.577)	5.138	-0.874	0.405
	GPC1-H : SPC1-H	3.978 (1.257, 6.698)	1.388	2.866	**0.019***
FPC2	Intercept	0.255 (-0.267, 0.777)	0.266	0.958	0.359
	SPC1-F	0.197 (0.045, 0.349)	0.077	2.547	**0.027***
FPC3	Intercept	-0.180 (-0.816, 0.457)	0.325	-0.554	0.591
	SPC1-F	-0.150 (-0.286, -0.015)	0.069	-2.170	0.053

3.5 Discussion

Of the 35 hypothesised directional links (or lack of) between morphology and flight performance found in the literature, only 9 (25.7%) of them were fully supported by my data. A further 11 may be supported but due to either vague definitions of the measure of linked flight performance, or connections with flight speed it is not certain whether these links are accurate. At least 42.9% (potentially up to 74.3%) of the assumptions found in the literature are not supported empirically. My study represents the first attempt to demonstrate *in vivo* the link between wing morphology and flight performance in multiple species of insects using relevant and comparable flight performance data instead of proxies (Berwaerts et al., 2002). The results show strong correlations among all measures of wing morphology, as the variation in both wing statistics and shape are primarily explained with a single principal component in the PCAs. In general the link between flight morphology and flight speed and acceleration is complex relying on multiple aspects of size and detailed shape of the hindwing. Flight efficiency and agility/manoeuvrability are less complex, being linked to the size and AR of the forewing (see Table 3.8).

3.5.1 The effect of wing morphometrics on flight ability

The results here show that steady flight speed has a complex relationship with measures of hindwing shape and size. Large and low AR hindwings that are more pointed and petiolate correlated with fast flight, but the same is true for small high AR hindwings so long as they are rounded and non-petiolate. The strong interaction between wing shape and size make flight speed and acceleration difficult to predict from wing morphology, so any prior assumptions might only be valid for small wings, whilst incorrect for larger wings. This complex relationship is why any assumption about the speed of flight (six assumptions concerning flight speed found in the literature) is only partially supported by my data as any trend is supported (except the complete lack of a trend) for a certain wing shape or size. Interestingly it is only aspects of the hindwing that significantly affect flight speed and acceleration. Perhaps the hindwings are used to provide the majority of aerodynamic power, whilst the forewings are more important for aerodynamic control. When the wings are considered separately the same trend remains for the hindwings, but for the forewing, the geometric morphometric shape of the wing is the only significant predictor of flight speed. Although some trend may exist for forewing shape and flight speed, the link between hindwing morphology and flight speed appears to be more important. Forewing shape may not be important due to lower levels of variation, or even that broader forewings would interfere with the hindwings during flight (Wakeling, 1997). The 3rd moment of area is proportional to profile power (Norberg and Rayner, 1987), but given the results here, high 3rd moments of area could still lead to poor flight speeds if the wings are too pointed and petiolate. At the lower Reynolds numbers under which Odonata operate, high aspect ratio wings may be more detrimental due to relatively higher profile drag. However, amongst insects Odonata have some of the highest aspect ratio wings and best flight performance, suggesting that a compromise in between high and low AR is important for insects (Ennos, 1989). The results here support a compromise in AR, as medium values for SPC1-H and GPC1-H tend to give the best flight speeds. Higher flight speeds are theoretically obtainable according to the model (see Figure 3.5 D), but it is likely that these extreme wing morphologies have other disadvantages – or may simply not be physically possible. Due to the complex relationship between wing morphology and flight speed and acceleration, wing morphology does not make a good proxy for flight performance – particularly as outside the Odonata, the geometric morphometric measures here are not necessarily repeatable (some of the landmarks involve structures not necessarily present or easily visible in other insect orders' wings).

Flight efficiency is best measured through respirometry, however here I have a measure of flight efficiency through biomechanical behaviour. Flight efficiency was positively correlated with the size and general shape of the forewing (SPC1-F), high efficiency seen in forewings with high aspect ratio, 2nd and 3rd moments of area and low size and loading. This relationship only supports 3 of the 11 assumptions made specifically about flight efficiency in Table 3.1, although one of these supported assumptions is the second most popular assumption found in the literature (seven separate studies making the assumption). Geometric morphometrics were not correlated suggesting that the finer intricacies of shape are not important over broader definitions of size and shape in terms of flight efficiency. It is possible that within the Odonata, despite appearances, the changes in wing geometric morphometrics do not reflect a large enough variation to see differences in flight efficiency.

Manoeuvrability and agility are generally considered as a single property by most authors so I will discuss them as a single entity. Here they are represented by flight PC3 which is negatively correlated with forewing size (SPC1-F), although when considering the hindwing in isolation SPC1-H is also significantly negatively correlated with flight PC3. At high forewing ARs and small forewing sizes and loading, turning performance is higher (tighter turns). This result supports 5 of the 11 manoeuvrability and agility assumptions made in Table 3.1, but does not support the most popular assumption in the literature: that low AR wings are linked with high agility and manoeuvrability (an assumption made by nine separate studies). Again, detailed but small changes to the wing shape do not appear to have a significant effect on manoeuvrability and perhaps agility, which seems unusual given that manoeuvrability is dependent on the wing working in a multitude of positions and airflows. The results here also conflict with the widely held idea that Zygoptera are slow, agile fliers whereas Anisoptera are fast but less agile (Corbet, 1999), with Anisoptera demonstrating tighter turns in general than Zygoptera here.

Measuring variance inflation factors (VIFs), the independent variables examined above all potentially have a high degree of collinearity (VIFs all above 5, one VIF above 10). Whilst high collinearity may not impact the model results per se (O'Brien, 2007), small changes in any value in isolation are likely to have disproportionate effects on the response variable. It is likely that changes to one variable are not seen without concurrent changes in the other in wild populations, as changes in wing size will almost invariably change the wing shape.

Table 3.8 – Statistically significant relationships between flight performance data and wing morphology. C: combined forewing and hindwing analysis. F: separate forewing analysis. H: Separate hindwing analysis. *Significant interaction term.

	Wing morphology PCs		SPC1	GPC1
FPCs	Low value ↔	Low value ↕ High value	Large, low AR wings. High mass. Small, high AR wings. Low mass.	Thin, petiolate wings Broad, rounded, non-petiolate wings
FPC1	Low speed & acceleration	High speed & acceleration	C -* F 0 H -*	C +* F + H +*
FPC2	Low speed, high acceleration	High speed, low acceleration	C + F + H +	C 0 F 0 H 0
FPC3	High path curvature	Low path curvature	C - F - H -	C 0 F 0 H 0

3.5.2 Comparative wing morphometrics

The measured morphometric properties of Odonata wings were as expected and similar to values previously obtained for Odonata (Wakeling, 1997). Again, as expected, anisopteran hindwings were considerably different in everything but length to their forewings, and given the empirical data here is likely to be the reason for higher flight speed and greater manoeuvrability and agility seen in Anisoptera.

The results of the geometric morphometrics PCA suggest that small changes in size independent wing structure can have a strong effect on altering the performance of the wings (see Figure 3.3). As expected there is strong differentiation between Anisoptera and Zygoptera in wing shape, with Zygoptera wings appearing less broad and more petiolate. It is difficult to say exactly what is responsible for the differences in shape, as all the landmark co-ordinates involved are highly correlated with the first principal component axis, but in general the axis seems to represent a more even spread of landmarks around the wing at higher values. This variation could be due to either larger wing cells between the landmarks, or increased numbers of cells. Looking at the wing images I suspect that it is a mixture of both with increased numbers of wing cells towards the tip of the wing and larger cells towards the base, but further more detailed geometric morphometric analyses would be required to confirm this. The movement of R4 and CuP towards the wing base and the movement of the nodus distally seem to be the greatest contributors to the change in shape (see Figure 3.4).

A notable feature of both wing size and shape here is that the Anisoptera have remarkably different forewings and hindwings but also differ considerably between species. On the other hand Zygoptera species have highly conserved wing sizes and shapes. The relatively high level of variation in Anisoptera is perhaps due to differing behaviour. The Libellulidae family consists primarily of ‘percher’ species whereas the Aeshnidae family are generally considered ‘fliers’ (Sacchi and Hardersen, 2013). Similar to May and Baird (2002) the results here do not show any evidence for different wing shapes for perchers and fliers although perches were not available in the filmed section of the flight arena used, so percher species may not have been flying as in the wild.

3.5.3 Future directions

The data here provide strong evidence that some aspects of wing shape and structure are related to flight performance in Odonata. It is reasonable to assume that the results here will also apply to other insect taxa, however dragonflies are unique in several aspects of their flight, for example being able to control each wing separately (Dudley, 2000), the specific interaction between their forewings and hindwings which is beneficial for their flight (Thomas et al., 2004), and often being considerably larger than other insect taxa. Future work will hopefully extend to other insect taxa to investigate whether these patterns hold for them. Respirometry work will also be useful in properly quantifying flight efficiency, and may reveal further patterns between wing morphology and flight ability. Something that I have not explored here is the extremes of morphology shown in the Odonata, for example the helicopter damselflies of the Pseudostigmatidae family which would allow for the exploration of morphological limits and much smaller Anisoptera species (e.g. *Nannothemis sp.*), which would be useful for testing for size-normalised differences in performance and morphology between Anisoptera and Zygoptera.

3.5.4 Conclusions

The results here are the first comprehensive and comparative empirical test of the effect of wing morphology on flight performance in insects. I show that the properties of Odonata wings are highly correlated and that different aspects of size and shape are responsible for variations in flight performance. There is also some evidence to show partitioning in aerodynamic function between hindwings and forewings. Empirical support is provided for a number of prior assumptions regarding insect wing morphology in the literature, however up to 74% of those found are not supported. This study demonstrates that several aspects of the wing morphology can be used effectively as proxies (although traits may need to be chosen carefully if studying a four-wing system, or examining flight speeds and accelerations) for flight performance but only if performance is carefully defined, as different aspects of performance can often require mutually exclusive wing properties.

Chapter 4 – Ontogenetic changes in locomotion: no correlation between larval and adult locomotory performance

4.1 Abstract

The Odonata (dragonflies) are insects with an aquatic larval stage and terrestrial adult stage. As larvae, swimming by either undulation or jet propulsion is used for general locomotion and occasionally escape responses or predation attempts. Adult dragonflies' primary mode of locomotion is flight, which uses a very different musculature to that of aquatic larvae. Studies have shown the performance of both Odonata flight and Odonata swimming, and whilst the change in muscle structure has been recorded, how emergence might effect locomotory performance change is unknown. Here I record swimming performance measures for 17 *Ischnura elegans* larvae and measures of their flight performance after emergence. The results show that there is no correlation between larval and adult locomotory performance, suggesting some resetting mechanism between the two life history stages, possibly differing methods of muscle development or muscle power outputs. The results also show that swimming performance is related to development time, which is possibly due to greater muscle development time. I show that there is no carry over effect of locomotory performance from larval to adult Odonata, but that variation in growing times is linked with swimming performance in Odonata larvae. This could represent a bet hedging strategy, allowing for different emergence times.

4.2 Introduction

4.2.1 Biomechanics and hemimetabolous development

There are three methods of insect development: ametabolous, hemimetabolous and holometabolous (Belles, 2011; Truman and Riddiford, 1999). The ametabolous insects do not undergo any metamorphosis between adult and larval stages and consist of some of the more basal insect orders, for example the silverfish

(Thysanura), as this is the ancestral condition within the Insecta. The larval stages are close to identical to the adult stage, with the exception that they lack genitalia. The advantages of this method of development are that there is no vulnerable metamorphosis stage involving extensive morphological changes, and it allows both adults and immature insects to remain within the same habitat or niche . This is also a potential disadvantage as adults and immature insects may be competing for the same resources (Truman and Riddiford, 1999; Truman and Riddiford, 2002). Hemimetabolous insects undergo an incomplete metamorphosis where larval insects are similar to adult insects, except they lack genitalia and rather than wings, carry wing buds from which the adult wings will develop in those species with winged adults (the majority of the hemimetabolous insects). These insects make a paraphyletic group of both primitive and more derived insect orders, for example the comparatively primitive Odonata and Ephemeroptera and the more derived Orthoptera, Hemiptera and Blattodea (Misof et al., 2014; Trautwein et al., 2012; Truman and Riddiford, 1999). For most hemimetabolous insects there are usually minimal changes between larval and adult life stages and the adults retain the terrestrial locomotory performance of the larva in addition to developing flight. The advantages and disadvantages to incomplete metamorphosis are similar to ametabolous insects, with the exception that greater partitioning can be seen between life stages. For example in the dragonflies (Odonata), nymphs are aquatic, whereas adults are terrestrial, allowing the exploitation of two separate habitats, or even further with mayflies (Ephemeroptera), where adults are a non-feeding dispersive and reproductive phase only (Truman and Riddiford, 2002). It is interesting to note that the vast majority of studies into insect embryogenesis are directed to holometabolous insects, with very little data for ametabolous and hemimetabolous insects (Simon et al., 2017). The monophyletic holometabolous insects (Endopterygota) undergo complete metamorphosis, involving large-scale changes in physiology between larval and adult life stages, including the degradation or complete loss of some tissues, restructuring of some and growth or regrowth of others (Tissot and Stocker, 2000; Truman, 1990; Truman and Riddiford, 1999; Truman and Riddiford, 2002). Complete metamorphosis has allowed them to exploit two separate environments and allows them to partition growth and reproductive resources (Truman and Riddiford, 1999), but also to have much more rapid life cycles (Truman and Riddiford, 1999; Truman and Riddiford, 2002). The separate life stages have been described by some as separate developmental modules (Raff and Sly, 2000; Von Dassow and Munro, 1999), i.e. the phenotypes of life stages are independent of each other, which for the “more modular” holometabolous insects makes them more adaptable, with faster radiations of species seen in the fossil record (Yang, 2001). Locomotory systems differ greatly between larval and adult holometabolic insects, with many larvae leading burrowing lifestyles, whereas adults show walking locomotion in addition to flight. In these insects there is a pupal stage lasting from days to years to accommodate significant changes needed to switch or develop a new locomotory system. In hemimetabolous insects, the only difference in locomotion tends to be the flight of adult stages, however in aquatic insects this is very different as most have aquatic swimming larval stages and terrestrial and/or flight capable adult stages.

4.2.2 Odonata locomotion

The Odonata are hemimetabolous insects. Despite being hemimetabolous, they undergo considerable morphological and ecological changes between larval and adult stages, with aquatic larvae and terrestrial adults. As adults, flight is their primary means of locomotion, and flight muscle makes up the majority of their mass (Anholt et al., 1991; Marden, 1989). The biomechanics of Odonata flight have been studied extensively, demonstrating how they provide lift (Azuma and Watanabe, 1988; Azuma et al., 1985; Bomphrey et al., 2016; Wakeling and Ellington, 1997c; Wakeling and Ellington, 1997a; Wakeling and Ellington, 1997b; Wang, 2008) and the specifics of airflow over the wing during flight (Bomphrey, 2006; Thomas et al., 2004). As a relatively primitive group Odonata musculature is different from most other insects, with muscles attaching directly onto the wings or aspects of the wing hinges. This muscle system is known as the direct flight mechanism and differs from the more common indirect flight mechanism where muscles attach to the exoskeleton and primarily deformations of the exoskeleton provide the movement of the wings. As a result the Odonata have active control over several flight parameters for each wing, allowing out of phase wing strokes, and generally more control over wing parameters (Dudley, 2000; Thomas et al., 2004; Usherwood and Lehmann, 2008). The swimming performance of Odonata is qualitatively well known, as the Anisoptera are the only insects to perform jet propulsion, however little quantitative data is available. Jet propulsion is only seen in the Anisoptera and is only described quantitatively by a handful of studies (Hughes, 1958; Mill and Pickard, 1975), showing reasonably fast swimming speeds of up to 50cms^{-1}, although noting that they are primarily used for escape. The Zygoptera swim by horizontal undulation of their abdomen and caudal lamellae (Burnside and Robinson, 1995), which has received a little more attention (McPeek, 2000; McPeek et al., 1996; Robinson et al., 1991; Stoks, 1999). Again, swimming is used as an escape mechanism, and can actually be disadvantageous in some habitats, where predators are able to out-swim the larvae (McPeek et al., 1996). Of particular interest is the function of the lamellae which act as gills, yet are often lost to autotomy. Whilst loss is disadvantageous the larvae are still able to swim without them (Robinson et al., 1991; Stoks, 1999).

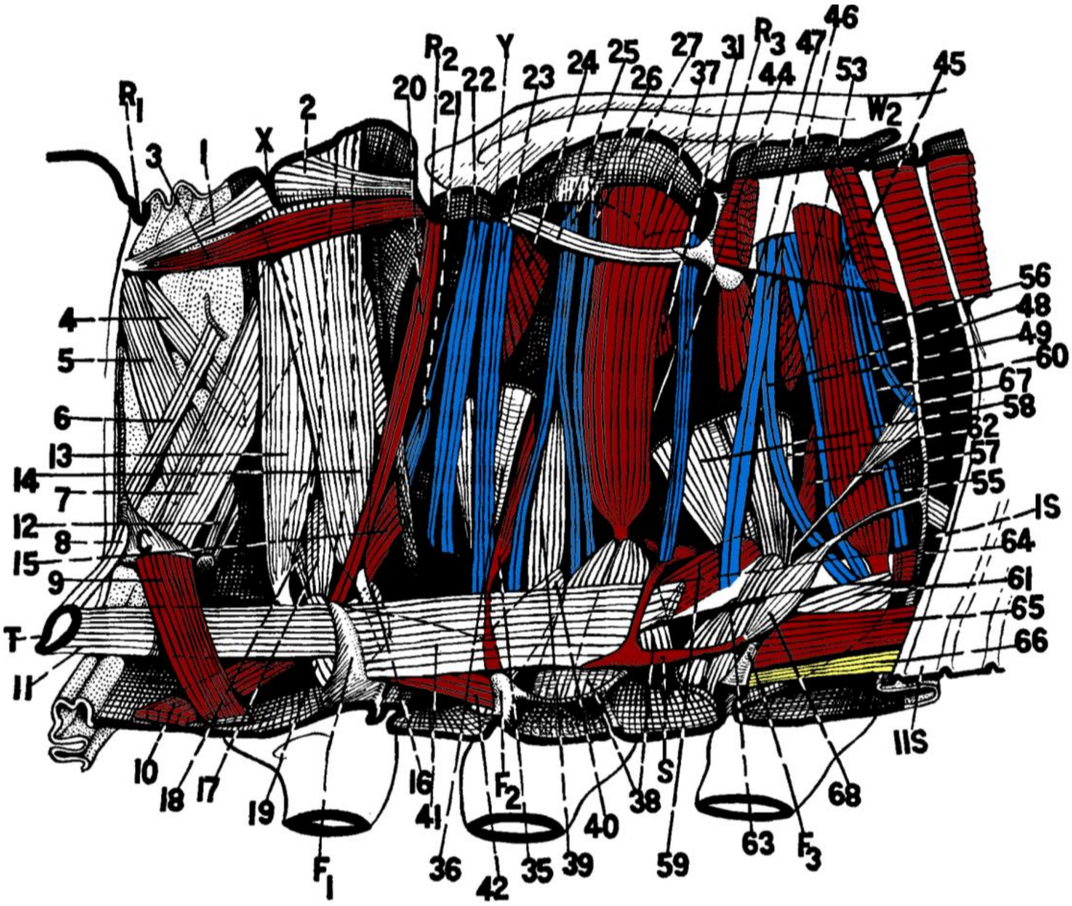


Figure 4.1 – See next page for full caption (p86).

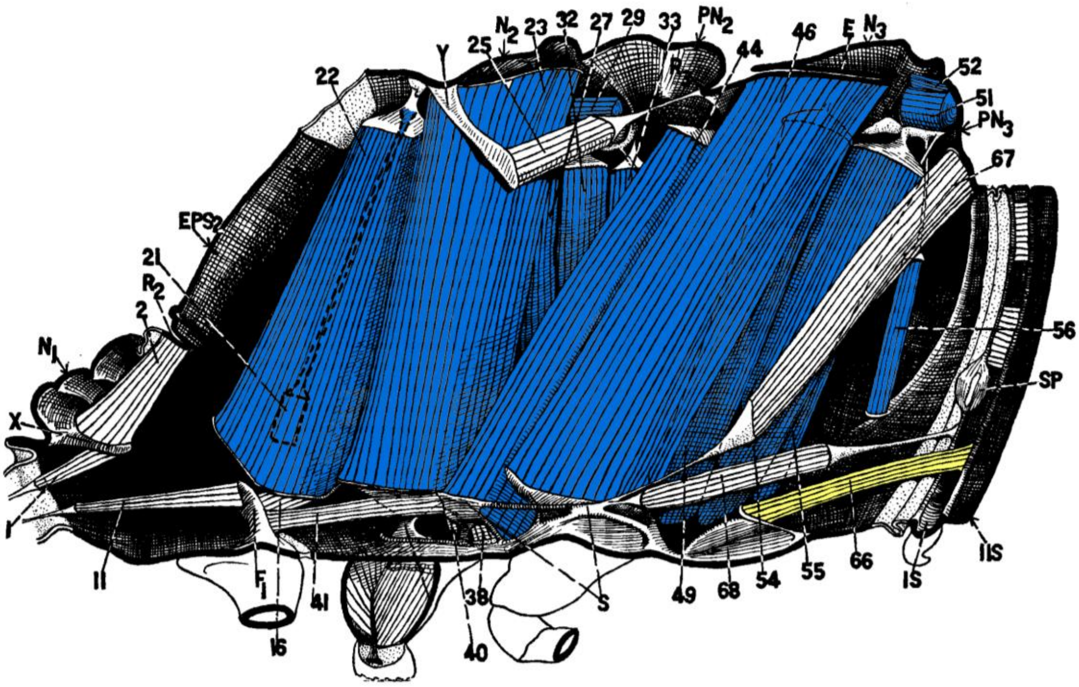


Figure 4.1 cont. – Figures adapted from Maloeuf (Maloeuf, 1935), showing differences between adult and larval muscle structure. Right half of an adult and larval *Plathemis lydia* thorax. The muscles in the adult (B) are considerably fewer and larger, running mostly vertically, whereas in the larva (A), the vertical flight muscles are mostly reduced and horizontal muscles are larger, allowing longitudinal contractions for jet propulsion in this species. To aid interpretation, I have coloured the image to highlight different muscle groups: flight muscles are coloured in blue and muscles and features absent in the adult are coloured in red. Muscle 66 is coloured in yellow as it may have abdominal function – but Maloeuf's description is unclear.

Odonata musculature has received limited attention but has been thoroughly described by Büsse (Büsse, 2013; Heckmann et al., 2013) in adults for the Zygoptera and both larval and adult life stages in the Anisoptera (Büsse, 2013; Büsse and Hörnschemeyer, 2013). Maloeuf showed that the larval stage of Anisoptera has all the muscles of the adult in addition to 'larval-only' muscles (Maloeuf, 1935, see Figure 4.1). Muscles presumably used in flight and other adult processes are much smaller than their adult counterparts, and thought to be inactive in the larva.

Whereas a number of muscles degenerate in the adult insect, so are presumably exclusive to larval locomotion or processes.

4.2.3 Odonata locomotor performance

Knowledge of general flight performance outside of the laboratory in the Odonata is poor and is only demonstrated through proxies such as predation trials (Outomuro and Johansson, 2015) or observations, or dispersal estimates through mark release recapture studies (Angelibert and Giani, 2003; Conrad et al., 1999; Hassall and Thompson, 2012; McCauley, 2013; Purse et al., 2003). A few studies have employed remote sensing in the field, to track Odonata movements, with varying results (Hardersen, 2007; Rüppell, 1989; Rüppell and Hilfert-Rüppell, 2010; Wikelski et al., 2006). As I showed in Chapter 2, there appears to be a significant difference in both species and individual flight performances, when measured in a laboratory context. Locomotor ability is similarly (if not more) neglected in the larval stage, with a handful of old studies making simple estimates about only the largest of Odonata species. Stoks and Cordoba-Aguilar reviewed carry-over effects in Odonata across separate life stages, showing that adult flight related characters such as flight muscle ratio and wing symmetry are reduced by various stressors experienced during the larval stage (Stoks and Córdoba-Aguilar, 2012). As of yet it is unknown whether locomotor performance carries over from larva to adult.

4.2.4 Locomotor carry-over effects

The process of emergence in Odonata is presumably energetically costly as a large number of changes are carried out, including the loss of gills, the atrophying of several muscle groups and finally the movement out of water (sometimes to a considerable distance) to exit from the last instar’s skin and the inflation of wings and abdomen with fluid. Whether the atrophy of some muscles is able to provide energy to the growth of others is unknown. Regardless of the mechanism, it seems logical that this switching of muscle tissues from larval to adult locomotion should have some effect on the biomechanical performance of the insect. To test whether there is a functional correlation between larval and adult locomotory performance we recorded the swimming and flight performance of larval and adult damselflies.

Previous studies have shown that generally the length of larval development and size at metamorphosis are important for determining early adult performance (Beck and Congdon, 2000; Schmidt et al., 2012). Here I predict that muscle anabolism will be driven via the same genetic and physiological processes in both the larva and the adult, so insects that exhibit greater swimming performance (greater speed and acceleration) will be similarly faster fliers (higher speeds, accelerations, and/or turning radii and turning frequency).

4.3 Methods

4.3.1 Time and location

Captive rearing of odonate larvae started in July 2016, with the last adult emerging roughly a year later. Reared insects came from eggs, which were collected from mated females caught from the following locations:

- Letchmire Pastures Nature Reserve, West Yorkshire, latitude 53.741°N, longitude -1.359°E, managed by the Yorkshire Wildlife Trust.

- Kemira Chemicals, West Yorkshire, 53.779°N, longitude -1.747°E, owned by Kemira Chemicals UK ltd.

Experiments were carried out from January 2017 through to July 2017, depending on when larvae reached a size threshold and when they emerged as adult insects.

4.3.2 Animal capture and husbandry

See section 2.3.2. for adult animal capture and husbandry.

Most insects did not lay eggs of their own volition in laboratory enclosures. To induce egg laying, females that had been observed mating were held with the tip of their abdomen in a petri dish of aged tap water with strips of filter paper in. If no eggs were laid after 5 minutes the insect was returned to its cage. Once laid, eggs were left in the petri dishes and water was topped up regularly to prevent drying out. When the eggs hatched, the prolarvae or young larvae were transferred to small trays of aged tap water with a substrate of strips of filter paper, and fed daily with washed brine shrimp (*Artemia sp.*) nauplii. Water in the trays was replaced once a week. Once the larvae were large enough to easily handle and see with the naked eye, they were transferred to individual plastic cups to avoid cannibalism, and their diet supplemented with *Daphnia sp.* After this stage each larva was photographed under a calibrated microscope (Nikon SMZ1500 and Nikon DS-U1, Nikon Instruments Europe BV, Amsterdam, Netherlands) to obtain two body length measurements (from mandibles to tip of caudal lamellae and from mandibles to end of last abdominal segment) and a head width measurement. Measurements were repeated each time a larva moulted. The head width was used as a proxy for size as the length of the larva changes during swimming and is more difficult to measure accurately as the body is usually curved to some extent. Each group of larvae from a single female parent was given a number at random to determine which insects to use in experiments (lower numbers have greater priority, 8 insects used from each parent where possible). When a larva died either before it reached an appropriate size or before flight experiments could be conducted, assigned numbers were shifted downward to provide replacements. When a larva reached a head width of 3mm or more, as head width has proven to be a good indicator of both size and mass (Harvey and Corbet, 1985), its swimming performance was recorded using a high speed camera, except in cases where a larva had lost or was in the process of re-growing a caudal lamella. When a larva that had already been tested for swimming performance emerged as an adult, its flight performance was recorded in flight arena experiments (Section 4.3.4). The flight and swimming was recorded for 17 insects from 5 parents (4:3:3:1:6, 7 males, 10 females).

4.3.3 Swimming kinematics

A glass tank (0.456m length x 0.309m width x 0.307m depth) was filled to a depth of 0.12m with distilled water. A Photron SA3 camera (FASTCAM SA3, Photron Ltd., Tokyo, Japan) with a 105mm f1-2.8 VR (Vibration reduction) macro lens (Nikon Corporation, Tokyo, Japan) was set up facing a mirror mounted above the tank angled at 45° so that the recording plane was parallel to the water's surface (see

Figure 4.1). Insects were then dropped or placed into the tank and allowed to swim freely. If the insect stopped swimming, or did not swim through the filmed area, after a break of 1-5 minutes it was gently encouraged to swim by touching the abdomen with a wooden rod. When the insect did swim whilst in view of the camera a video sequence was recorded (250fps, 1/250 second shutter, 1024x1024 resolution, f1.0) using Photron Fastcam Viewer (Photron Ltd., Tokyo, Japan). This process was repeated until 10 sequences were recorded or the insect refused to swim further. After the experiment, the insect was photographed under a calibrated microscope (Nikon SMZ1500 and Nikon DS-U1, Nikon Instruments Europe BV, Amsterdam, Netherlands) to obtain total length measurements and head widths (as in section 4.3.2). A measured grid was placed in the tank after experiments parallel at the level of swimming, and an image was taken using the same camera setup to calibrate the space. As part of a separate experiment, the tank had a laser sheet projected into it and was also seeded with aluminium oxide particles to capture data particle image velocimetry data (see Figure 4.2 for experimental setup).

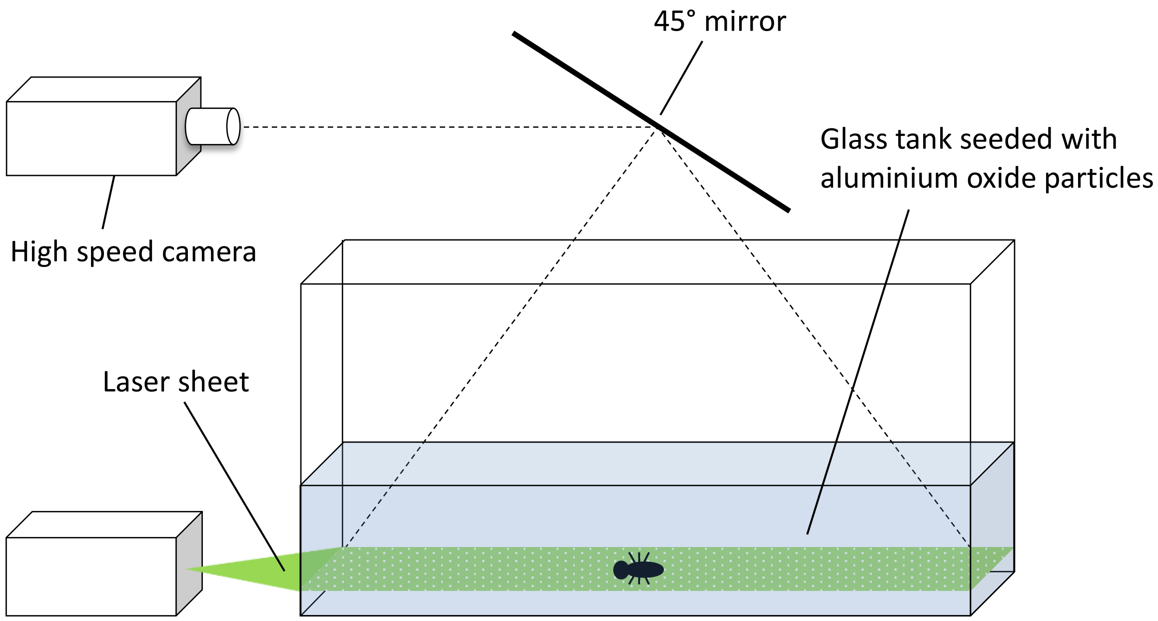


Figure 4.2 – Experimental setup (not to scale)

4.3.4 & 4.3.5 Flight kinematics and image processing

See section 2.3.3. and 2.3.4.

4.3.6 Image Processing: Swimming

Video footage from the flight arena was saved as images in a TIFF file format from the Fastcam camera and converted to AVI using Photron Fastcam Viewer (PFV version 3.3.4.1, Photron Limited 2006). The idTracker 2.1 program (Pérez-Escudero et al., 2014) was used to track the two dimensional movements of the insect larvae in the video. The insect was automatically detected in the image by thresholding the image by grayscale intensity and looking for areas large enough to match the size of the insect. Using the two-dimensional coordinates of the insect from the video frames and the calibration image, speed, acceleration and turning performance were calculated using the same method for flight (see chapter 4.3.5), but assuming that the insect does not change height (i.e. two dimensions, no z-axis).

4.3.7 Statistical Analysis

Statistical analysis was carried out in R (R Core Team, 2017, https://www.r-project.org) using a model II regression using the "lmodel2" R package (Legendre, 2004) between adult and larval biomechanical data due to the presence of error in both variables.

The average speed, acceleration and path curvature of the wild *Ischnura elegans* (see chapter 2) was compared to that of the reared individuals here using generalised linear models (and a general linear model for acceleration data which fit the necessary assumptions), with the data points being the average values for each individual across all flight or swimming sequences. Reared insects were significantly different to wild animals, with wild animals flying at on average 10.88 ms^{-1}, whereas reared individuals flew at on average 7.85 ms^{-1}, 3.03ms^{-1} slower. The opposite trend was seen for acceleration with wild individuals accelerating at on average 164.33ms^{-2} and reared individuals at 169.08 ms^{-2}, 4.15ms^{-2} more. Path curvatures in wild individuals were 9.39 on average and 22.37 in reared individuals. Whilst the differences in acceleration are minimal, the difference in flight speed and curvature is considerable and will be discussed (see section 4.5.4).

In addition the above methodology was attempted with *Sympetrum striolatum*, and detailed swimming measurements were obtained but not enough individuals survived to emergence to analyse flight performance.

4.4 Results

4.4.1 – Swimming performance

Larvae swimming sequences were generally quite short, as the larvae would not remain at the depth of the laser sheet for too long. Instead they preferred to be able to stand or cling to a surface. Larvae swam at average speeds between 0.052 and 0.130ms^{-1} per trial, with an overall average speed of 0.075ms^{-1} across all trials. One individual achieved a momentary peak swimming speed of 1.566ms^{-1}.

4.4.2 – Flight performance

Adults flew at an average speeds of between 5 and 14 ms^{-1} per trial, flying at 7.9ms^{-1} on average across all trials. One individual momentarily achieved a peak flight speed of 23.8ms^{-1}. The overall average flight speed is slightly lower than the average of 10.6ms^{-1} seen in the wild individuals in chapter 2 (see section 4.5.4).

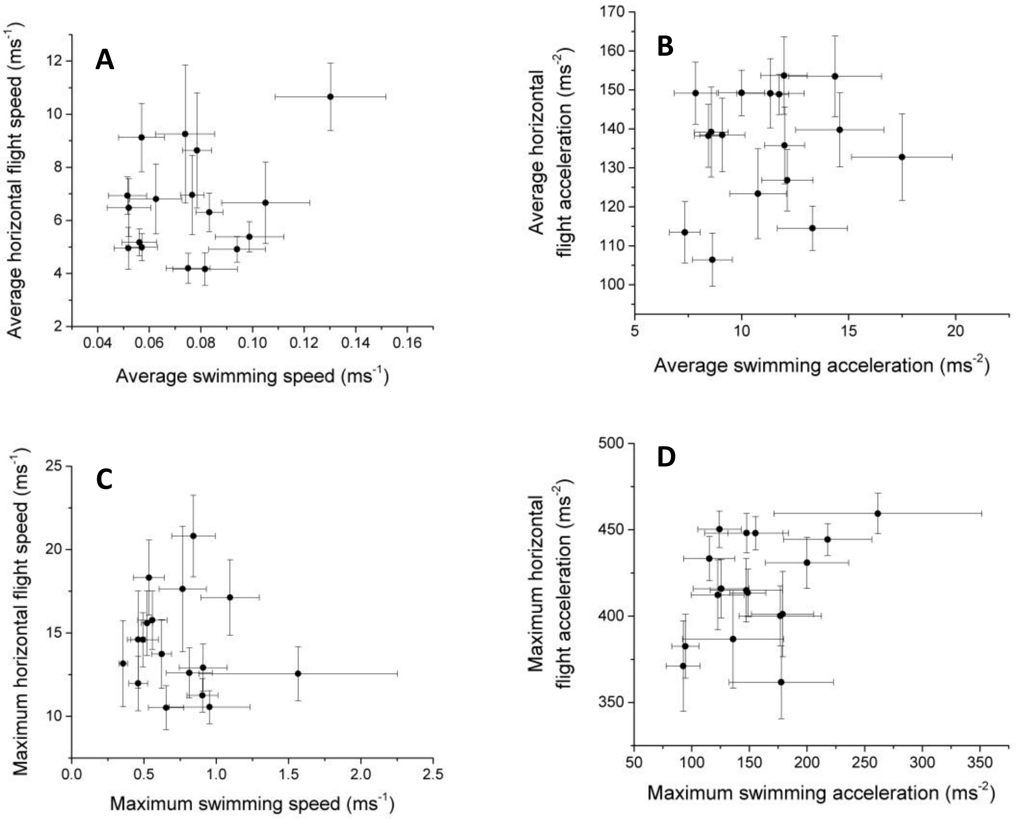


Figure 4.3 – Model II regression graphs. A) Average horizontal swimming speed vs. horizontal average flight speed. B) Average horizontal swimming acceleration vs. average horizontal flight acceleration. C) Maximum horizontal swimming speed vs. horizontal maximum flight speed. D) Maximum horizontal swimming acceleration vs. maximum horizontal flight acceleration.

4.4.3 – Ontogenetic correlation

Our results show no correlation between larval and adult swimming performance (see Figure 4.3, all p-values >0.05). In addition, neither flight nor swimming performance appears to differ significantly between the sites at which the parents were collected. Growth and development time also did not reveal any correlation between adult and larval performance once taken into account. A correlation can be seen (ANOVA, F = 13.551, p = 0.002) between the time from the egg being laid to the time of swimming trials and swimming performance (both speed and acceleration, see Figure 4.4). The time in question is the inverse of growth rate, as insects were put through swimming trials as soon as they reached a head width of 3mm. Hence, individuals with slower growth tended to show faster swimming speeds and greater acceleration.

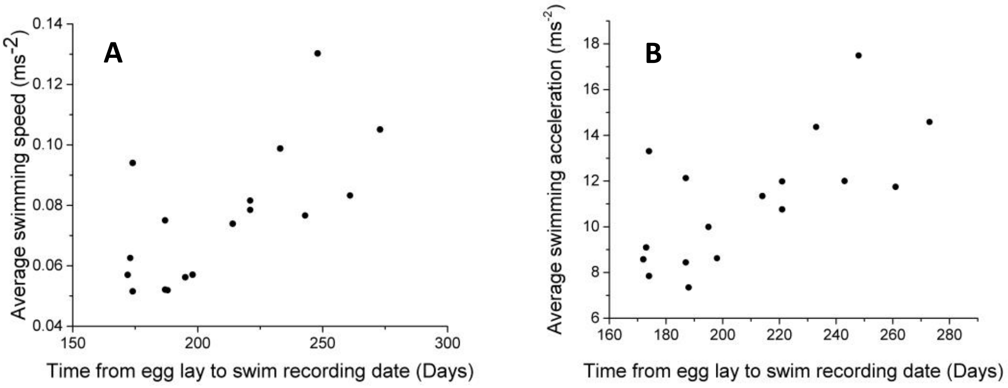


Figure 4.4 – Time from egg laid to time of recording of swimming data vs. A) average swimming speed and B) average swimming acceleration. The time is representative of growth speed up until the larvae grows a head width of 3mm.

4.5 Discussion

The experiment detailed here is the first test of carry-over effects of locomotory performance in Odonata, the results of which suggest that there are no effects or the process of metamorphosis is able to decouple any effects that do exist. The study did however show for the first time that swimming performance is positively correlated with growth time, possibly due to longer intervals to develop muscle mass, but further investigation is required.

4.5.1 Ontological correlation

The results here show no correlation, positive or negative between larval and adult locomotory performance. The lack of correlation suggests that muscle development for swimming and flight is not tightly regulated by genes or environment, as the latter was kept constant and muscle was presumably not developed in the same way given the variation in locomotory abilities. It seems that there may be two different mechanisms of muscle development occurring between adult and larval locomotor systems - perhaps mediated through flight muscles spending the entirety of the larval stage non-functional. The results here contradict numerous observations showing direct ‘carry-over’ effects of size, mass and activity levels (Stoks and Córdoba-Aguilar, 2012). Evidence for larval effects on flight performance is relatively scarce, but flight muscle mass and wing symmetry have been shown to be influenced by larval environments and muscle ultrastructure is suggested to follow the same pattern given evidence from the fall armyworm (*Spodoptera frugiperda*) (Marden et al., 2008). There are also several examples of traits unaffected between larval and adult stages through decoupling mechanisms during, pre and post metamorphosis (emergence), for example larval food shortage has been shown not to affect adult fecundity (Richardson and Baker, 1997) and compensatory growth. Stoks and Córdoba-Aguilar (2012) suggest that underdeveloped individuals are able to ‘catch up’ to more developed individuals through compensatory growth when food or temperature are not limiting, both in the larval (De Block and Stoks, 2008a; De Block and Stoks, 2008b; Stoks et al., 2006) and adult stages (Anholt, 1991). In addition emergence may be such a stressful event that other effects are essentially voided (Campero et al., 2008; Stoks and Córdoba-Aguilar, 2012). The data here were collected under as optimal conditions as possible, with food provided *ad libitum*. As previously mentioned, adult insects in the laboratory often chose not to feed, so it is possible that carry-over effects were lost through poor food conditions for the adult. However, adult flight performance did not correlate with growth time, or the time between emergence and flight recording, suggesting that food conditions are unlikely to be responsible for variation in adult flight ability.

4.5.2 Larval muscle development

The results here show a correlation between the time taken to grow to a certain size and swimming performance. Yet this correlation is not seen when analysing flight performance. In theory a longer growth time allows for more muscle development, which is presumably how greater swimming performance is achieved. Why there is variation in growth time under the same environmental conditions is unclear, as a number of studies have shown strong interactions with growth rate and biotic factors (Johansson et al., 2001; Mikolajewski et al., 2015; Stoks et al., 2005; Stoks et al., 2006). Responses to biotic factors allow larvae to take advantage of unusually good or poor conditions – emerging as fast as possible when necessary, or spending as much time as possible as a larva gaining size and/or mass. Given that no carry-over effect was observed in those insects that took longer to grow, this seems unlikely unless the carry-over effect was in a non-locomotory trait, a number of which have been shown (Stoks and Córdoba-Aguilar, 2012), primarily effects on size and mass (Harvey and Corbet, 1985; Johannes Mikolajewski et al., 2007), but also behaviour such as activity level (Brodin, 2009). Perhaps growth time stays variable as a necessity to avoid stochastic environments, ensuring at least some larvae survive regardless of when they emerge, a process known as 'bet-hedging' or risk spreading (Hopper, 1999; Poethke et al., 2016; Simons, 2011), in this case 'diversifying bet-hedging' with growth time remaining variable. If so, increased swimming performance could remain an artefact of this. There remains the possibility that not all larvae in the experiment were responding maximally to stimuli. Regardless of whether larvae were responding maximally, variation in swimming performance could represent behavioural strategies in predator avoidance in addition to or instead of variation in swimming abilities. Odonata larvae with higher growth rates take more risks with fish predators, reducing foraging activity less within the presence of fish predators (Stoks et al., 2005). The higher swimming performance seen here in quicker growing larvae could be an increase in risky behaviour (fish predators often rely on sight and can outswim larvae), although this seems unlikely as the stimulus provided here is more similar to invertebrate predators than fish, for which swimming is a more successful evasion strategy (McPeek et al., 1996).

4.5.3 Swimming performance

The average swimming speed of 0.075ms^{-1} shown here for *Ischnura elegans* is similar to some speeds of other damselfly species previously recorded, with various species recorded from around 0.02ms^{-1} up to around 0.18ms^{-1} (Burnside and Robinson, 1995) a number of *Enallagma* species between 0.02ms^{-1} and 0.37ms^{-1} (McPeek et al., 1996) and an average speed of 0.375ms^{-1} was shown for *Lestes sponsa* (Stoks, 1999). Whilst the method for eliciting swimming is the same here as in previous experiments, comparing the differences between data collected here and previous studies is difficult given that the maximum depth of water provided in these studies is 2-6cm and no recording is made of the depth at which larvae swam. If larvae swim along the bottom of the tank, which is likely in some species given their preference for solid surfaces (Corbet, 1980; Corbet, 1999) hydrodynamic ground effects will affect the swimming performance of the larva (Webb, 1993) although in what way is not yet established. Regardless of surface effects, the majority of interspecific variation in swimming performance is presumably down to differing sizes and morphologies (Burnside and Robinson, 1995).

4.5.4 Flight performance

Adult insects flew on average around 7.9ms^{-1}, and accelerated at 170.22ms^{-2}, which is significantly lower than the average performance recorded for *I. elegans* in Chapter 2. The lower flight speed is not surprising given that all the reared insects here were flown within 3 days of emergence and so were still immature. It is likely that the insects won't have fully developed flight muscles by this time, especially given their tendency to not feed in laboratory conditions, but testing them at this stage also ensures that all insects were at the same developmental stage for the flight trials. The age and condition of the insects recorded in chapter 2 is unknown but it is almost certain that they were mature individuals, as they were caught around water and usually engaging in mating behaviour (copulation or territory defence). Mature individuals are known to have considerably greater flight muscle mass than immature individuals (Marden, 1989; Marden et al., 1998), which will lead to better flight performance. Thus age probably explains the difference in flight performance seen here, although further experiments on immature wild individuals would help confirm that laboratory rearing has no effect on flight performance.

4.5.5 Conclusion

In the first experimental test of carry-over effects of Odonata locomotion across life stages, I found no correlation between larval and adult locomotory performance, suggesting that some decoupling mechanism is likely to occur during metamorphosis (emergence). The study demonstrates the novel result of correlation between swimming performance and growth time in *I. elegans* larvae, presumably brought about by longer times allowed for muscle development. Whether this correlation represents a trade-off between larval survival and an earlier emergence remains to be seen. The results of this experiment also add to the relatively small body of data documenting swimming performance of Odonata larvae, which measured here is reasonable if somewhat low compared to other studies. The flight performance measured here was also lower than that seen in wild-caught individuals in chapter 2. To conclude, the lack of carry-over effects in Odonata locomotion, may be brought about by differing muscle development in larva and adults, and muscle development is shown to be important for locomotion in the larvae as it is known to be in the adult. Further work is required to verify whether there is potential reduction in locomotory performance in laboratory reared populations compared to wild populations.

Chapter 5 – Modelling the effects of reversible polarotaxis on Odonata dispersal

5.1 Abstract

Dispersal is a fundamental aspect of biology and has roles in a host of ecological processes. With increasing and varied climate induced dispersal by multiple species, predictive species range modelling is becoming increasingly important. One of the most significant hurdles for these models is the lack of useful data for both validation and parameterisation. Here I develop a spatially explicit individual based model for dispersal in the Odonata, testing the effects of reversible polarotaxis behaviour, where immature adult Odonata are repelled by polarised light found in freshwater habitats, and then attracted by polarised light as mature adults. The model shows how this behaviour interacts with the amount of available reproductive habitat to reduce distances travelled (gross dispersal) in the Odonata by an average of 280m (11.5%), in exchange for earlier arrival at feeding habitats (on average 0.8 days earlier) and and increase of 15% in the probability of successfully returning to freshwater habitats to reproduce . My results suggest that this behaviour might be one of the primary drivers of philopatry in Odonata, and that the loss of this behaviour in urban populations due to polarised light pollution has mainly negative consequences. Polarotaxis appears to provide benefits by reducing potential dispersal related mortality by reducing the amount of time spent in unsuitable habitat. In addition, individuals may be able to spend more time reproducing as they are more likely to return to a breeding habitat and are likely to return earlier within their lifespan.

5.2 Introduction

5.2.1 Dispersal modelling

Dispersal is an important and essential aspect of ecology (Bowler and Benton, 2005; Clobert et al., 2012; Jønsson et al., 2016; Nathan et al., 2008; Trakhtenbrot et al., 2005). It is required to allow populations to expand to new habitats, but also to help tolerate local extinctions through repopulation of habitats (Hansson, 1991; Harrison, 1991; Taylor, 1990). Movements like migration also help tolerate fluctuating or stochastic conditions by avoiding extinction in the first place (Chapman et al., 2015; Nathan et al., 2008; Rota et al., 2016). Predicting the movement of populations is important for conservation efforts, whether understanding the necessary connectivity of habitat patches for the maintenance of metapopulations, or the distance a population might move under environmental change (Bowler and Benton, 2005; Morales et al., 2010; Ponchon et al., 2015). Whilst movement of populations can be measured through mark release recapture programs (Conrad et al., 1999; Stevens et al., 2010), or telemetry/GPS tracking (Kissling et al., 2014), predicting population movements requires the modelling of dispersal. Individual- or agent-based models (IBMs) are particularly useful for this as they can easily incorporate real landscapes and are able to provide insights on how individual dispersal behaviour can contribute to population level patterns. IBMs operate by simulating all individuals in a population allowing dynamic interactions between individuals and abiotic factors more easily than previous mathematical models based on diffusion and population-level characteristics. IBMs also allow models to operate at a more realistic scale for evolution with individuals being units of natural selection not populations. IBMs were initially used as an alternative to existing state-variable models as there was considerable debate around the efficacy of those models to predict real world trends – in particular long-term trends (Huston et al., 1988; Judson, 1994; May, 1976b). With increasing computer power and better prediction/representation of real world processes, IBMs have become increasing popular methods for modelling ecology and evolution (Grimm, 1999), although opinion is still divided on the extent of the applicability of IBMs (DeAngelis and Grimm, 2014; DeAngelis and Mooij, 2005; MacPherson and Gras, 2016).

5.2.2 Animal movement

To model animal movement accurately and, hence, produce realistic estimates of population dispersal, we need to know how animals move. For simple microscopic organisms in infinite homogenous habitat a random walk pattern of movement (Brownian motion) might suffice (Codling et al., 2008), but most organisms have some method of sensing their environment, live in heterogeneous surroundings (both spatially and temporally) and display a variety of behaviours that vary their movement patterns – even microscopic organisms will display chemotactic or other movement related behaviours (Kim and Or, 2016). For example, birds are known to follow roads and other linear structures whilst navigating long distance journeys (Guilford et al., 2004; Lipp et al., 2004), mountains, rivers or other abiotic features of the environment can be barriers to species movements (Lövei et al., 1998; Mader et al., 1990) and both interspecific and intraspecific interactions can affect movement (Denno and Roderick, 1992; Matsumura and Suzuki, 2003; Sullivan et al., 2017).

Generally, population dispersal has been modelled in two different ways – density dependence and habitat suitability/quality. A third and often overlooked driver of dispersal is ontogenetic shift in habitat use (Nakazawa, 2015; ten Brink and de Roos, 2017). Ontogenetic habitat shifts are most commonly known from fish (Dahlgren and Eggleston, 2000; Snover, 2008), invertebrates (Grof-Tisza et al., 2015) and amphibians (Nakazawa, 2015; ten Brink and de Roos, 2017), but to some extent are present in most organisms. It is generally thought to represent a predator avoidance vs. growth rate trade off, with younger life stages favouring safe habitats and older life stages favouring more productive habitats allowing faster growth rates. Within insects the strong differences between larval and adult stages through metamorphosis maintain ontogenetic variation in habitat and food use (ten Brink and de Roos, 2017), and these appear to be driven generally by predation avoidance in the larva (Grof-Tisza et al., 2015). However, within the Odonata, whether the balance between mortality and growth rate dictates the timing of metamorphosis and emergence of the adult is not yet fully understood (Plaistow and Siva-Jothy, 1999) – in part due to a lack of knowledge of adult mortality drivers (Anholt, 2008). Within the Odonata additional ontogenetic habitat or niche change exists between immature and mature individuals, with immature insects leaving breeding sites to forage and returning to reproduce once mature (Corbet, 1999). This mechanism is thought to be driven through reversible polarotaxis behaviour.

5.2.3 Polarotaxis

Polarotaxis is the attraction of an individual to polarised light. The ability to detect polarisation and modify behaviour in response has been found in many organisms from microscopic algae to vertebrates (Adler and Phillips, 1985; Häder, 1987; Horváth et al., 2011; Kriska et al., 2009; Via et al., 1975; Waterman and Forward Jr, 1972). In general there are three purposes that polarisation is used for. First is orientation in a fluid (Häder, 1987; Hawryshyn, 2010; Hawryshyn et al., 1990), second is navigation using a polarisation based “sky-compass” (Adler and Phillips, 1985) and finally the locating of water through reflected polarised light (Bernáth et al., 2004; Csabai et al., 2006; Gál et al., 2001; Horváth et al., 2011; Kriska et al., 2009; Molnár et al., 2011; Schwind, 1991). The latter of these is generally found in either fully aquatic insects or those with an aquatic larval stage and is thought to allow the insects to find mating habitat (i.e. above or beside water) as the winged adults search for mates or new habitat. Even those insects that never actually leave the water surface still have this polarotaxis (Kriska et al., 2007). For these insects polarotaxis is positive i.e. they are attracted to polarised light above a certain threshold.

With increasing urbanisation, polarised light pollution (PLP) is becoming a problem, particularly for aquatic insects. Many urban objects or surfaces, for example tarmac, windows or cars, reflect horizontally polarised light in a pattern similar to – but to a greater extent than – that seen from water surfaces. A number of insect taxa have already been shown to be affected by PLP (Horváth and Varjú, 1998; Horváth et al., 1998; Szaz et al., 2015; Villalobos-Jiménez et al., 2018), although the long term effects on populations are yet to be elucidated.

Very few studies have looked at ontogenetic changes in polarotaxis, and those that have, only studied the development stage at which polarotaxis first occurs (Via et al., 1975) or shown that polarotactic retina cells were removed through programmed cell death in older individuals (Hawryshyn, 2010; Waterman and Forward Jr, 1972). The Odonata demonstrate a reversible polarotaxis, initially negative in newly emerged adults repelling them from water bodies, but then switching to positive attracting mature adults to breeding habitat (water bodies) (Corbet, 1999; Villalobos-Jiménez et al., 2018), possibly shared with some other insects although the evidence is far weaker and/or timescales far shorter (Boda et al., 2014; Szaz et al., 2015). There is an a priori reason to expect reversible polarotaxis to impact landscape ecological processes, as the behaviour encourages movement through the repulsion from certain habitats and then subsequent attraction to them. However, empirical evidence is lacking due to the paucity of studies and the focus on reproductively mature animals in previous mark release recapture studies.

5.2.4 An IBM for reversible polarotaxis

Here I develop a dispersal IBM to simulate movements of multiple generations of Odonata through real landscapes with and without reversible polarotaxis. I expect to find that simulated individuals under reversible polarotaxis disperse further and travel greater distances overall. I also expect that they are more likely to end their lifecycle in suitable habitat than those under non-polarotactic conditions as the positive polarotaxis in their mature state should encourage this. Finally, I expect individuals with reversible polarotaxis will find feeding habitat faster and as a result spend longer times there than those without.

5.3 Methods

5.3.1 Model construction

An individual-based model for dispersal was developed in R (R Core Team, 2017, https://www.r-project.org). The model simulated dispersal north across a landscape to quantify poleward range shifts.

The experimental landscapes were created using phase I habitat survey data for Wales[1]. The Phase I habitat survey of Wales is a vector land cover data classifying landscape into 138 different categories from 10 broad categories (Woodland and scrub, grassland and marsh, heathland, mire, swamp marginal and inundation, open water, coastland, exposure and waste, miscellaneous). Grids of 2km width and 25km height were selected at random from the phase I habitat data (avoiding overlap and any grids that had more than 5% sea cover) until 9 grids were found, 3 with low levels of freshwater habitat (<2.5% cover), 3 with medium levels of freshwater habitat (2.5 – 7.5% cover) and 3 with high levels of freshwater habitat (>7.5% cover). For each grid, habitats were assigned as either reproductive habitat for Odonata, phase I habitat codes “E“ (mire), “F“ (swamp, marginal and inundation) and “G“ (open water), feeding habitat, phase I habitat codes “A“ (woodland and scrub), “B“ (grassland and marsh), “C” (tall herb and fen) and “D“ (heathland), and unsuitable habitat for Odonata, phase I habitat codes “H“ (coastland), “I“ (exposure and waste) and “J“ (Miscellaneous). Additionally phase I habitat codes only used in the Wales survey, “m“, “NA“ and “?“, (mosaic i.e. multiple habitat types, land not accessed and unknown, respectively) were assigned as unsuitable habitat.

Models were run with or without simulation of reversible polarotaxis (“polarotaxis” and “non-polarotactic” respectively). At the start of a model, an individual began from the centroid of the most southerly freshwater habitat within a grid. Individuals started in a reproductively immature state with a lifespan of 26 days. Their reproductive state switched to mature at 13 days of age (Banks and Thompson, 1985; Brooks et al., 1997; Corbet, 1999). The reproductive state governed which habitat types an individual would prefer in the polarotaxis models – i.e. reproductive habitats reflect polarised light, whereas feeding habitat does not.

Each day of the simulation an individual had a percentage chance of moving based on the habitat they were currently in. This percentage was either 50% for non-polarotactic runs, or varied with age where polarotaxis was present (see above and

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[1] Attribution statement: Contains Natural Resources Wales information © Natural Resources Wales and Database Right. All rights Reserved. Contains Ordnance Survey Data. Ordnance Survey Licence number 100019741. Crown Copyright and Database Right. http://nationalarchives.gov.uk/doc/open-government-licence/version/2/

Section 5.3.2). If the individual dispersed it was allowed up to 5 independent trial movements all starting from the same origin – the individual’s current location. Movement stopped when one of these movements crossed into or ended in suitable habitat given the individual’s current state (mature or immature). If no suitable habitat was found the individual moved to the end location of the 5th trial movement. Each trial movement was generated by a uniformly random heading (compass direction) and a random distance value drawn from an exponential distribution (see Section 5.3.2), i.e. a single step from a random walk. If any movement would take the individual off the landscape grid it was repeated until the movement remained within the grid.

Once run, the model saved the location co-ordinates for each step of each individual and the habitat type they were in at that location.

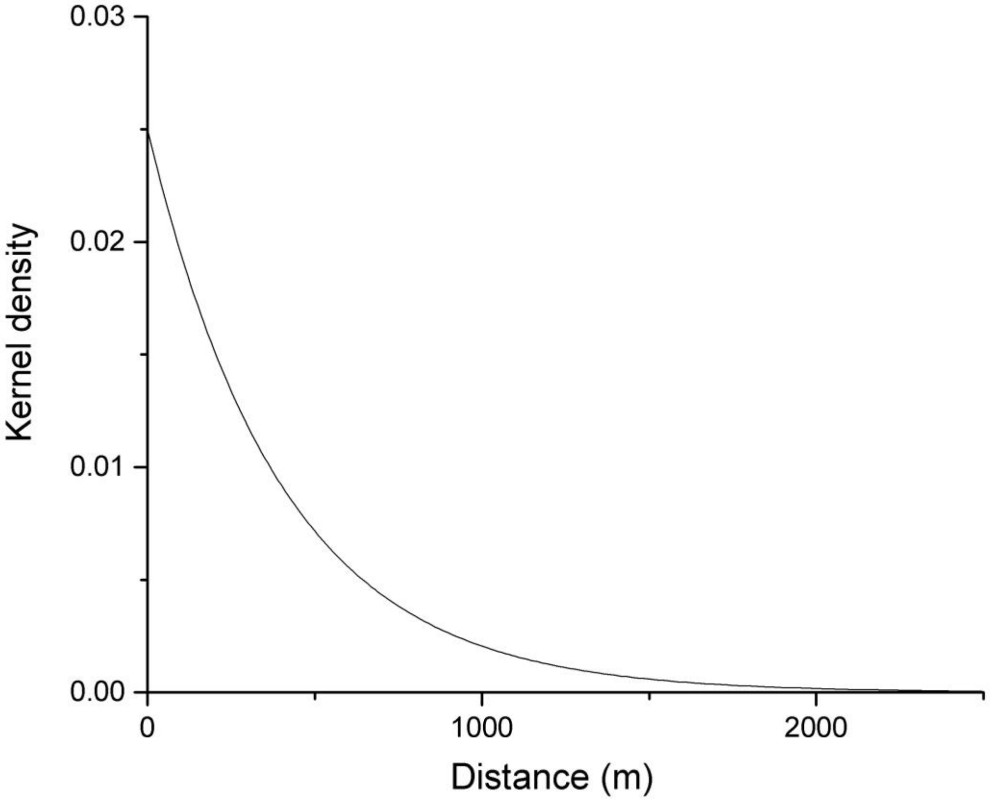


Figure 5.1 – Dispersal kernel used in trial movements

5.3.2 Model parameterisation

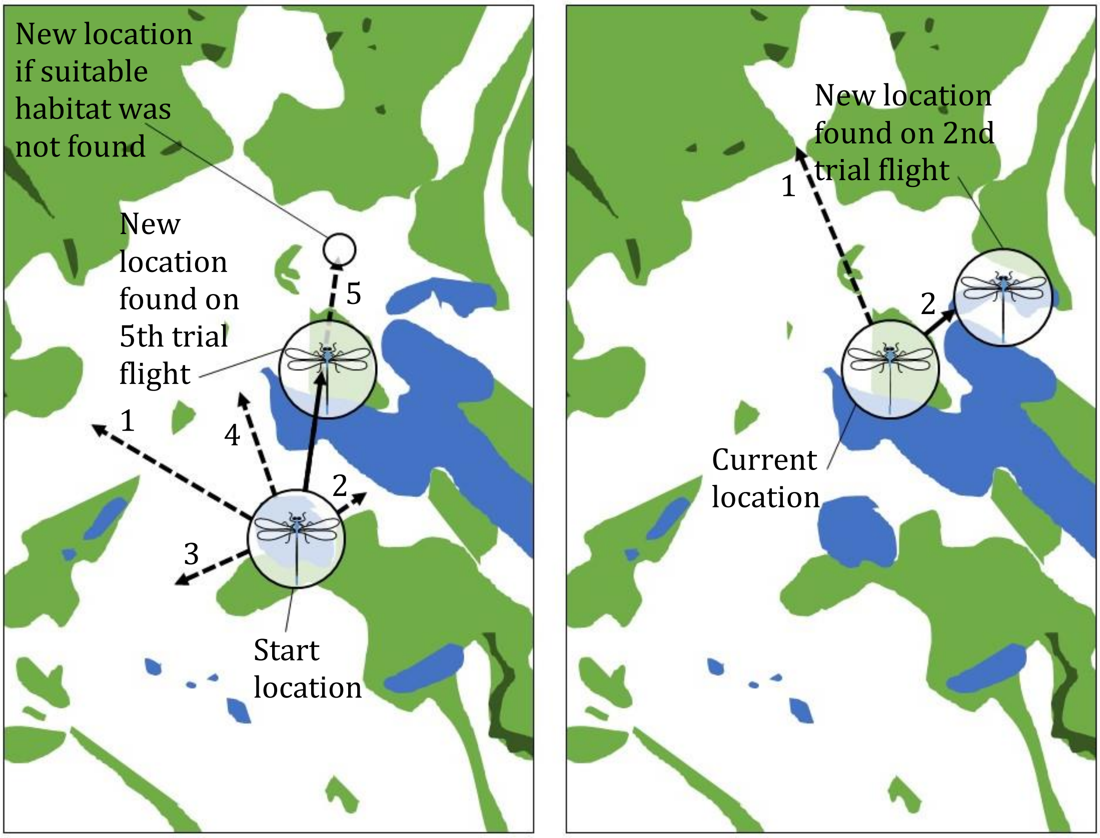
For each model run, 50 “damselfly” individuals were simulated over 10 years and 9 landscapes (4500 individuals simulated in total per model run). For each year the start point was moved to the furthest north reproductive habitat reached in the previous year and a new 50 individuals were simulated starting from this origin. The model was run eight times, four times with reversible polarotaxis and four times without.

The lifespan of 26 days with a 13 day pre-reproductive period was selected to be representative of a typical damselfly, set between an average and maximum lifespan – average adult lifespan is around 10 days in *I. elegans* with on average 5 days reproductive period, but longer lifespans occur in other species (Banks and Thompson, 1985; Cordero-Rivera and Stoks, 2008) and some individuals have been known to live for 7-8 weeks (Brooks et al., 1997; Corbet, 1999). However, the sizes of natural populations of damselflies are much larger than the 50 individuals simulated here, and so the animals in the model can be considered the longer-lived component of a wider population.

The percentage chance of dispersal was based on empirically derived behavioural preferences for polarised light in *I. elegans*, with an 80% preference for non-polarised light during the pre-reproductive period and a 75% preference for polarised light once mature (Villalobos-Jiménez et al., 2018).

The trial movements were parameterised using an exponential distribution as mark release recapture surveys have generally shown fewer long distance movements in damselfly species (Allen and Thompson, 2010; Conrad et al., 1999; Watts et al., 2004). The exponential distribution rate ($\lambda = 0.025$, and distance was then multiplied by ten as preliminary experiments saw no dispersal, see Figure 5.1) was chosen so that only a low number of trial movements (roughly 27% chance of a movement more than 2000m happening at least once across 50 individuals) met or exceeded 2000m, a distance derived from the average range shift per year in *I. elegans* (see Chapter 2).

Figure 5.2 – Diagram of model process. Green represents foraging (immature) habitat and blue represents breeding habitat (mature). The process pictured here is initiated if a random number between zero and 100 generated at each time step is less than the percentage chance of moving based on the current habitat. The left panel shows an immature insect (green habitat is suitable habitat), the right panel shows a mature insect (blue habitat is suitable habitat).



5.3.3 Statistical analysis

Statistical analysis was performed in R (R Core Team, 2017, https://www.r-project.org). To evaluate the effect of reversible polarotaxis on movement, the distances each individual travelled each step of the model were extracted and summed to find the total distance travelled by an individual in a year (gross dispersal). In addition, the distance from the start point (day 1) to the end point (day 26) for each individual each year (net dispersal) and the potential area they may have covered (bounding box measured from maximum and minimum northings and eastings recorded) were calculated. To quantify the effect that reversible polarotaxis has on potential dispersal-related mortality, I recorded whether individuals ended their lifespan in reproductive habitat (see section 5.3.1), the time it took each individual to reach feeding habitat (see section 5.3.1) and the time they spent there. Generalised linear models were constructed for each of these six statistics as dependent variables and five combinations of predictors: (i) a null model with a floating intercept, (ii) the percentage freshwater habitat content of a grid, (iii) whether reversible polarotaxis was simulated (polarotaxis or non-polarotactic), (iv) freshwater and polarotaxis as additive effects, and (v) freshwater and polarotaxis as additive effects plus an interaction between the two. Model comparison was conducted using AIC (see Table 5.1).

5.4 Results

See Figure 5.3 for a visual example of the simulation outputs. The model shows dispersal values of on average 0.14km north per year, average total dispersal values (including longitudinal movement) per year of 0.83km and average potential areas covered of 1.10km^2. On average it took 2.75 days for individuals to reach feeding habitat and they spent on average 5.38 days feeding (of those that did reach it at all – 243 of 72000, or 0.3%, did not reach feeding habitat). Across all runs 80% of individuals ended in reproductive habitat.

The results of the model runs suggest that reversible polarotaxis is an important factor in helping Odonata arrive at feeding habitats earlier and increasing their chances of returning to reproductive habitat. However, contrary to predictions, polarotaxis does not increase dispersal distances. Instead it decreases the distance dispersed (for example, see Figure 5.3) and does so slightly more in higher densities of reproductive habitats.

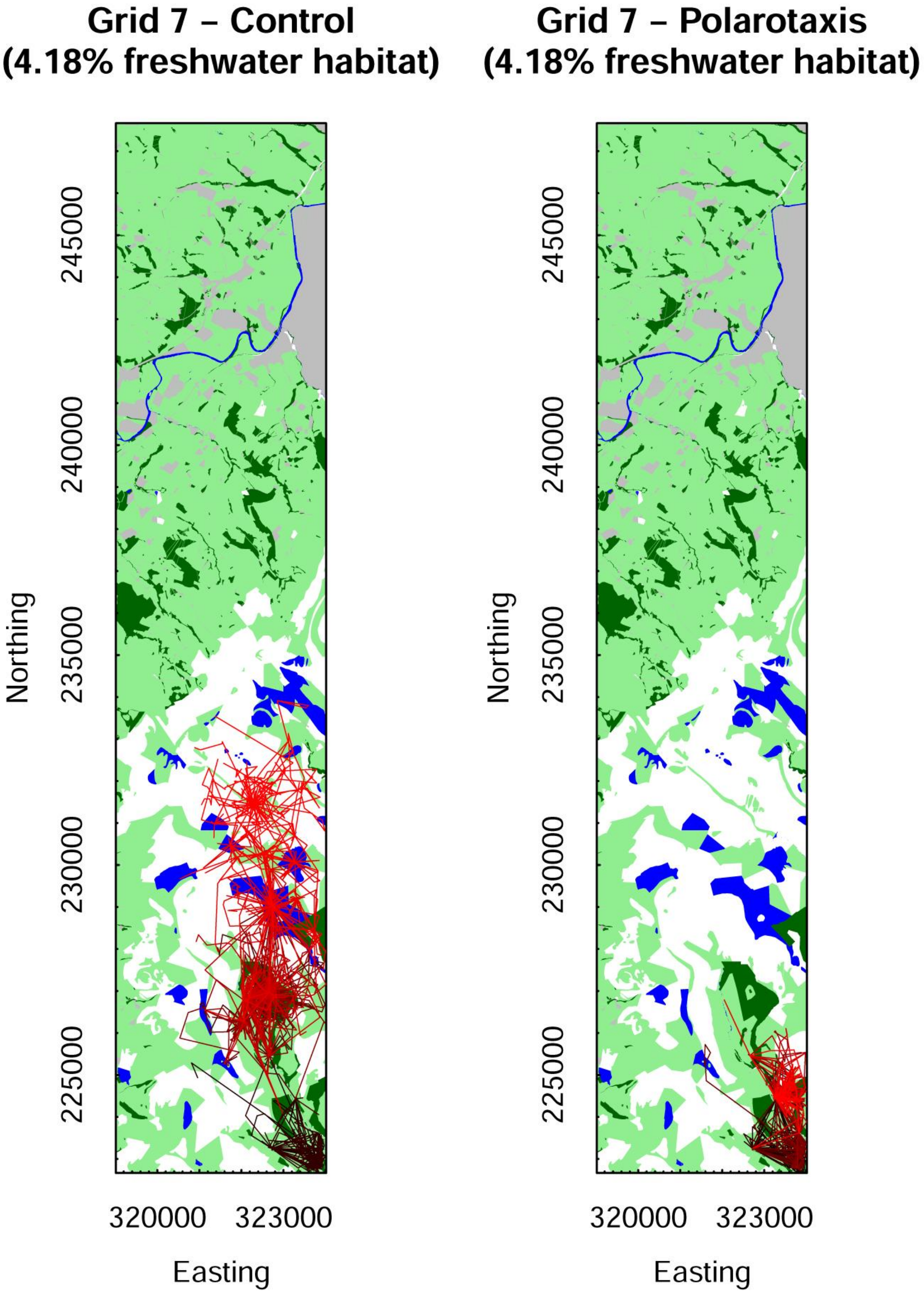


Figure 5.3 – A comparison of paths taken by 50 individuals for 10 years (left) without and (right) with reversible polarotaxis, showing greater dispersal in the non-polarotactic run. Line colour is related to the year of the model run with bright red being year 10 and dark red being year 1.

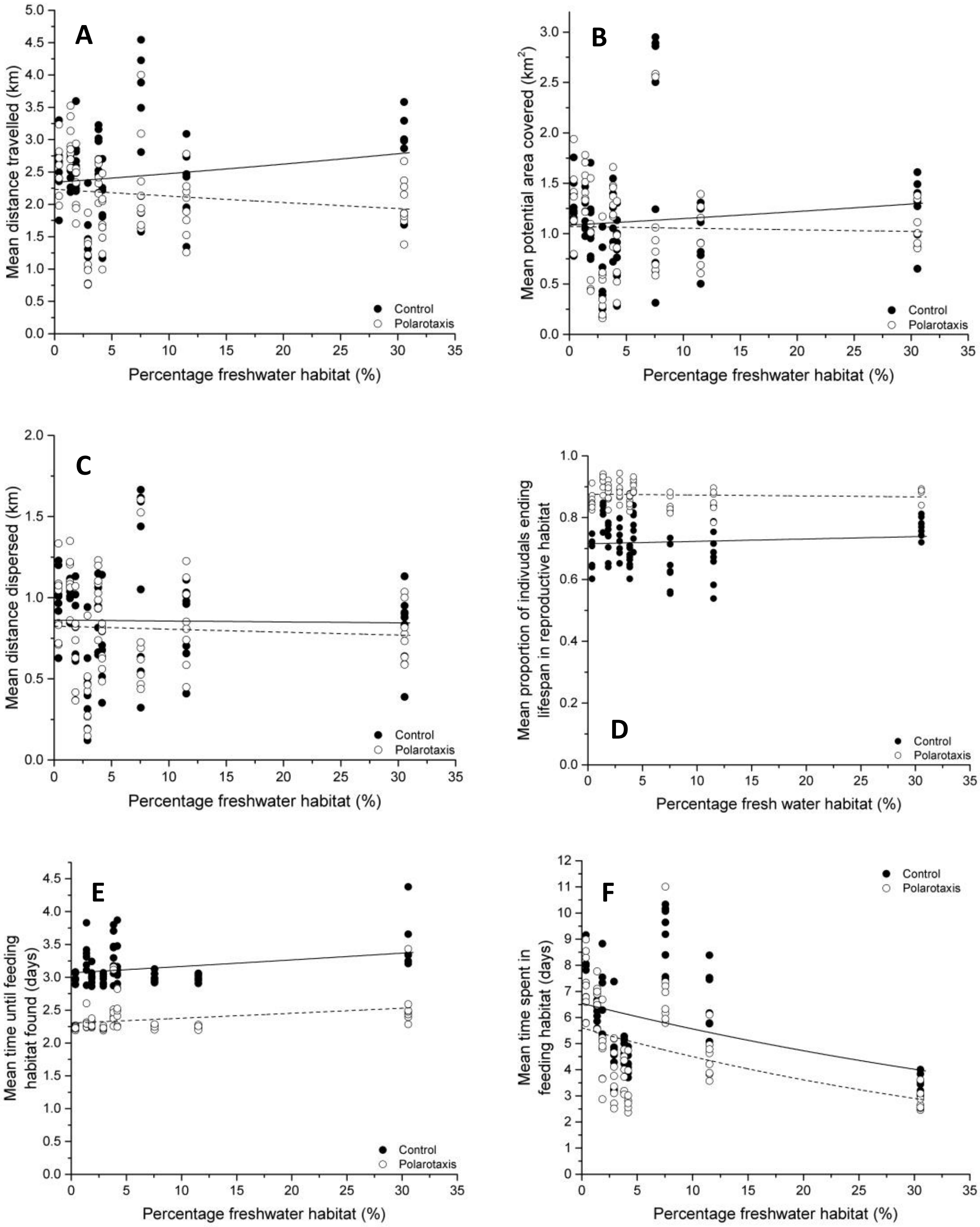


Figure 5.4 – Scatter graphs of freshwater habitat area against average dependent variables. Points are mean values for each year within each grid, averaged across all 50 individuals. Filled circles represent non-polarotactic simulations, open circles represent simulations with reversible polarotaxis. Lines are minimum adequate glm fits of non-averaged data, with dashed lines for reversible polarotaxis and solid lines for non-polarotactic. A) Distance travelled, B) Potential area covered, C) Distance dispersed (displacement), D) Proportion of individuals ending lifespans in reproductive habitat, E) Time taken to reach feeding habitat and F) Time spent in feeding habitat.

Table 5.1 – AICc tables for all generalised linear models constructed. Habitat availability refers to the percentage freshwater habitat available.

Response variable	Model terms	df	AICc	ΔAICc	Weight
Gross dispersal	Polarotaxis * Habitat availability	5	266947.4	0.000	1.000
	Polarotaxis + Habitat availability	4	267232.9	285.555	0.000
	Polarotaxis	3	267242.7	295.354	0.000
	Habitat availability	3	267718.8	771.404	0.000
	Null model	2	267728.5	781.151	0.000
Potential area covered	Polarotaxis * Habitat availability	5	211431.0	0.000	1.000
	Polarotaxis + Habitat availability	4	211499.7	68.758	0.000
	Polarotaxis	3	211527.4	96.458	0.000
	Habitat availability	3	211567.9	136.897	0.000
	Null model	2	211595.6	164.580	0.000
Net dispersal	Polarotaxis * Habitat availability	5	169642.1	0.000	0.697
	Polarotaxis + Habitat availability	4	169643.8	1.687	0.300
	Polarotaxis	3	169653.2	11.085	0.003
	Habitat availability	3	169696.2	54.092	0.000
	Null model	2	169705.6	63.484	0.000
Chance of ending in reproductive habitat	Polarotaxis * Habitat availability	5	69872.0	0.000	0.924
	Polarotaxis + Habitat availability	4	69878.3	6.375	0.038
	Polarotaxis	3	69878.4	6.413	0.037
	Null model	2	72539.8	2667.805	0.000
	Habitat availability	3	72539.8	2667.841	0.000
Time taken to reach feeding habitat	Polarotaxis + Habitat availability	4	237670.4	0.000	0.713
	Polarotaxis * Habitat availability	5	237672.3	1.822	0.287
	Polarotaxis	3	237822.0	151.597	0.000
	Habitat availability	3	241665.9	3995.468	0.000
	Null model	2	241815.1	4144.618	0.000
Time spent in feeding habitat	Polarotaxis * Habitat availability	5	417828.0	0.000	1.000
	Polarotaxis + Habitat availability	4	418000.2	172.262	0.000
	Habitat availability	3	421409.0	3581.071	0.000
	Polarotaxis	3	426659.5	8831.489	0.000
	Null model	2	430068.3	12240.298	0.000

5.4.1 The effect of reversible polarotaxis on dispersal

The models show that both the habitat availability and polarotaxis were significantly correlated with aspects of individual movement, and feeding behaviour metrics (Table 5.1 and 5.2 and Figure 5.4). Gross dispersal and potential area covered were both similar for non-polarotactic and polarotactic individuals at low densities of freshwater habitat. At high densities of freshwater habitat gross dispersal and potential area covered increased for non-polarotactic individuals but decreased for polarotactic individuals (see Figure 5.4 A and B). Polarotactic individuals showed slightly lower net dispersal than non-polarotactic individuals. Net dispersal decreased slightly with increasing freshwater habitat density, but this decrease was lower in non-polarotactic individuals (see Figure 5.4 C). The maximum distance dispersed over 10 years across any one grid was 170.9km. The chance of ending in reproductive habitat decreased very slightly with increasing freshwater habitat density for polarotactic individuals. Non-polarotactic individuals had a lower chance of arriving at reproductive habitat across all freshwater habitat densities studied, but the chance increased with freshwater habitat density (see Figure 5.4 D). Polarotactic individuals arrived at feeding habitats earlier than non-polarotactic individuals and the time of arrival was shifted later with increasing freshwater habitat density at the same rate for both groups (see Figure 5.4 E). Finally, the time spent in feeding habitat decreased with increasing freshwater habitat density, with non-polarotactic individuals generally spending more time feeding, and a slightly shallower rate of decrease in time spent feeding in relation to increasing freshwater habitat density (see Figure 5.4 F).

Table 5.2 – Minimum adequate model parameters. Habitat availability refers to the percentage freshwater habitat available. *Indicates a Wald's test has been carried out, otherwise t tests were performed.

Response variable	Term	Parameter	SE	t or z	p
Gross dispersal	**Polarotaxis**	**0.0099**	**0.0015**	**6.385**	**<0.001**
	Habitat availability	**-0.0012**	**0.0001**	**-13.691**	**<0.001**
	Polarotaxis × habitat	**0.0022**	**0.0001**	**16.356**	**<0.001**
Potential area covered	Polarotaxis	0.0032	0.0032	0.981	0.326
	Habitat availability	**-0.0015**	**0.0002**	**-7.909**	**<0.001**
	Polarotaxis × habitat	**0.0019**	**0.0002**	**6.699**	**<0.001**
Net dispersal	**Polarotaxis**	**0.0109**	**0.0026**	**4.235**	**<0.001**
	Habitat availability	0.0002	0.0002	1.005	0.315
	Polarotaxis × habitat	0.0004	0.0002	1.782	0.075
Chance of ending in reproductive habitat	**Polarotaxis**	**1.0335**	**0.0254**	**40.764**	**<0.001**
	Habitat availability	**0.0038**	**0.0013**	**2.860**	**0.004**
	Polarotaxis × habitat	**-0.0064**	**0.0022**	**-2.906**	**0.004**
Time taken to reach feeding habitat	**Polarotaxis**	**-0.2862**	**0.0046**	**-62.910**	**<0.001**
	Habitat availability	**0.0031**	**0.0002**	**12.500**	**<0.001**
Time spent in feeding habitat	**Polarotaxis**	**-0.1548**	**0.0041**	**-37.820**	**<0.001**
	Habitat availability	**-0.0162**	**0.0003**	**-57.570**	**<0.001**
	Polarotaxis × habitat	**-0.0057**	**0.0004**	**-13.170**	**<0.001**

5.5 Discussion

This is the first investigation of the population level effects of reversible polarotaxis in Odonata, with clear application to the general effects of polarotaxis in other groups with similar behaviour. The model produced here suggests that reversible polarotaxis has a fairly small effect on Odonata dispersal, with polarotactic individuals predicted to disperse 37m per year (2%) less than non-polarotactic individuals at freshwater habitat densities close to zero percent. At freshwater densities of 30% this reduction increases to 77m – still a relatively small reduction of only 4%. However, reversible polarotaxis does help reduce the time taken to find feeding habitat and the chance of returning to freshwater habitats. The impact of freshwater habitat density is relatively small for all response variables, except time spent in feeding habitat, which decreases considerably with increasing freshwater habitat density – presumably due to concurrent decreases in the proportion of feeding habitat available, and thus the need to travel longer to find feeding habitat. It also has a considerably diverging effect on movement patterns between polarotactic and non-polarotactic individuals. Polarotactic individuals show negative correlations with freshwater habitat density and distance travelled, area covered and distance dispersed, whereas the correlation is positive for non-polarotactic individuals for distance travelled and area covered (and a shallower negative correlation with distance dispersed).

5.5.1 Polarotaxis and dispersal

Beyond the role of polarotaxis in determining behavioural interactions with breeding habitat, the ecological function of the phenomenon has received little attention. I expected that there would be a "push-pull" effect of polarotaxis, which would first move the immature animals away from their natal waterbody and then attract them to a water body that was further away. Such a mechanism would result in greater overall (net) dispersal distances in polarotactic individuals. However, the model here shows that individuals with reversible polarotaxis disperse shorter distances and travel generally shorter distances than those without – even more so at high densities of freshwater habitat. As such reversible polarotaxis does not promote dispersal as expected, but rather help to find the shortest route to feeding habitat, then encourage relatively sedentary behaviour before a return to probably the natal body of water (philopatry), as opposed to a new habitat which is likely a longer distance away from the individual. Given the relatively low percentages of dispersers usually seen in a population (Conrad et al., 1999; Conrad et al., 2002), it may be that dispersers do not have this reversible polarotaxis behaviour, or show very different behaviour when dispersing, but due to their relative rarity and the scarcity of studies on polarotaxis that this has not yet been detected. It certainly warrants further study involving the combination of mark release recapture and behavioural trials in the field.

For both polarotactic and non-polarotactic individuals, dispersal is increased in areas with limited freshwater availability, presumably a mechanism to avoid or escape isolated habitats (Harabiš and Dolný, 2012; Keeler and Chew, 2008; Schlaepfer et al., 2002), whereas at higher freshwater habitat densities dispersal is not as important as there is the habitat is suitable. This in direct contrast to models of “corridor” habitats, which can be considered as areas of low density habitat, where dispersal is decreased (Travis and Dytham, 1999) – as dispersing individuals are more likely to disperse into unsuitable habitat. The difference in this study is that mortality has not been simulated, so individuals dispersing into unsuitable habitat survive long enough to find new habitat or return to an existing one.

Dispersal-related mortality is an important aspect of animal movement models (Dytham, 2009) – which has only been considered here in reference to return to a breeding habitat. Here our model suggests that reversible polarotaxis although reducing the distance dispersed and travelled, helps ensure that individuals return to reproductive habitat, increasing their fitness (an individual cannot or is very unlikely to reproduce if it doesn’t return to reproductive habitat). Whether this is the only drive minimising dispersal related mortality (ending up in unsuitable habitat by accident) remains to be seen, but given the reliance of Odonata on vision it seems likely the reversible polarotaxis is one of the primary drivers. Any future models might want to consider giving dispersal a distance related cost representing mortality through increased predation or insufficient energy reserves. However, at least within the Odonata, adult mortality drivers are generally unknown or have little empirical evidence (Anholt, 2008) and given their strong flight ability (see Chapter 2 and 3) dispersal-related costs could be considerably lower for the Odonata than for other groups. The average zygopteran daily survival rate is 0.86 (Cordero-Rivera and Stoks, 2008). Assuming that survival is indifferent between habitats, the simulations here suggest that polarotactic individuals which spend on average 4.9 days feeding have a higher feeding survival rate (proportion surviving until their return to reproductive habitat) of 0.48 as opposed to non-polarotactic individuals which have a feeding survival rate of 0.41 (based on an average 5.9 days spent feeding).

5.5.2 Polarotaxis and foraging ecology

Flight is involved with almost all aspects of adult life for the Odonata, and they are known to not only have one of the highest flight muscle ratios of any insect but also to develop flight muscles quickly after emergence (Marden, 1989). This is the theorised function of reversible polarotaxis, in that newly emerged Odonata are repelled by polarised light (i.e. water) to find feeding habitat, build muscle mass (and ovary mass in females) before returning to water to breed (Corbet, 1999). There is usually only anecdotal evidence for this behaviour, although recent studies have started to investigate the degree of change in polarotaxis (Kriska et al., 2009; Villalobos-Jiménez et al., 2018) and the particulars of maiden flights (Rüppell and Hilfert-Rüppell, 2010). The model here suggests that initial repulsion from polarised light is helpful for finding feeding habitat earlier, whereas in other groups with ontogenetic niche shifts intraspecific competition appears to enforce movement away from mature adult habitat (Van Kleeck et al., 2018). The focus on enhancing fitness through feeding ecology rather than dispersal suggests that reversible polarotaxis is a behaviour associated with routine movements as opposed to less common dispersal movements (Van Dyck and Baguette, 2005). Unlike my predictions however, the time spent feeding is reduced in polarotactic individuals. Although at first this would seem to have negative consequences for individual fitness, I suspect that the increase in feeding time in non-polarotactic individuals is due to time spent in feeding habitat during the mature part of the adult lifespan, whereas polarotactic individuals have already returned to reproductive habitats. It is currently unclear what cue prompts the return to reproductive habitat as it cannot be polarotaxis if the individual is not within visual range of freshwater. The potential increase in fitness for arriving in feeding habitats earlier is dependent on areas such as grassland and forest acting as feeding habitat for Odonata, which appears to be the case for many Odonata species but has limited empirical evidence to date (Anholt, 1992; Kirkton and Schultz, 2001). It may be the case that freshwater habitats provide enough prey that initial negative polarotaxis is only required to get the individual away from the water's surface (as opposed to into new habitats).

5.5.3 Ecological traps

When presented with polarised light pollution in urban environments, the Odonata appear to have lower affinities for polarised light. This could be through removal of high affinity individuals from the population (either through mortality or more likely failure to reproduce as eggs are not laid in water etc.) or alternatively there may be some behavioural plasticity allowing suppression after unprofitable experiences with polarised light pollution (Villalobos-Jiménez et al., 2018). The results of the model here suggest that through either method the remaining individuals with reduced polarotactic responses are likely to expend more effort by travelling further, for relatively minimal dispersal gains. This effect is exacerbated at higher levels of freshwater habitat availability – although urban environments generally have lower densities of suitable habitats (Mckinney, 2002; Zedler and Kercher, 2005), so the effect is unlikely to be present in actual urban populations. Urban individuals with weaker polarotactic responses would also spend longer reaching a feeding habitat and perhaps spend more of the mature lifespan in feeding habitats than is necessary. Given that urban environments are likely to have fewer and smaller feeding habitats (Mckinney, 2002; Zedler and Kercher, 2005), this is likely to cause a significant reduction in urban individuals' fitness – particularly those with weaker movement abilities and in conjunction with higher chances of not being able to find reproductive habitat once mature. This phenomenon is also known as "habitat split", seen in amphibians where different life stages utilise different habitats, which are increasingly separated in urban environments (Becker et al., 2007).

5.5.4 Model performance

Freshwater habitat percentage within a grid can be a poor indicator of the actual freshwater habitat density experienced by an individual, particularly if dispersal does not cover the entire grid (as has happened here with our model). The actual density of freshwater habitats may be considerably different in smaller compartments of the grid, as their distribution in landscapes is heterogeneous. Having checked more local densities of the grids the values do change but the relative classification of the grids remains mostly the same (i.e. the grid with the largest percentage of freshwater habitat remains the same – only one grid changes its rank). Future efforts could use raster surfaces to identify the minimum distances to other freshwater habitat in any given location, and the relative availability of freshwater habitat could be included for each step of the model based on the individual's current location.

The overall northwards dispersal values of on average 0.14km north per year are relatively low, given the recent roughly 2km per year range expansion (Hickling et al., 2005, also see Chapter 2). However, the lack of climate data included in the model, and the ability of individuals to disperse in any direction probably has an impact on this, as the range shifts detected in these species are likely to be driven by increasing temperatures making higher latitude habitat available and perhaps of higher quality than current habitat patches (closer temperatures to the species thermal optimum). The model here assumes that all habitat patches are of equal quality and movement decisions are based solely around the presence of polarised light. This means that individuals are not discouraged from returning to their natal habitat which they could be if that habitat became less suitable due to climate change. The average total dispersal values are considerably higher (0.83km per year), and again these are likely smaller than real world scenarios due to the lack of directed movements within the model, but more importantly the small population sizes considered here. Fifty individuals represents a very small percentage of total invertebrate populations, so if the model were run for more realistic population sizes, I would expect to see increased dispersal distances.

Although not a limitation in relation to the results discussed above, the model developed here has considerable potential to include further detail. Of particular interest would be the inclusion of population maintenance (i.e. the integration of birth and death rates and the habitation of multiple habitat patches) and habitat quality, which is particularly important in determining predation success, territory choice and dispersal (Crumrine et al., 2008; McPeek, 2008). Habitat quality will also have a strong influence on how viable or useful a feeding habitat is. Further details not simulated are the potential ability of individuals to direct their dispersal, whether by wind direction (Srygley, 2003), active discrimination for landmarks of certain habitats (e.g. treelines of forests or polarised light from freshwater habitats) (Lojewski and Switzer, 2015), or temperature driven latitude or altitude movements (Hassall and Thompson, 2008; Hickling et al., 2005), which would help predict real world movements. However much of this detail requires knowledge of the underlying drivers of movement behaviour and the sensory systems of the individuals involved – which may not yet be available.

5.5.5 Conclusions

To conclude, reversible polarotaxis does not promote dispersal as initially expected, but instead seems to encourage less movement, to increase the chances of finding feeding habitat quickly and increase the chances of an individual returning to reproductive habitat. Interestingly my model suggests that reversible polarotaxis promotes philopatry more strongly in areas with more reproductive habitat, which may be a mechanism to help individuals exploit more abundant resources when or where available. The implications of these results for polarised light pollution and the ecological traps they create seem to generally reduce fitness in individuals with loss of polarotaxis through polarised light pollution related selection. Reduction in fitness is brought about by increasing travel distances (gross dispersal), but there is a slight promotion of net dispersal, increasing the chance of escaping potentially poorer and isolated habitats. Despite some limitations, the model here seems a reasonable predictor of the processes influenced by reversible polarotaxis and will hopefully facilitate further more detailed study.

Chapter 6 – General Discussion

Here I lay out the key findings of each preceding chapter and then explain how the synthesis of these findings contributes to the field as a whole. After this I explore the synthesis in a wider context and suggest possible future directions in the field of Odonata and flight ecology.

6.1 Key findings

6.1.1 Chapter 2

In chapter 2 I demonstrated that range shifts are related to some dimensions of flight performance in the Odonata. This link is contrary to previous studies on range shifts (Hill et al., 1998; Mair et al., 2014; Therry et al., 2014; Therry et al., 2015), but these studies have used proxies for flight performance rather than measuring flight performance directly. The relationship displayed by the data in chapter 2 suggests that flight performance imposes a limitation on range shift magnitude, as several species exhibit smaller range shifts than would be predicted based on their flight performance (see Figure 2.5). Range shifts are not solely dependent on flight performance, but are influenced by a range of other factors which will interact with this limitation. Significantly, *Coenagrion mercuriale* stands out as a species that is exhibiting considerably smaller range shifts than would be predicted from the kinematic analysis, which is consistent with the reliance of this species on very specific, fragmented habitats. Thus, I have confidence that the relationships seen in that chapter are accurate reflections of interspecific variation.

Flight performance is a complex entity which is difficult to measure with a single value, as it encompasses average flight speed, specific aerial manoeuvres, maximum speed and acceleration and the efficiency with which all of these can be performed – between which there are potentially trade-offs. In chapter 2 it is a measure of flight efficiency that appears to impose limitations on range shifts. Rather than absolute speed or power of flight, it is the minimisation of energy expenditure that is important. Efficiency is particularly important in long distance movements, which represent a significant energy cost in the life of an individual. For range shifts to occur, colonisation of new habitats is required with individuals having to disperse to populate new areas. Depending on the quantity and configuration of suitable habitat that is available to a species, the distance any individual will have to travel to be able to establish a new population will vary. In fragmented habitats like those seen for freshwater organisms, the distance required to travel to new habitats is high, hence why efficiency appears to be so important.

6.1.2 Chapter 3

In chapter 3 I showed that there is a correlation between actual flight performance and wing morphology. In general, larger wings, lower aspect ratios, and broader chords towards the wing base produce faster flight speeds, greater accelerations, and better agility, but are less efficient. The exact shape of the wing is less important, only influencing speed and acceleration of flight, with less petiolate, broad, rounded wings being faster and with better acceleration. It is possible that shape does have an influence on other flight performance traits, but not within the range of shape variation seen in Odonata. Given the considerable differences between Zygoptera and Anisoptera wing forms, I suspect that outside of extreme morphological differences, the general shape of the wing beyond aspect ratio and 2nd moment of area is unlikely to have an effect outside the Odonata, at least in those insects with four functional wings. There is a wide variety of conflicting assumptions regarding the impact of wing morphology on flight performance which seem to have originated from a couple of primarily theoretical studies. My results are in agreement with about half of the previous assumptions made, showing that greater care is needed when using wing morphology as a proxy for flight performance and that flight performance should be properly defined from the outset.

This study is also the first comparative look at the influence of wing morphology on flight performance. Where previous studies have only considered a single study species, my study considers almost the entire range of variation within an order (with the exception of some of the more unusual species, for example the helicopter damselflies or the extremely small *Nannothemis sp.*). Whilst variation in detailed shape parameters remains small between closely related species, size is more variable, suggesting that certain wing plans are advantageous, but can be scaled up or down in terms of size. It remains to be seen whether the four individually controlled wings of the Odonata have a different relationship between wing morphology and flight performance than other insects that have only two functional wings, or interlocked wings (where the forewing and hindwing are held together by some mechanism, effectively creating one wing from two).

6.1.3 Chapter 4

In chapter 4 I found no carry-over effects on locomotory performance in Odonata. Adult performance is therefore independent of larval performance, suggesting that energy invested in swimming musculature is not converted to adult flight muscles, nor is it invested at the cost of investing in adult flight musculature. The results here also lend support to the idea that immature Odonata adults spend the majority of their time feeding to develop flight muscles before returning to mate. Although carry-over effects are present in Odonata from larva to adult (Stoks and Córdoba-Aguilar, 2012), most of these are seen under stressful conditions (food shortage, chemical exposure etc.) which was not the case here.

I did find evidence that slower growth rates lead to faster swimming speeds and greater accelerations in the larvae. What is responsible for this pattern is unclear but I suggest that it could be longer times available for locomotory muscle development, i.e. a trade-off between growth rate and performance, as longer growth times may cause late emergences. Although the individuals studied were the same size, the nature of insect exoskeletons means that the actual muscle mass inside the exoskeleton might vary. Further study is required to find out whether this is the case and whether the same is true in adult Odonata.

6.1.4 Chapter 5

The model constructed in chapter 5 shows that reversible polarotaxis behaviour seen in Odonata does not increase potential dispersal distances across realistic habitat, but reduces it slightly. Interestingly, polarotaxis decreases the distance travelled and areas covered by individuals, more so in dense freshwater habitat, the opposite trend to non-polarotactic individuals. It also reduces the time spent feeding, but causes individuals to arrive earlier in feeding habitat and have better chances of returning to a reproductive habitat after feeding. This pattern suggests that it is primarily a mechanism to increase fitness by reducing energy expenditure and promoting philopatry – particularly in dense areas of suitable habitat. The amount of available freshwater habitat has different effects on distances travelled, and area covered depending on whether reversible polarotaxis is simulated, but only small effects on other model outputs. In urban populations where insects with stronger polarotactic responses are removed from the population, reversible polarotaxis is likely to decrease the remaining insects' fitness as they will travel further without necessarily finding feeding habitats and are less likely to be able to find reproductive sites.

6.2 Synthesis

Taking all of these results together they show that flight performance does affect the way in which populations spread, and that it is based upon in part wing morphology. Larval conditions, except where stressed, are unlikely to have strong influences on wing shape, at least in the Odonata. It shows that if properly defined, many different measures of wing morphology represent suitable proxies for flight performance, although generally size seems to have the largest impact. The complexity of dragonfly (and, more broadly, insect) flight has led to a number of equivocal assumptions about the link between morphology and function. These findings also raise questions as to why previous studies have not detected any influence of flight-related morphology in range shifts.

6.2.1 Flight Ecology

The ultimate aim of my work is to inform and assist conservation efforts, predicting where species of concern will be able to move to, and whether flight performance is a limiting factor. The findings can also help to predict the movement patterns of potentially or known invasive species (Gallien et al., 2010; Rocchini et al., 2015). With increasing anthropogenic change in natural habitats, including environmental warming, habitat loss and fragmentation and the introduction of new species, the capacity of species to respond will be reduced (Hassall and Thompson, 2008; Palmer et al., 2017; Walther et al., 2002). Implementing effective conservation measures requires knowledge of the ecology of a species and its ecosystem (Araújo et al., 2005; Estrada et al., 2016; Harris, 2015; Watson et al., 2016). Creating a nature reserve which, due to increasing temperatures, loses all the species it was set up to protect is a futile endeavour. The relationship demonstrated in Chapter 2 helps to show the physical limits to dispersal in Odonata species – if the distances between habitats are too large, species such as *Calopteryx splendens* and *Aeshna sp.* may not be able to disperse between them. Through Chapter 3 I have demonstrated a relatively quick and easy way of assessing a species dispersal capacity by measuring relatively simple morphological statistics. Although I measured many different aspects of the wing, all were correlated with a small number of primary principal components. The average chord had the highest correlation coefficient so I recommend that this is perhaps the best proxy of flight efficiency for future use, allowing dispersal ability to be quickly assessed. The limiting relationship of flight performance on range shifts should help to provide insights to existing work on range shifts, as, if a species is not reaching its potential range shift, some other factor is likely responsible, for example habitat availability (Mair et al., 2014). For declining species I have confirmed that flight performance in relation to dispersal at least is unlikely to be important, as colonisation is not usually relevant for species with declining abundances (Mair et al., 2014).

My results showing a link between range shifts and flight efficiency, correlated with wing morphology raise the question of why some studies have not found any link between range shifts and flight morphology. I have shown that the flight performance proxies used previously are all good indicators (not including “expert opinion”) of flight ability even if the expected relationship is the reverse of the true relationship. It seems likely that in these cases either the taxon is declining or limited by habitat availability, in which case flight performance is not relevant or its limit is not reached (for example, Hill et al., 1998; Thomas et al., 1998), or in some cases the variation in flight performance was studied within a population, in which case perhaps intraspecific variation in some aspects of flight morphology are simply not large enough to produce a difference, (for example, Therry et al., 2014; Therry et al., 2015). Flight performance could still be having an effect in these cases, just not necessarily in dispersal or colonisation, instead its effects on predator avoidance or intrasexual competition (agility and manoeuvrability) may be more important (Gyulavári et al., 2017; Marden and Cobb, 2004; Marden et al., 1998; Outomuro and Johansson, 2011; Outomuro and Johansson, 2015; Outomuro et al., 2014; Takeuchi et al., 2016).

As expected, there were significant differences in both morphology and performance between Anisoptera and Zygoptera species. However, the differences were not quite in agreement with previously established hypotheses. Previously, it was thought that the Anisoptera were fast but not agile fliers, whereas the Zygoptera were slow but agile fliers. My results indicate that there is some truth to this dichotomy as in general the Anisoptera are very slightly faster and less agile fliers, but the difference is small with many being very similar in performance to Zygoptera species, and Zygoptera flight efficiency is also much higher (*Calopteryx splendens* excepted). In all the flight performance of the Zygoptera seems to be greater in most respects (more agile, more efficient, similar speeds) than the Anisoptera which makes sense given their more derived lineage (Dumont et al., 2010) and previous work showing more efficient performance (Rüppell, 1989; Wakeling and Ellington, 1997b). If Zygoptera are more efficient, why do we not see lengthy Zygoptera migrations as in some Anisoptera (May, 2013)? The answer is likely to be that although more efficient, their smaller size prevents the insects from developing energy stores large enough to carry out movements of those distances.

The *Calopteryx* genus is well studied in ecology, perhaps due to their slightly more conspicuous nature and generally being easier to manipulate for field studies. However, as my data shows *Calopteryx splendens* occupies an unusual position with intermediate wing morphology between Anisoptera and Zygoptera, similar flight speeds and agility, yet the lowest flight efficiency. *C. splendens* is one of two species in this analysis with marked wing colouration, the other being *Libellula quadrimaculata* (whose colouration is significantly less obvious). In *C. splendens*, its wing spot is thought to be used for territorial displays and is under sexual selection. It may be that reductions in flight efficiency are accompanied by increases in reproductive fitness via these means, driven by an intermediate wing morphology between two aerodynamically adapted states. In all, data for *Calopteryx* species should be considered with care given the evidence that they are not necessarily as strongly adapted for aerodynamic performance as other Odonata species.

6.2.2 Flight biomechanics

My data shows some evidence that reared individuals have lower flight speeds than wild individuals – at least within one species of Odonata. However, I suspect that this difference is more to do with the age of insects involved, in that reared individuals' flight was tested shortly after emergence (so immature insects) whereas all wild caught animals were mature individuals (as most if not all were engaged with mating activity or behaviours when caught). This ontogenetic variation in flight performance is interesting in and of itself, as age-related declines in odonates have received little attention in the literature, and were previously thought not to exist in invertebrates (Hassall et al., 2015; Hassall et al., 2017; Sherratt et al., 2010; Sherratt et al., 2011).

In addition, my data provides several measurements of flight performance of a range of Odonata from small *Coenagrion mercuriale* to large *Aeshna grandis*. These should be of further use to future biomechanical studies, in addition to further demonstrating the mirror corner cube technique as a viable and effective method of quantifying insect flight performance.

6.2.3 Biomechanics and ecology

As I've shown, biomechanical flight performance is a complex quantity with several different aspects. Within ecology, many authors refer to flight performance, sometimes under the guise of dispersal ability, as a single quantity related to relatively few morphological aspects of an animal. My results here show the need for caution in defining flight performance or dispersal ability. Dispersal ability is often recorded as maximum distance travelled in previous studies. Whilst maximum distance travelled is a useful quantity in helping to predict movements of species, it must be acknowledged as a quantity that is affected by a suite of different traits, including proportion of a population dispersing, habitat availability, flight efficiency and behavioural responses to environmental cues. Many of these are limiting factors, for example here I show that range shifts are limited by the flight efficiency of the Odonata, but in other species the limitation of habitat availability may be more severe. In other words, if the distance species are travelling is measured, it must be acknowledged that this metric is not necessarily an indication of physical performance, as is the case with *Coenagrion mercuriale*, where previous studies on its dispersal distance have brought about the assumption that it is a poor flier, whereas the data here shows otherwise. Understanding which limitations are likely to be most important in a given species should be a key area for future investigation.

There has been little investigation of how specific aspects of wing morphology affect flight (Ray et al., 2016), perhaps due to the complexities involved as the wings are potentially under multiple selective pressures, for example, aerodynamic, sexual selection and perhaps camouflage in some species. The data I've collected support previous comparative studies showing that most measures of wing morphology have an impact on flight performance. Knowing which aspects of wing morphology might be selected for by aerodynamic selection pressures will help identify which selective pressures are important in a species, but also which aspects of wing design affect which aspects of an individuals' fitness.

6.3 Future directions

The work here opens up a number of new and exciting directions primarily for the inclusion of further biomechanical data in ecology but also for advances in both fields. Here I will briefly suggest and outline future work and the rationale behind it.

6.3.1 Real world dispersal

Now we know empirically that flight efficiency is important for allowing dispersal, and that it is smaller but higher aspect ratio wings that improve flight efficiency, it is important to consider within populations which individuals are carrying out dispersal. The number of individuals in a population that are likely to disperse is not always known, and in Odonata percentages of dispersers can vary from 3.5% to 95% of a population, with considerable differences in between males and females (Beirinckx et al., 2006; Conrad et al., 1999). Once identified, the actual distances dispersed by individuals within a population are not well known – at least in Odonata. Whilst mark release recapture studies are useful for identifying the proportion of dispersing individuals within a population, they can be limited by the area covered, effort invested or timescale (Hassall and Thompson, 2012). With increasingly small radio or even GPS tags and detectors, radio telemetry or GPS tracking represents a useful avenue of investigation to look at actual movements in Odonata. Radio tags could be fitted to a large number of Odonata at a site and then nearby – or perhaps even distant sites monitored for arriving signals. Alternatively, active tracking could be carried out, which whilst an intensive exercise from the ground, drone mounted detectors could effectively receive signals from much greater areas. Additionally studies like this could provide insight into territorial movements, which are as of yet, poorly understood (Dolný et al., 2014; Lojewski and Switzer, 2015).

6.3.2 Flight efficiency

Now that I have demonstrated the implications of flight efficiency for range shifts, further investigation is required to determine whether my measure of efficiency is behavioural-based (i.e. the insect’s style of flight minimises energy expenditure) is related to the actual mechanical efficiency of the musculature system of flight, and what this relationship may be. Measuring flight efficiency is best done through respirometry, measuring O_2 intake and/or CO_2 production, as this methodology can quantify the exact amount of energy used by an animal during flight. Respirometry of Odonata is not yet possible in flight arenas like the one used here, as the volume covered by flight manoeuvres is too large in comparison to the small amounts of O_2 used or CO_2 produced by an Odonata. However, small scale wind tunnel experiments are possible, quantifying the energy expended at different flight speeds. Future work should focus on measuring this efficiency and discovering how it links to kinematic data.

In the study here, the two *Aeshna* species exhibited relatively low flight efficiency, which seems unusual as some members of this genus are known for long distance migrations (Corbet, 1999; May, 2013; Russell et al., 1998; Schröter, 2011; Wojtusiak, 1974). Within the UK the migrant hawker (*Aeshna mixta*) is known to migrate from continental Europe, and is slightly smaller than the other *Aeshna* species known in the UK. These traits makes it a good candidate to investigate efficiency in relation to long distance movements.

6.3.3 Comparative studies

Whilst the work here is one of the first comparative investigations into ecologically relevant flight performance, there is still opportunity to increase the scope of the species and flight systems involved. Initially, comparison to other four-winged insects such as locusts (already well studied within flight biomechanics) would be useful to corroborate the data here. More importantly, comparison outside four winged insects is necessary, determining whether the patterns I've demonstrated here are applicable to two-winged insects like the Diptera or insects with effectively two wings, for example the Lepidoptera (which have their forewings and hindwings linked together and an extensive background of ecology work) and the Coleoptera whose forewings are modified to protective wing cases. The methodologies could remain roughly the same, although as mentioned in Section 6.3.2 respirometry should be included if possible. Some of these groups already have some data (Bomphrey et al., 2009a; Ray et al., 2016), whereas others are lacking, but regardless an over-arching pattern across these groups with very different morphologies is required.

Additional scope could be implemented with the use of particle image velocimetry (PIV) studies. PIV is a technique that provides quantitative data on air (or liquid) flow, and is a powerful comparative technique that has helped describe leading edge vortices in insect flight among other aerodynamic patterns (Bomphrey, 2006). Whilst flight PIV has already received some attention, the swimming performance of Odonata larvae is restricted to a handful of studies measuring only speed or pressure. Future PIV studies can fully quantify the flow around, and produced by, Odonata larvae (see Figure 6.1), which will allow the calculation of hydrodynamic efficiency and power of Odonata swimming in addition to performance measures such as speed and acceleration.

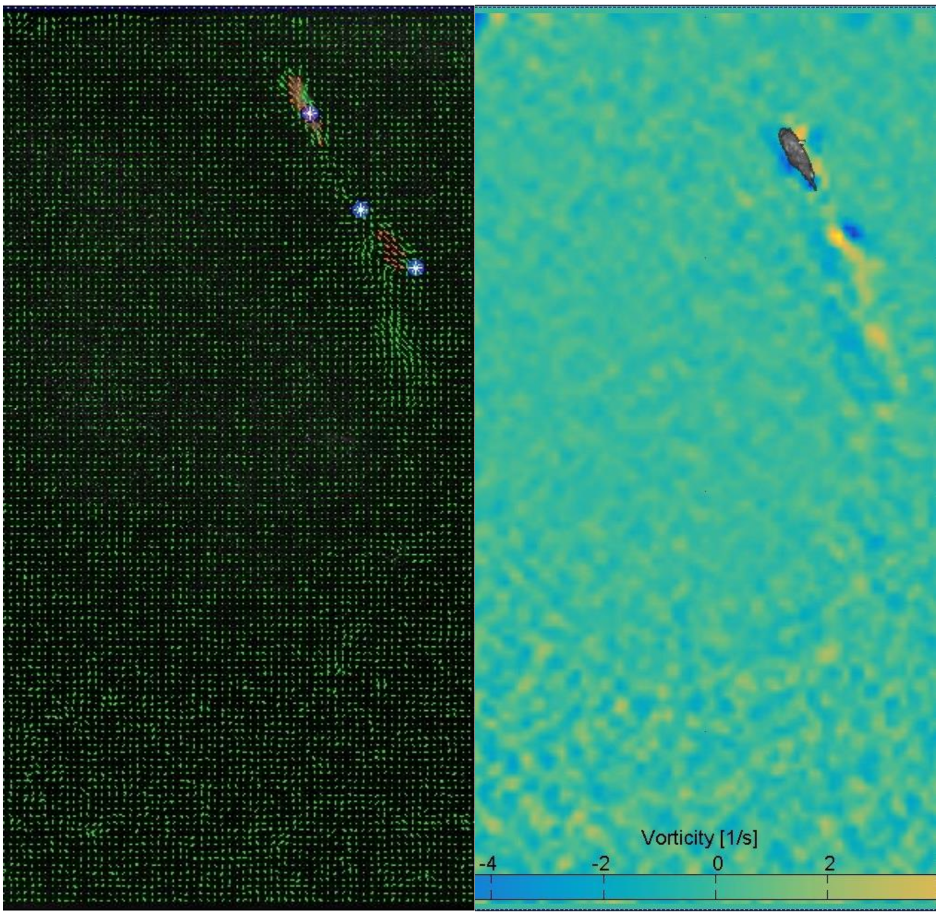


Figure 6.1 – A) Vector field produced during a swimming (jet propulsion) trial of a *Sympetrum striolatum* larva, showing a single jet produced by the larva. B) Vorticity calculated from 6.1 A

6.3.4 Validation of laboratory experiments

The vast majority of biomechanical work on flight has been conducted in laboratory settings, due to the advantages of being able to control the experimental environment amongst other logistical issues. Laboratory environments or setups are likely to have an impact on animal behaviour and performance but the extent of this impact and whether it will disrupt naturally occurring patterns is still debated in some areas for example tethered insect flight (Heisenberg and Wolf, 1979; Minter et al., 2018; Ribak et al., 2017). Here I looked at wild and laboratory reared insects' flight, both of which have advantages. Wild individuals have successfully survived the larval stage and emerged in the wild and are caught usually on the wing so we can be sure that their ability to fly is natural and intact. We do not have this reassurance in reared individuals, but we can control for larval carry-over effects if they are known and more importantly can control for parentage. Further study examining the effects of senescence on flight ability would be useful to help understand the drivers of senescence, following the proof of senescence in the Odonata and its links to climate but not to reproductive activity (Hassall et al., 2015; Sherratt et al., 2010; Sherratt et al., 2011).

Perhaps more exciting would be to capture field-based flight performance. Until now technology has not been advanced enough to carry out field tests of flight performance, beyond measuring distances travelled or perhaps estimates of flight speed. The biggest difficulty to overcome here is the ability to automatically record the position of an insect within an image – otherwise digitisation by hand is incredibly time consuming. Within the laboratory, powerful lights and plain backgrounds allow for automatic detection of insects but this is not possible in the field. However if a number of cameras could be set up at water level observing an area attractive to dragonflies, the contrast of the insect against the sky may be enough to record detailed natural flight patterns and show whether laboratory and field flight patterns are the same.

6.4 Conclusion

In conclusion, I have shown that multiple aspects of wing morphology are responsible for producing variation in flight ability in a range of Odonata species. Small but thin wings are more efficient and agile, but generally affect slower flight with lower accelerations, whereas larger broader wings show the opposite trend. I have also shown that flight efficiency (small, high aspect ratio wings) is correlated with range shifts in the UK Odonata, in what seems to be a limiting fashion, i.e. flight efficiency affects the maximum range shift able to be exhibited by a species, but does not specifically set the distance travelled by a range margin. There is no correlation between larval and adult locomotion, confirming that the musculature systems underlying these separate modes of locomotion are likely different. Finally the presence of polarotactic behaviour in Odonata does not seem likely to have an effect on dispersal distances and, as such, range expansion. Rather it is a mechanism that benefits adult Odonata by allowing them to spend as long as necessary in higher quality feeding habitat. Future research should be directed towards a better understanding of flight efficiency in Odonata and other insects and how this translates to actual movements in the field.

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