The adaptive significance of allopreening

Elspeth Kenny

A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy

Department of Animal and Plant Sciences

The University of Sheffield

December 2017

Allopreening common guillemots *Uria aalge*. Photo by Duncan Jackson.

Acknowledgements

I am extremely grateful to my supervisor Tim Birkhead for the opportunity to work on this project, and to the Department of Animal and Plant Sciences at the University of Sheffield, the Louise Hiom Fund and the Wildlife Trust of South and West Wales for financial support.

Thank you to everyone who has worked on the Skomer guillemot project, especially Julie Riordan for being the best field work pal I could have imagined. Thank you to all Skomer Island staff and volunteers whom I had the pleasure of working alongside for three field seasons, especially wardens Bee Büche and Eddie Stubbings, and assistant warden Jason Moss. Special thanks to Howard for designing and constructing a hide for me, and to Jamie Thompson for not dropping me off a cliff when I got too annoying.

Thank you to Sophie Wilcox for access to, and help with, the Alexander Library of Ornithology, and to Duncan Jackson for help with data collation. Many generous people gave their expertise, equipment and time to my GuilleMonitor project for which I am extremely grateful: Patrick Fairclough, Chris Rose, Chris Smith, Wendy Birtwistle, Ashley Cadby, Stuart Littlefair, Ros Green, Joanne Edgar and especially Nic Mullin.

Thank you to John Jackson, Carly Lynsdale, Joel Pick and Gavin Thomas for statistical advice. Thank you to Chris Cooney, Jonathan Green, Ben Hatchwell, Nicola Hemmings and Nyil Khwaja for your thoughtful and constructive feedback on chapter drafts, as well as being constant sources of encouragement, guidance and support. I would also like to thank past and present members of the TRB lab group and the Life History and Behaviour group for your advice, discussions and cheer, as well as the table tennis competitions, squash injuries and enthusiasm for cake.

Thank you to my wonderful friends and family, in Sheffield and beyond, for your support, encouragement and understanding. I am extremely fortunate that you are too many to name, but please know that I am tremendously thankful for your presence in my life.

Finally, thank you to Charlie, who introduced me to the joy of dogs.

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Statement of contributions

As well as supervision from Tim Birkhead, the research chapters (2-5) presented in this thesis have benefitted from collaboration with a number of colleagues, which are detailed here.

Chapters 2 and 3: These chapters use long-term data on a study population of common guillemots on Skomer Island, Wales, UK from 1997. Guillemots were monitored by Sherry Wilson (1997-2000), Tom Clarke (2001), Darrel Porter (2002, 2003), Katrina Fellerman (2004), Katherine Bradley (2005), Kat Munro (2006), Jess Meade (2007, 2011), Samantha Patrick (2008, 2009), Katherine Bowgen (2010), Tom Finch (2012), Jodie Crane (2013), Julie Riordan (2014, 2015), and Lorraine Chivers (2016).

Chapter 4: I conceived this study with Jonathan Green who, along with Duncan Jackson, helped to collect data from sources both online and at the Alexander Library of Ornithology, Oxford. Gavin Thomas and Chris Cooney advised on phylogenetic methods of analysis. This chapter is published in Behavioral Ecology, where all co-authors (Tim Birkhead and Jonathan Green) and 4 anonymous reviewers made comments that improved the manuscript.

Chapter 5: Patrick Fairclough designed the initial egg file for printing, Chris Rose and Chris J Smith altered the egg design for printing, and Wendy Birtwistle printed the artificial eggs. Ashley Cadby designed and built the first prototype GuilleMonitor, including all software coding. Nic Mullin improved the electronic design of the GuilleMonitor and built nine GuilleMonitors. Joanne Edgar demonstrated the method of measuring heart rates of broody hens using ECG monitors, and provided access to broody hens at University of Bristol Veterinary School. Henry Castle and Jamie Thompson helped with access to guillemot breeding sites, and Ros Green helped with access to razorbill breeding sites and placement of GuilleMonitors, on Skomer Island. Joel Pick provided data mining code, and Stuart Littlefair provided code and advice on signal estimation using ACF.

All other work in this thesis including all analyses was carried out by Elspeth Kenny.

Summary

Despite its many benefits, group living incurs significant costs for individuals; most notably increased competition for food and resources. Animals have evolved complex behaviours to cope with these competitive conditions, including forming social relationships with other group members. Social relationships consist of a series of predictable interactions, and may in part be built and maintained by affiliative behaviour such as social grooming (allogrooming). In birds, social grooming is performed using the bill to preen another bird's feathers, and is referred to as allopreening. In this thesis I investigate the role of allopreening in maintaining social relationships with group members and breeding partners.

To understand social interactions between group members it is vital to understand the composition and structure of the group, so first I use a long-term data set to describe the population structure of a colony of ringed common guillemots *Uria aalge*. I find that the social structure of this population is stable, although related birds are no more likely to associate with each other than unrelated birds, and that familiarity with neighbouring breeders over multiple breeding seasons is associated with higher breeding success in young and inexperienced breeders. I also find that guillemots that have been breeding at adjacent sites for 5 or more years allopreen each other significantly more than those that have been neighbours for fewer than 3 years, suggesting that allopreening with neighbouring conspecifics is associated with longer social relationships. Next, I test the hypothesis that species in which breeding pairs allopreen have a stronger pair bonds. Incorporating 503 species in a phylogenetic study, I demonstrate that species that allopreen within the breeding pair are more likely to contribute equally to offspring care, and are more likely to breed with the same individual in consecutive breeding seasons (less likely to divorce). Lastly, I develop and test a prototype heart rate monitor in an artificial egg to be used on group-living incubating birds in remote and difficult conditions. This novel prototype accurately measures heart rates in humans, but is not able to accurately measure heart rates in common guillemots, razorbills *Alca torda* or domestic chickens *Gallus gallus domesticus* via the brood patch, possibly due to the type of pulse sensor used.

My findings demonstrate that allopreening in birds plays a social role, and is involved in social relationships both within and between breeding pairs. This thesis highlights the importance of considering social relationships in non-primates.

Chapter 1

General introduction

Group living

Group living is common throughout the animal kingdom, and animal groups vary enormously in their size, permanence and composition. Animal aggregations range from unrelated individuals that have grouped together at random (e.g. some fish: Peuhkuri and Seppä 1998; Russell et al. 2004; Kolm et al. 2005), to exclusive nuclear families living in stable groups (e.g. some birds, Ekman et al. 1994; wolves *Canis lupus* Mech 1999). Groups also comprise complex mixtures of breeders and non-breeders (e.g. lions *Panthera leo*, Schaller 1972; gorillas *Gorilla gorilla*, Stewart and Harcourt 1987; some birds, Stacey and Koenig 1990), and vary in terms of sex ratios (e.g. elephants *Loxodonta africana*, Douglas-Hamilton 1972; spotted hyena *Crocuta crocuta*, Kruuk 1972; killer whales *Orcinus orca*, Ford et al. 2000) and relatedness between group members (e.g. birds: Clutton-Brock 2009; Hatchwell 2009).

Group living incurs costs and benefits for each individual (Alexander 1974). In order for sociality to be favoured by selection, the benefits must outweigh the costs. Advantages of sociality over solitary living include improved predator vigilance, mobbing and swamping behaviour, increased foraging efficiency and greater mating opportunities (Krause and Ruxton 2002). However, close proximity to, and daily interactions with, conspecifics within a group can be disadvantageous due to increased conspicuousness to predators (because a group of individuals can be more easily detected than a solitary individual) and competition (Alexander 1974). Competition for food, mates, territory and space can affect fitness directly, by preventing individuals from reproducing due to lack of a breeding site or mate, or indirectly by increasing aggressive interactions between individuals, which may be detrimental to health and survival (Alexander 1974). Additionally, the increased proximity to other individuals that comes with group living increases the risk of disease transmission and the chance of misdirected parental care through brood parasitism or cuckoldry (Alexander 1974).

Since selection acts to minimise the costs associated with group living and increase the fitness pay-off from social interactions, species have evolved specific behaviours. One such behaviour is to form social relationships (long-term bonds) with other group members. Social relationships are defined as a series of interactions between two individuals, and are described by the number and types of interactions (e.g. play, grooming), their quality (e.g. rough or gentle) and their temporal patterning (Hinde 1976). Such interactions are the basic elements of social structure, yet interactions are also *influenced by* social relationships, and therefore social structure. In other words, social relationships depend on the composition (e.g. age, sex ratio, relatedness) of the group, and vice versa (Hinde 1976). Long-term bonds may form between related individuals (through direct or indirect fitness) and between unrelated individuals (through direct reciprocity, or reciprocal altruism), and as such, knowing the composition of the group aids our understanding of the evolution of long-term relationships.

Cooperation theory

Cooperation is widespread in the animal kingdom, ranging from cooperative breeding (where individuals raise offspring that are not their own) (Cockburn 2006) to coalitionary aggression (where individuals intervene in fights, or multiple individuals attack a common conspecific target) (Smith et al. 2010; Bissonnette et al. 2015), food-sharing (Carter and Wilkinson 2013) and grooming another conspecific individual (allogrooming) (Schino and Aureli 2008a). Cooperative behaviour provides a benefit to another individual (recipient), and is selected for because of its beneficial effect on the recipient (West et al. 2007). Cooperative behaviour may be initially costly to the actor, in which case for cooperative behaviours to evolve they must yield a fitness benefit that outweighs this cost. The choice of partner in these cooperative interactions is generally non-random, and ultimate explanations for cooperative behaviour include kin selection (Hamilton 1964), reciprocity (Trivers 1971) and mutualism (West-Eberhard 1975). I discuss each of these mechanisms below.

Kin selection

Kin selection is the process that favours enhancing a close relative’s fitness because of shared genes (Hamilton 1964). Individuals will be selected to perform altruistic behaviours for the benefit of relatives when $rb>c$, where r is their genetic relatedness, b is the fitness benefit to the beneficiary and c is the fitness cost to the altruist. Altruistic behaviour is defined as costly to the actor and beneficial to the recipient, in terms of the lifetime direct fitness consequences. The altruist, or donor, gains indirect fitness by passing their genes on to the next generation through close relatives. Each individual act is advantageous to the actor in terms of inclusive fitness, and no reciprocation is required. For example, cooperative breeding typically occurs within populations where delayed or limited dispersal of young creates a population genetic structure in which relatives are physically close to one another, so by helping their parents to raise more offspring on the home territory, helpers (often failed breeders) can gain inclusive fitness (Emlen

1982; Preston et al. 2013). However, in some species cooperative interactions also occur between non-relatives, which cannot be explained by kin selection.

Reciprocity

Reciprocity, also known as reciprocal altruism, may explain cooperative interactions between non-relatives. Cooperative actions which are performed at a cost to the actor but confer a fitness benefit to the recipient can evolve because the donor will receive an equivalent fitness benefit in return at some point in the future. Reciprocity can be (a) direct (Trivers 1971), (b) indirect (Alexander 1987) or (c) generalised (Hamilton and Taborsky 2005).

a) Direct reciprocity

Direct reciprocity can be defined as an exchange of altruistic acts between the same two individuals such that in total both participants obtain a net fitness benefit (Trivers 1971). Here, an altruistic act is one in which the actor suffers a fitness cost in order for the recipient to gain a fitness benefit. The cost of the act to the donor is smaller than the benefit to the recipient, so if the act is returned then both participants gain. For example, cotton-top tamarin monkeys *Saguinus oedipus* give food to conspecifics who give food back (Hauser et al. 2003) and pairs of coral reef rabbitfishes (f. Siganidae) regularly alternate between positions of upright vigilance (which is costly) and foraging, which results in a balanced distribution of foraging activity and higher foraging efficiency compared to solitary individuals (Brandl and Bellwood 2015). Direct reciprocity evolves where individuals can reciprocate previous cooperative behaviour of their partners (Trivers 1971), and therefore requires either (1) individuals to be able to recognise their present partner and remember the outcome of their previous encounter with that specific partner (as appears to be the case for tamarin monkeys) or (2) individuals to interact with just one partner for a long time (Dugatkin 2002) (as is the case with rabbitfishes). Direct reciprocity therefore requires either specific cognitive capabilities of the interacting individuals (Milinski and Wedekind 1998) or a population structure in which individuals interact repeatedly with the same individual.

b) Indirect reciprocity

In contrast to direct reciprocity, indirect reciprocity is where return benefits come from a third observing individual, rather than from the direct recipient of the beneficial act (Nowak and Sigmund 1998a). As such, indirect reciprocity involves reputation and status: members of the group assess and ‘score’ other group members and discriminately direct their assistance to those with a higher score (Nowak and Sigmund 1998b; Nowak and Sigmund 2005; McNamara and Doodson 2015). In other words, a donor provides help if the recipient is likely to help others, generally if the recipient has helped others in the past, and can be thought of as "direct reciprocity occurring in the presence of interested audiences" (Alexander 1987). Evidence for indirect reciprocity is so far limited to humans, whereby in a cooperation game humans donated more frequently to receivers who had been generous to others in earlier interactions (Wedekind and Milinski 2000). The lack of evidence supporting indirect reciprocity in non-human animals may be due to the inherent cognitive complexity of recognising social partners and remembering their previous behaviour (Milinski and Wedekind 1998; Stevens and Hauser 2004).

c) Generalised reciprocity

Generalised reciprocity is where individuals who have experienced cooperation in the past will reciprocate by indiscriminately cooperating with the next individual they meet; decisions taken to cooperate are dependent on anonymous social experience. Unlike direct and indirect reciprocity, generalised reciprocity may be evolutionarily stable without individual recognition or spatial structure (Hamilton and Taborsky 2005). Cooperation can evolve and be maintained if individuals interact repeatedly in small groups and if individuals base their behaviour towards the present partner on the outcome of the last encounter they had, irrespective of the identity of the partner (Pfeiffer et al. 2005). For example, female rats *Rattus norvegicus* that were trained in an instrumental cooperative task (pulling a stick in order to produce food for an unknown conspecific but not for herself) pulled more often for an unknown conspecific after they were helped than if they had not received help before (Rutte and Taborsky 2007). Thus, generalised reciprocity does not depend on advanced cognitive skills such as partner recognition and memory of previous encounters, but instead relies only on the ability of an individual to judge the outcome of its most recent interaction.

With regards to the cognitive capacities required for these different types of cooperation to evolve and be maintained, indirect reciprocity requires the highest level of cognitive capacity as individuals are required to observe interactions between other individuals and base their behaviour on these observations. Direct reciprocity can evolve with sufficient cognitive capacity for recognising and remembering interactions with specific partners, but can also evolve without this cognitive ability, but with a population structure limiting interactions between few individuals over a long period of time. Generalised reciprocity requires considerably less information than direct reciprocity as the basis for future behaviour.

Mutual benefit

Mutual benefit differs from kin selection and reciprocity, because where kin selection and reciprocity involve behaviours that are costly to the actor and beneficial to the recipient (altruistic), mutualistic acts are beneficial to both the actor and the recipient (West et al. 2007). (This is not to be confused with mutualism, which is cooperation between species and will not be discussed here.) A typical example of mutually beneficial cooperation is synchronised mobbing of predators (e.g. Pettifor 1990; Graw and Manser 2007; Krams et al. 2009), or synchronised roaring of lions faced with intruders (Heinsohn and Packer 1995), whereby the cost of contributing to the group behaviour is cheap but the potential cost of predation or intrusion is large for all group members.

Mutually beneficial interactions between unrelated individuals can be explained using ‘biological market models’, where traders exchange commodities to their mutual benefit (Noë and Hammerstein 1995). The value of such a social relationship depends on the quality and abilities (referred to here as ‘individual value’) of the individuals participating in the exchange, or relationship. Characteristics such as sex, age, strength, skills, and experience, the likelihood of performing certain acts, and the influence of external factors can all affect the potential fitness gain for the interacting individuals (Kummer 1978). Since individuals vary in qualities (e.g. strength and experience), and there is a preference for partners offering the highest individual value, the exchange and value of commodities is a source of conflict and contests among the competitors may determine which individuals trade (Noë and Hammerstein 1995).

In summary, social behaviours may be classified into each category – altruism or mutual benefit – based on whether the behaviour immediately benefits the recipient only, or both the actor and the recipient (Hamilton 1964). It is important to note that the benefit or cost of a behaviour is defined by the lifetime consequences of the behaviour and the absolute fitness effect rather than short-term consequences i.e. whether the behaviour increases or decreases the number of offspring surviving to adulthood. However, measuring lifetime fitness can be very difficult, so specifying the classification of cooperative behaviours can be difficult. For example, a cooperative behaviour which is costly in the short-term but provides a benefit which outweighs the cost in the future would be classed as altruistic, unless the future benefit is measured and therefore the behaviour is found to be mutually beneficial. Even when we do not know whether a cooperative behaviour is altruistic or mutually beneficial, useful predictions can be made and tested.

Allogrooming and social relationships

Allogrooming, whereby individuals groom other group members, appears to be an altruistic behaviour because the groomer (actor) invests energy and time that could otherwise be spent on vigilance or feeding behaviour. As such, allogrooming is presumed to be costly to the groomer. The energetic cost of grooming has been calculated as 0.39 calories per minute for a 5 kg animal (Veà et al. 1999), yet Dunbar and Sharman (1984) argue that the small energetic cost of allogrooming is unlikely to impact on the groomer's reproductive success overall. Additionally, the groomer may gain some potential benefits, such as reduced tension (Keverne et al. 1989), which would further lower the cost of such interactions. Allogrooming captive macaque *Macaca mulatta* mothers reduced their rate of vigilance of their infants, who were more likely to be harassed by other group members; since the rate of surveillance of infants and the potential for rapid intervention is reduced during allogrooming, under natural conditions in the wild the reduced vigilance associated with allogrooming may expose an individual and its offspring to an increased risk of predation (Maestripieri 1993). Reduced vigilance during allogrooming was also observed in wild blue monkeys *Cercopithecus mitis stuhlmann* suggesting that grooming individuals were more at risk of being preyed upon than non-grooming individuals (Cords 1995). However, there is no direct evidence of increased predation during allogrooming interactions in primates, and it is possible that vigilance of the group as a whole remains at a sufficient level to minimise predation risk. Despite the lack of quantification of the ultimate costs of allogrooming, the assumption that allogrooming is costly to the groomer remains widespread.

In order to be evolutionarily stable, allogrooming is likely to benefit the groomer in some way, and more than make up for the time invested in grooming other group members. Primates spend up to 20% of their time allogrooming (Dunbar 1991), and this considerable time investment suggests that allogrooming plays an important role in fitness. As an affiliative interaction, allogrooming is thought to be the basis of social relationships. Social relationships are linked to increased survival and reproductive success in primates and other mammals (baboons *Papio cynocephalus*, Silk et al. 2003; Silk et al. 2009; Silk et al. 2010; Archie et al. 2014; macaques *Macaca assamensis* and *M. sylvanus*, Schülke et al. 2010; McFarland and Majolo 2013; horses *Equus ferus*, Cameron et al. 2009; dolphins *Tursiops* sp., Frère et al. 2010; Stanton and Mann 2012; rats *Rattus* sp., Yee et al. 2008; mice *Mus domesticus*, Weidt et al. 2008). However, allogrooming has no direct link to survival or reproduction, so *how* does allogrooming, and the associated social relationships, benefit individual fitness?

One way in which allogrooming could impact fitness is through maintaining hygiene by removing ectoparasites from the recipient. There is considerable evidence supporting a hygienic function of allogrooming: (1) allogrooming removes ectoparasites effectively from fur (Freeland 1981; Tanaka and Takefushi 1993; Zamma 2002), (2) allogrooming is targeted at areas of the body where the receiver cannot reach (Pérez and Veà 2000; Zamma 2002), and (3) allogrooming rates correlate with ectoparasite load (Sánchez-Villagra et al. 1998; Madden and Clutton-Brock 2009; Akinyi et al. 2013). Some researchers have suggested that removing ectoparasites by allogrooming and eating them is essentially insect-feeding behaviour, and therefore is an entirely selfish behaviour (Tanaka and Takefushi 1993). However, since there is little nutrition available from ectoparasites it is unlikely that allogrooming evolved for this reason. Removing ectoparasites from other group members could be altruistic because this reduces the risk of the recipient to disease, or could be considered selfish behaviour because this reduces the risk of ectoparasites being transmitted to the groomer. If allogrooming occurred purely for hygienic reasons, we may expect allogrooming interactions to occur between any group members, because removing ectoparasites from any individual would benefit the donor through reduced disease risk. However, allogrooming in long-tailed macaques was more often directed towards individuals which had previously donated grooming than non-grooming individuals (Majolo et al. 2012), suggesting that grooming was allocated according to past social interactions i.e. direct reciprocity. This reciprocity of allogrooming constitutes a social relationship, and indicates that allogrooming has value other than improving hygiene.

In primates, allogrooming is also reciprocally exchanged for other benefits (also referred to as interchange), including agonistic support (reviewed in Schino 2007; Schino et al. 2007; Berghänel et al. 2011; but see Silk et al. 2004), reduction of received aggression (Silk 1982), tolerance during feeding (Ventura et al. 2006; Tiddi et al. 2012), increased access to clumped, contestable resources (de Waal 1986; Kapsalis and Berman 1996), sex (Gumert 2007) and protection (Palombit et al. 1997; Cords 2002). Higher-ranking strong individuals can bestow better benefits on the donor compared to lower ranking weaker group members (Seyfarth 1977), so animals distribute their grooming among group members accordingly: primates tend to direct allogrooming up the hierarchy (Silk 1982; Schino 2001; Ventura et al. 2006; Tiddi et al. 2012). However, the exchange of benefits depends on the gradient of the dominance hierarchy i.e. the relative differences in strength, experience or resources available to each individual: individuals exchange grooming for grooming when the dominance gradient is shallow, and exchange grooming for rank-related benefits when the dominance gradient is steep (Barrett et al. 2002; Schino and Aureli 2008b). The exchange of benefits also depends on the ecology of the species or population. For example, groups of female capuchin monkeys *Cebus apella nigritus* are supported in fights by the alpha male of the group, so do not need to trade allogrooming for agonistic support with other females in the group; instead, female capuchin monkeys exchange allogrooming among themselves for tolerance at food sources (Tiddi et al. 2012). This interchange of allogrooming and other commodities can be understood by biological market theory (Noë and Hammerstein 1995) and constitutes a social relationship.

These allogrooming functions – maintaining hygiene and forming social relationships – are not mutually exclusive. Since natural selection does not operate on one specific behavioural strategy at a time, it is likely that these roles are evolutionarily linked. For example, the intrinsic rate of increase of lice populations on hosts means that hosts need to be groomed every day, so they need to find grooming partners for daily grooming (Zamma 2002). Since allogrooming is a costly, albeit low-cost, behaviour, the donor must be sufficiently likely to gain a benefit in return for this behaviour to be evolutionarily stable. Structural and physiological, rather than social, adaptations are more likely to have been initially selected for in order to control diseases brought about by ectoparasites (Alexander 1974; McKenna 1978). Dunbar (1991) takes this suggestion further, and argues that allogrooming seems to have been 'captured' by a different functional system during the course of primate evolution, and has been intensified so that primates spend much more time engaged in this activity than is required for purely hygienic reasons. Regardless of the evolutionary origin of allogrooming, it is clear that grooming exchanges and the associated social relationships are valuable to fitness in many social species.

I have discussed how allogrooming is reciprocated and exchanged for services or resources, and how these series of interactions constitute a social relationship which positively impacts fitness of participants. But what is the proximate mechanism by which allogrooming builds social relationships? In other words, how is allogrooming, an apparently low-cost behaviour, sufficiently valuable to be exchanged for goods and services that impact fitness?

The 'tension-reduction' hypothesis states that allogrooming (1) reduces tension and (2) restores integration of individuals into the group, resulting in increased group solidarity (Terry 1970). Recipients of grooming have reduced heart rates (Boccia et al. 1989; Feh and de Mazière 1993; Aureli et al. 1999; Madden and Clutton-Brock 2009), lower beta-endorpin levels (Keverne et al. 1989) and engage in less self-directed behaviour (a sign of anxiety) (Schino et al. 1988) compared to individuals receiving less grooming. Furthermore, Japanese macaques *Macaca fuscata* direct allogrooming towards individuals from whom they had received most aggression (Schino et al. 2005), and Indian langur monkeys *Presbytis entellus* engaged in allogrooming immediately following an aggressive interaction, indicating that allogrooming "enables an animal to manipulate a tense situation into a peaceful one" and restores the relationship (McKenna 1978). Indeed, allogrooming is thought to be the 'glue' that maintains social cohesion because time spent allogrooming increases with group size, up to a certain group size where the proportion of time spent allogrooming asymptotes (Dunbar 1991; Lehmann et al. 2007). As group size increases, the costs of group living increases as tensions rise, so individuals must alleviate the increased tension by forming social alliances in order to maintain the benefits of group living. Likewise, as group size increases, the number of available social partners increases, so individuals need to spend more time servicing social relationships (Dunbar 1991; Lehmann et al. 2007). Taken together, this evidence provides support for the tension-reduction hypothesis because (1) the physiological response to allogrooming is a reduction in stress, and (2) the behavioural response to allogrooming is improved group dynamics and better integration of individuals into the social group.

So how does the physical interaction and sensation of allogrooming reduce stress and help create cooperative relationships? Recent studies suggest that the hormone oxytocin is involved in creating and maintaining social relationships (Beery and Zucker 2010; Crockford et al. 2013; Romero et al. 2014). Physiologically, oxytocin acts in the brain to enhance social memory (Lim and Young 2006; Insel 2010; Soares et al. 2010), reduce anxiety and fear (reviewed in Churchland and Winkielman 2012) and activate neural reward circuits (Lim and Young 2006). Experimentally administered oxytocin increased both allogrooming rates (Carter and Wilkinson 2015) and cooperative behaviours (Dreu et al. 2010; Madden and Clutton-Brock 2011), indicating that oxytocin could explain the positive effects arising from social contact. In chimpanzees *Pan troglodytes* it appears that oxytocin is involved with long-term social relationships specifically, because higher urinary oxytocin concentrations were associated with grooming among long-term social partners compared to non-bonded conspecifics (Crockford et al. 2013). Neither the occurrence of grooming nor the presence of a social bond partner alone was sufficient to increase oxytocin levels, suggesting that grooming with a friend is more emotionally rewarding than engaging in the same behaviour with a less preferred partner. Other candidate hormones include vaopressin (Lim and Young 2006) testosterone (Hirschenhauser 2012) and endorphins (Keverne et al. 1989; Dunbar 2010), but regardless of the specific physiological mechanism, it is clear that long-term affiliative social relationships matter to the participants over and above the reduction of stress.

In summary, there has been considerable research into the proximate and ultimate functions of allogrooming in mammals, especially non-human primates. This taxonomic bias in research has arisen partially because the advanced cognitive abilities of primates was thought to be required for cooperative acts, such as allogrooming, and social relationships to occur (Brosnan et al. 2010).

However, more recently it has been suggested that complex cognition is not necessary for social relationships to occur (Pfeiffer et al. 2005), and consequently such social relationships may also exist in non-primate groups. For example, many bird species live in groups, and perform a similar affiliative behaviour to allogrooming in primates, triggering the assumption that social grooming in bird groups has the same effect as in primate groups: to form and maintain social bonds.

Allopreening in birds

Allopreening (also called allogrooming, social preening or mutual preening), whereby birds use their bill to run through another bird's feathers, is performed in a similar way to how birds preen their own plumage (autopreening, or self-preening). The energetic cost of preening is approximately twice the basal metabolic rate (reviewed in Goldstein 1988; loggerhead shrikes *Lanius ludovicianus,* Weathers et al. 1984*;* black ducks *Anas rubripes*, Wooley and Owen 1978; budgerigars *Melopsittacus undulates,* Buttemer et al. 1986); for the common guillemot, the metabolic rate of preening on water is ~18 W kg^{-1}, a 107% average increase from resting metabolic rate (Croll and McLaren 1993). Despite the variation in bill shapes across avian taxa, the movements involved in allopreening are remarkably similar: birds receiving allopreening erect their feathers in the preened area, tilt their heads away from the preener's bill (perhaps to facilitate the allopreening) and close or narrow their eyes, while the preener (allopreening donor) runs their bill through the feathers, perhaps appearing to search through the feathers with the bill, or nibble or pull at the bases of the feathers (Harrison 1965; Gaston 1977). Until Harrison's (1965) paper, allopreening received little attention, such that the full extent and distribution of allopreening was difficult to determine. Recently, allopreening has garnered more attention, and, similar to allogrooming in mammals, the potential roles of allopreening in maintaining both hygiene and social relationships are being investigated.

As in primates, one key proposed function of allopreening in birds is hygiene, specifically the removal of ectoparasites from feathers. Consistent with this hypothesis, the morphology of the bird bill is adapted to remove ectoparasites from the feathers (Clayton and Walter 2001; Clayton et al. 2005) and allopreening movements appear to be very similar to autopreening, which effectively removes ectoparasites (Clayton et al. 2010). Indeed, higher rates of allopreening are correlated with fewer ectoparasites in a range of species (Brooke 1985; Radford and Du Plessis 2006; Villa et al. 2016), providing support for the hygienic role of allopreening. Furthermore, allopreening mainly occurs on areas of the body that are inaccessible to autopreening such as the head and neck (Clayton et al. 2010). However, it is unlikely that hygiene is the only function of allopreening because many species do not allopreen, and may instead rely on scratching, water-bathing, dusting or feather toxins to combat ectoparasites in their head and neck area (Clayton et al. 2010). Preliminary evidence suggests that allopreening is more likely to occur in species forced to live in close proximity to their neighbours, due to high density nesting or spatially restricted environments, compared to species living in non-restricted environments (Harrison 1965). This correlation could be due to group-living species having more ectoparasites, because disease transmission increases with increasing population density (Alexander 1974; Møller et al. 2001), but it could also be due to some other factor associated with living in close proximity to conspecifics.

Allopreening also plays a social role in birds. Most allopreening occurs between breeding partners, where allopreening correlates with several aspects of the pair relationship: pairs of allopreening buff-breasted wrens *Cantorchilus leucotis* were less likely to divorce than pairs that did not allopreen (Gill 2012), and allopreening within pairs of captive cockatiels *Nymphicus hollandicus* and common guillemots *Uria aalge* correlated positively with coordination of offspring care (Spoon et al. 2006; Takahashi et al. 2017) and post-conflict reconciliation (Ikkatai et al. 2016). It is assumed that these associations between allopreening and pair bond strength are beneficial to the fitness of the participants, yet a direct association between within-pair allopreening and fitness have been shown in two species only: (1) cockatiels, in which pairs that allopreened at higher rates had higher breeding success, probably due to incubation coordination (Spoon et al. 2006), and (2) breeding pairs of common guillemots that allopreened at higher rates had higher average breeding success, possibly due to reduced aggression (Lewis et al. 2007). Despite this sparse evidence on few species, the notion that allopreening behaviour ‘strengthens the pair bond’ is widespread (e.g. Harrison and Harrison 1997; Dagg 2011; Mandal 2015).

In several species, allopreening also occurs outside the breeding pair bond, where, similar to allogrooming in groups of primates, allopreening may be exchanged for resources and services. In buff-breasted wrens, jackdaws *Corvus monedula* and rooks *Corvus frugilegus*, allopreening other group members is associated with sharing food (Emery et al. 2007; Gill 2012), and in jackdaws, rooks, ravens *Corvus corax* and green woodhoopoes *Phoeniculus purpureus* allopreening is associated with agonistic support (Emery et al. 2007; Radford 2011; Fraser and Bugnyar 2012). Preening is donated according to which individuals best can provide necessary benefits. For example, subordinate ravens are weaker and less experienced in fights so are more likely to require aid in fights than dominant individuals. As such, subordinate ravens donate more allopreening to dominant individuals, which were more likely to provide agonistic support to group members who donated preening than those that did not (Fraser and Bugnyar 2012). In contrast, green woodhoopoe groups engage in territorial fights with other groups, and the relatively larger group is more likely to win a territorial conflict than a smaller group (Radford and Du Plessis 2004). Consequently, dominant green woodhoopoes donate more allopreening to subordinate helpers than vice versa, especially in areas of high conflict, to persuade subordinates in the group to help protect the breeding territory (Radford 2011). Within family groups of buff-breasted wrens, allopreening between parents and offspring was proposed to be involved in persuasion of juvenile offspring to delay dispersal and partake in mobbing predators, building nests and defending territory (Gill 2012). Testing the direction of causation in each of the above studies is difficult, and as such these findings could be interpreted in the opposing direction: allopreening could be donated in response to offspring delaying dispersal and helping on the family territory. Nevertheless, these studies demonstrate clear correlations between allopreening and services that can be given by certain individuals only.

It is important to note that the possible social functions of allopreening are not necessarily mutually exclusive from a hygienic function of allopreening. Since birds cannot reach their own heads with their bill to remove parasites, some rely on neighbours and partners to remove parasites from this part of their body, and this physical interaction has downstream effects that are beneficial to the participants in another way. In one species, the green woodhoopoe, the hygienic and social functions of allopreening are observed separately and simultaneously, because, unusually, both the inaccessible (head and neck) and accessible (body) areas of the recipient are preened by other group members: allopreening directed at the head and neck area appeared to serve a hygienic function, because the frequency of allopreening was constant throughout the year, whereas allopreening directed to the body area appeared to serve a social function, because allopreening rates varied with season, group size and the relative rank of the participants (Radford and Du Plessis 2006).

Allopreening also appears to be linked with reduced aggression: a negative correlation between allopreening and aggression has been observed in common guillemots (Birkhead 1978a; Lewis et al. 2007), cockatiels (Spoon et al. 2006), jungle babblers *Turdoides striatus* (Gaston 1977) and monk parakeets *Myiopsitta monachus* (Hobson et al. 2015). Harrison (1965) suggested that allopreening prevents aggression, because the recipient of an aggressive attack offers their head for allopreening rather than moving away, and so the attack is replaced by allopreening. This preening invitation posture may be considered as an appeasement or submissive posture to be used when an individual cannot escape from an attack, so the recipient is able remain in the vicinity of the aggressor without aggression (Sparks 1964; Harrison 1965). Allopreening tends to be present in species which breed at restricted sites (such as a ledge, hole or nest platform) (Harrison 1965) which supports this idea that allopreening in an appeasement behaviour, yet allopreening may actually correlate with a third factor: close physical proximity with a conspecific increases the risk of transmission of ectoparasites, so these species may allopreen to maintain hygiene in these situations. Despite the ambiguity of the evolution of allopreening, the association between allopreening and reduced aggression appears to enable individuals to maintain social cohesion (in a breeding pair or group) in order to benefit from group/pair living.

In this thesis, my principal aim was to determine whether allopreening is involved with maintaining social relationships in groups of birds and within breeding pairs. I also aimed to discover whether allopreening was associated with reduced stress in birds.

Current study

Chapters 2 and 3 use data from a long-term study of common guillemots. Common guillemots show high site fidelity and live for up to three decades (Swann and Ramsay 1983; Hatchwell and Birkhead 1991; Harris et al. 1996; Kokko et al. 2004; Reynolds et al. 2011). This life history, combined with their typically high density breeding environments, provide the opportunity for guillemots to build long-term social relationships with neighbouring conspecifics. Additionally, guillemots allopreen both their breeding partners and neighbouring breeders, which creates the opportunity to study the role of allopreening in social relationships outside the pair bond. A long-term study of ringed common guillemots provides a unique opportunity to study the social structure of a guillemot colony, and to investigate individual differences in allopreening. Since each chapter is written to be published, relevant information on the study system and data collection is included in each chapter. However, below I give more general information on common guillemots and the field site.

The common guillemot Uria aalge

Common guillemots are long-lived colonial seabirds which breed between 76°N and 40°N on islands and coastal cliffs in the northern hemisphere. The birds breed on ledges on steep cliffs and on flat low-lying islands, without constructing a nest; the single pyriform egg is laid on bare rock and held in position against the brood patch between the feet. Guillemots generally incubate in direct physical contact with conspecifics where the average density on broad, flat rocky areas is 20 pairs per m^2 (Nettleship and Birkhead 1985), although densities may reach up to 70 pairs per m^2 (Birkhead 1993). During the breeding season, both sexes take turns to incubate the egg (approximately 32 days) and rear the chick (15-28 days) (Nettleship and Birkhead 1985). Once fledged, the father alone takes the chick to sea until the chick is independent at 10-12 weeks (Gaston and Jones 1998). Chicks return to their natal colony in their second year (Birkhead and Hudson 1977; Swann and Ramsay 1983; Hatchwell and Birkhead 1991) forming 'clubs' on the rocks nearby, and eventually begin to breed after their fourth year or later (Birkhead and Hudson 1977). Guillemots are sexually monomorphic and socially monogamous, and show a low frequency of extra-pair copulations (<10% of all copulations; Hatchwell 1988) and low extra-pair paternity (<8% Birkhead et al. 2001). Extra-pair copulations are associated with breeding density, such that forced extra-pair copulations are more frequent at high breeding densities compared to low breeding densities, demonstrating that extra-pair copulations tend to occur between neighbouring breeders rather than between strangers from different areas of the colony (Hatchwell 1988).

Field site

This study was undertaken on Skomer Island, Wales, UK (51^o 40′N, 05^o 15′W). Skomer Island is a volcanic rock island with an area of 2.92 km^2, generally tableland 60 m above sea level. The island was farmed until 1948, and is now covered with extensive areas of bracken, with bluebells and red campion giving way to thrift and sea campion on the coastal slopes. Skomer was permanently inhabited until 1950 and is now a popular tourist destination, although direct access to guillemot colonies is forbidden to the public. With no mammalian predators, Skomer Island is one of the most important seabird sites in southern Britain. The biggest predator of guillemots on Skomer Island is the greater black-backed gull *Larus marinus* (108 individuals on Skomer in 2016: Stubbings et al. 2016). The island and surrounding sea area is a National Nature Reserve, Special Protection Area, Site of Special Scientific Interest and a Marine Nature Reserve, and is managed by The Wildlife Trust of South and West Wales.

The number of guillemots breeding on Skomer Island has changed dramatically in the 20th century. The population declined after 1930 and reached its lowest levels in the early 1970s (Birkhead and Ashcroft 1975), before beginning to increase from 1980 at a rate of 5% per year (Meade et al. 2013). Current numbers (~24000 in 2015: Stubbings et al. 2016) remain well below the records present before 1930 (Birkhead 2016). Outside the breeding seasons guillemots from Skomer Island tend to move towards Brittany and the Bay of Biscay in August to November, although others remain in the Irish Sea (Mead 1974).

Thesis aims and outline

The main objectives of the study were to investigate: (1) the potential for development of social relationships outside the pair bond in a common guillemot colony, (2) the role of allopreening in forming or building social relationships both within and outside the breeding pair bond, and (3) to develop a method to test the proximate mechanism by which allopreening reduces stress.

I first describe the social structure of a common guillemot colony on Skomer Island, UK, and ask how social structure affects breeding success (Chapter 2). Due to the consistent social structure, I then investigate whether common guillemots use allopreening in forming social relationships outside of the pair bond (Chapter 3). To complement this, I ask whether allopreening within the pair bond is associated with strong pair relationships across bird species (Chapter 4). To test whether this association between allopreening and social bonds is linked with reduced stress, I develop and test a novel method for measuring stress in incubating birds (Chapter 5). Finally, in Chapter 6, I summarise my results and discuss their implications, and conclude by suggesting directions for further work.

Chapter 2

Social stability, familiarity and reproductive success in a common guillemot *Uria aalge* colony

The social organisation of a population is a crucial element of an individual's environment and can have important consequences for the ecology and behaviour of individuals. Common guillemots *Uria aalge* breed in dense colonies and frequently interact with adjacent breeders, yet little attention has focussed on the identity of these neighbouring conspecifics and how they may impact fitness. I explored site fidelity and natal philopatry of common guillemots using data on identifiable individuals present in a sub-colony on Skomer Island, Wales (UK) between 1997 and 2015, to assess the potential for familiarity and kinship between adjacent breeders. Breeders returned to the same site in consecutive seasons 90% of the time, and, conforming to the 'win-stay, lose-switch' model, failed breeders were more likely to move breeding site than successful breeders, demonstrating that productivity influences colony social structure. Furthermore, site fidelity resulted in stability of the social structure allowing familiarity to build between adjacent breeders, which in turn enhanced the likelihood of breeding success: young and inexperienced birds with familiar neighbours had higher fledging success than similar birds with unfamiliar neighbours. Natal philopatry measures suggested population genetic structure in the colony, which may have implications for the evolution of cooperative behaviours. Understanding social structure allows a deeper understanding of the adaptive value of social interactions between group members, and this study provides the basis for further enquiry into colony social behaviours.

Introduction

The social organisation of a population is a crucial element of an individual's environment and can have important consequences for the ecology and behaviour of individuals. For example, social structure can fundamentally affect the transmission of information (Couzin et al. 2005; Aplin et al. 2012) and diseases (Cross et al. 2004), as well as migration patterns (Guttal and Couzin 2010) and cooperative behaviour (Sih et al. 2009). Group structure can be determined by (or emerge from) individual traits such as personality, dominance, age, sex and morphology (e.g. Krause et al. 2007; Krause et al. 2009; Croft et al. 2008; Pike et al. 2008; Farine et al. 2012; Spiegel et al. 2017), or genetic relatedness and familiarity between group members (e.g. Barber and Ruxton 2000; Ross 2001; Holekamp et al. 2012). On the other hand, groups may be structured by extrinsic factors such as the quality of habitat patches (Willson 1974; Pulliam 1988; Rodewald and Yahner 2001). Indeed, several mechanisms may contribute to forming the structure of a population. Understanding how individuals are organised in a population can elucidate the adaptive significance of social interactions between individuals.

In territorial migratory species, familiarity with previous neighbours may reduce time and energy costs of re-establishing territory boundaries (Eason and Hannon 1994), and repeated encounters with the same individuals provide opportunities for reciprocity and the evolution of other cooperative behaviours (Trivers 1971). In birds, benefits of familiarity have been demonstrated through improved reproductive success in red-winged blackbirds *Agelaius phoeniceus* (Beletsky and Orians 1989, but see Weatherhead 1995) and great tits *Parus major* (Grabowska-Zhang et al. 2012). Alternatively, if a population is sub-divided into kin groups, social interactions may confer indirect fitness through kin selection (Hamilton 1964).

Group structure may be dynamic with respect to time and ecological context (Hobson et al. 2013). The ability to adjust the group member(s) with which an individual associates and interacts may be possible for only a limited time period. For example, individuals are less mobile during offspring rearing, especially during incubation in birds, so the ability to modify social associations is restricted. Social interactions affect fitness (Silk et al. 2003; Silk 2007a; Cameron et al. 2009) so it would be beneficial to individual fitness to breed next to individuals with whom interactions will be positive. In colonial species, opportunities to move between neighbouring breeders may be further constrained by limited space. Such changes may also be avoided because their destabilising effect on social structure reduces breeding success (Ebensperger et al. 2016). These constraints confer a strong selective pressure on choosing an optimal breeding site next to suitable conspecifics within the population.

Common guillemots *Uria aalge* (hereafter, 'guillemots') breed more densely than any other bird, typically at densities of 20 pairs per square metre, but up to as high as 70, often in direct physical contact with breeding conspecifics (Birkhead 1977; Birkhead 1993). This close proximity provides continuous opportunities to interact with adjacent birds throughout the breeding season, yet little attention has focussed on the identity of these neighbouring conspecifics. This is especially surprising for two reasons. First, as typical seabirds, guillemots show high site fidelity (Swann and Ramsay 1983; Harris, Wanless and Barton 1996; Kokko et al. 2004) and may breed for several decades (Hatchwell and Birkhead 1991; Reynolds et al. 2011), thereby providing the opportunity to develop long-term associations with familiar neighbours. Second, neighbouring conspecifics influence reproductive success positively through predator protection, timing of breeding and alloparenting, and negatively through aggressive interactions (Birkhead 1977; Tschanz 1979; Birkhead and Nettleship 1984; Hatchwell 1991; Ashbrook et al. 2008). Combined, these characteristics suggest that colony social structure may play a considerable role in reproductive success of guillemots. However, studies assessing productivity in guillemots have so far focused on the physical characteristics of breeding sites and density of individuals (Birkhead 1977; Birkhead 1978a; Birkhead et al. 1985; Harris et al. 1997; Kokko et al. 2004), while the identity and stability of the social environment is yet to be investigated.

The aim of this study was to identify fundamental characteristics of a guillemot colony in order to test hypotheses about social interactions between breeders. First, I investigated the stability of the arrangement of individuals within the colony by measuring site fidelity. Second, I investigated factors influencing return rates (including age, breeding experience and productivity) to understand the causes of colony social structure. I expected to find high site fidelity in the population, and support for the 'win-stay, lose-switch' model, which states that successful breeders are more likely than failed breeders to return to the same breeding site in the consecutive year (Switzer 1993). Third, I used site fidelity measures to document familiarity between neighbouring breeders, and tested the impact of familiarity with neighbouring breeders on breeding success. I expected birds with familiar neighbours to have higher breeding success than birds without familiar neighbours. Finally, I investigated the potential for kin structure in the population by measuring natal philopatry. I found my predictions to be supported: reproductive success was positively associated with familiarity with neighbouring breeders, and guillemot colonies have a degree of population genetic structure. I discuss the impact of these findings for social behaviour in guillemots.

Methods

Study site

A sample of breeding adult guillemots and chicks at sub-colonies on Skomer Island, Wales, has been ringed annually since 1985. The metal British Trust for Ornithology (BTO) ring and a unique colour ring combination, or more recently a coloured identity (Darvic) ring, allow individuals to be identified using a telescope from a distance of 100 m in good conditions. Standard protocols were used to collect information on the breeding behaviour of identifiable birds each year (Birkhead and Nettleship 1980). Careful searches for ringed birds present on the island occurred daily. Data on timing of breeding, productivity, identity of partners and breeding location for individual ringed birds were collected. Guillemots lay a single-egg clutch, but if the first egg is lost early in the season a replacement egg may be laid (Gaston and Jones 1998). Breeding was considered successful if the chick disappeared after 16 days, as guillemot chicks develop sufficient plumage to survive at sea (continuously immersed in water) by 15 days old (Mahoney and Threlfall 1981). I did not differentiate between first and replacement eggs. Birds were recorded as breeding partners if they were observed bill-arring, allopreening extensively with each other on multiple occasions or swapping incubation duties of an egg (Birkhead 1978a). Sex was established by observing copulations, and in some cases, from blood samples, although a few birds could not be classified.

The age of birds ringed as chicks was defined as the number of calendar years after ringing: a chick hatched in 1998 and found breeding in 2007 was described as being 9 years old. This method of aging is the same as that used on the Isle of May (Harris et al. 1994). Most birds were ringed as adults, therefore their age at capture was estimated to be the average age of first breeding. Lindner (2000) found most guillemots on Skomer attempted to breed at six years old, so breeding adults were assumed to be seven years old in the year subsequent to ringing. These minimum estimates of age have been shown to provide a suitable proxy for age because the use of this proxy did not create any bias nor did it greatly reduce the power of tests (Crespin et al. 2006).

One guillemot colony on the south side of Skomer Island, known as the Amos, has been particularly closely monitored between 1997 and 2015, and is the subject for this study. Henceforth, I define the Amos as a ‘colony’, and the island as a ‘population’. Breeding sites of colour-ringed guillemots were recorded on large digital photographs of the Amos each year: the breeding site (~25 x 25 cm) is defined as the specific location on the cliff where birds lay and incubate the egg, and care for the chick. These photographs reveal the identity of ringed pair members at each breeding site in each year, allowing measures of site fidelity, natal philopatry and neighbour identities to be calculated.

Locations of breeding sites were recorded by a different observer each year. To minimise the impact of observer error in recording breeding site locations, the breeding sites used in this study were near obvious physical markers, such as boulders or walls, and breeding sites on open ledges were not used. The total sample size comprises 797 observations (‘bird years’) from 138 birds (53 female, 65 male, 20 unsexed individuals). Breeding site information was inadequate in 2012: few breeding sites had been recorded on the photograph despite recordings of ring sightings and breeding successes. It appeared that many birds from the previous year were present, but since their breeding sites were not marked, this year was excluded from analyses. Consequently, for analyses requiring data between consecutive years, data between 2011 and 2012, and 2012 and 2013, were excluded. This is unlikely to bias my results because even without these data, the dataset consists of information over 15 years. Breeding outcome was unavailable for some birds in some years so sample sizes vary between analyses. Non-breeding birds were not included in the analyses.

Social stability: site fidelity

Using plotted breeding locations, I determined whether an individual had returned to the same breeding site as the previous year, or had moved to another site. In each case where a bird had not returned to the same site as the previous year, I determined whether the bird had moved to the adjacent site, elsewhere on the ledge, elsewhere in the colony, or had left the colony (either to another colony within the island population, or to another population) (figure 2.1). Exhaustive searches occurred at other colonies on Skomer, so if the bird was breeding elsewhere in the island population it is highly likely to have been recorded. However, if the bird was breeding in a different population (i.e. if the bird was not breeding on Skomer Island), we would not know whether it was dead or breeding elsewhere, because such close monitoring does not happen at other nearby colonies. We therefore assumed that if a bird was not seen in the Skomer population for one year before being seen again, it was assumed to have left the population for that year before returning.

To investigate influences on site fidelity, I tested whether sex, age, or breeding experience predicted the likelihood of returning to the same site using generalised linear mixed effects models (GLMMs) in the *lme4* package of R (R Core Team 2013; Bates et al. 2015). Site fidelity was the binary response variable (1 = returned to the same breeding site as the previous year, 0 = returned to different breeding site from the previous year) so binomial distributions were used. Predictor variables included breeding outcome in the previous year (0 = did not fledge chick, 1 = fledged chick), number of previous breeding attempts (number of years an egg was seen), number of previous successful breeding attempts (number of years a chick was raised to at least 15 days), age (years since ringing) and sex. Age was correlated with number of successful breeding attempts (r = 0.8) and number of previous breeding attempts (r = 0.9), and the latter two variables were also correlated with each other (r = 0.9), consistent with the interpretation that as individuals get older, they have more breeding experience. Due to these high correlations, these variables were reduced to one component by principal component analysis with a varimax rotation using the *psych* package of R (Revelle 2011). The component(s) retained for further analysis were those with eigenvalues greater than one (Jackson 1993). Bird identity was included as a random effect to account for multiple observations of birds throughout the years. To test the hypothesis that the relationship between return rate and breeding outcome in the previous year differed with age or breeding experience an interaction term was included. The maximal model was simplified to include only significant terms (to form the minimal adequate model) using backwards stepwise deletion based on the Akaike's Information Criterion (AIC), deleting terms with the lowest χ^2 if it produced a model with a significantly lower AIC value. Likelihood ratio tests were used to compare models with and without the term or interaction of interest. Type III Wald chi-square tests ('Anova' function, car library) were used to obtain probabilities and p-values (Bolker et al. 2009), and the estimates (β) ± estimated standard error of fixed factors are presented for each term: for nonsignificant terms, these were calculated from the maximal model, whereas for significant terms, these were calculated from the minimum adequate model. Marginal and conditional coefficients of determination were estimated using the r.squaredGLMM function in package MuMIn (Nakagawa and Schielzeth 2013).

Social stability: neighbour retention

To explore the potential for building long-term associations with neighbours, I generated an overall summary statistic. I first calculated the number of consecutive breeding seasons for which individuals retained the same neighbour. I define 'neighbour' as an adjacent breeder, breeding sufficiently close to be involved in physical interactions (such as allopreening; figure 2.1a, b). Birds breeding at adjacent plotted breeding sites on the digital photographs were assumed to be neighbours i.e. close enough to physically interact. I compared the identity of each focal bird's neighbours with the identity of its neighbours in the consecutive year using plotted breeding sites. Next, I calculated the expected probability of a breeding adult guillemot retaining the same *n* neighbours between consecutive years using site fidelity probabilities calculated in the previous section. I could not calculate the observed number of neighbours each focal bird had in each year because only ringed birds were plotted at breeding sites, so the 'observed' number of neighbours of each focal bird would likely be underestimated. Instead, to calculate the expected number of neighbours each guillemot retained in consecutive breeding seasons I used the following model:

$$R(n) = p^n$$

Where R is the probability of n number of birds breeding at adjacent sites in two consecutive breeding seasons; p is the probability of a bird returning to the same site as the previous year; n is the potential number of neighbours. For example, the expected probability of three birds remaining neighbours in consecutive years would be calculated as p^3.

Impact of neighbour retention

To investigate the impact of familiarity with neighbours on breeding outcome, I tested whether breeding next to the same neighbour in consecutive years predicted fledging success using GLMMs in the *lme4* package of R (R Core Team 2013; Bates et al. 2015). Breeding outcome was the binary response variable (0 = did not fledge chick, 1 = fledged chick), so binomial distributions were used. Predictor variables included familiarity with direct neighbours (unfamiliar = first year breeding at adjacent breeding sites, familiar = second or more year breeding at adjacent sites), and I took into account the number of previous breeding attempts, number of previous successful breeding attempts and age of each member of the dyad. Again, to account for the high correlation, these variables were reduced to one component by principal component analysis with a varimax rotation using the *psych* package of R (Revelle 2011). I define 'dyad' as two neighbours i.e. adjacent birds breeding in sufficiently close proximity to be involved in physical interactions (e.g. allopreening) from their respective breeding sites. An interaction term was included to test the hypothesis that the relationship between breeding success and neighbour familiarity differed with age or breeding experience. Bird identity and neighbour dyad identity were included as random effects to account for multiple observations of birds throughout the years, and birds being involved in multiple dyads. The maximal model was simplified to include only significant terms using backwards stepwise deletion based on the Akaike's Information Criterion (AIC), deleting terms with the lowest χ^2 if it produced a model with a significantly lower AIC value. Likelihood ratio tests were used to compare models with and without the term or interaction of interest. Type III Wald chi-square tests ('Anova' function, car library) were used to obtain probabilities and p-values (Bolker et al. 2009), and the estimates (β) ± estimated standard error of fixed factors are presented for each term.

Social identity: natal philopatry to estimate relatedness of neighbours

To assess the potential for neighbours to be related, I measured natal philopatry in the Amos colony. I use the term natal philopatry when birds return to breed in the same area where the individual was ringed. I use the term emigrant for a bird recorded breeding anywhere outside its natal area. The Amos is divided into 13 areas, five of which are easily accessible to ring birds, so I used information from these areas since these had the highest number of chicks ringed (figure 2.2). This non-random selection of areas for my sample could bias my results if some areas contained more or less optimal breeding sites. Potential recruits could be more attracted to those areas with better quality breeding sites. Furthermore, the number of breeding pairs dispersed over a series of slopes and ledges in each group varied between 300 and 50 pairs, so the areas may differ in the potential for growth and hence recruitment. The size of the group may affect measures of natal philopatry, yet logistical problems inherent with working on cliffs prevented rigorous standardisation of group size. However, post-hoc tests revealed that natal philopatry did not differ between the five areas ($\chi^2 = 1.36$, df = 5, p = 0.9) despite the potential differences in ‘attractiveness’ to recruits, or prospects for growth and hence recruitment.

Each season, daily searches were made throughout the Amos colony using a telescope to find any birds that were breeding, so it is unlikely that ringed birds went undetected. Regular searches were also made at other colonies on Skomer Island, so if a bird was breeding at another colony on the island it is likely to have been recorded. However, birds that bred away from Skomer Island will not have been recorded, so the degree of natal philopatry will be overestimated if there was movement to other populations. A chi-square test was used to compare the number of chicks which returned to breed in their natal area on the Amos with the number of chicks which later bred outside their natal area (emigrants seen breeding in other areas of the Amos colony or elsewhere in the island population). To assess the potential for kin structure in the colony, I calculated the probability of guillemot chicks later breeding within the same area (figure 2.2) as a parent using the measurement of natal philopatry in the following model:

$$P = a^6 c$$

Where P is the probability of a chick breeding within the same area as a parent; a is the probability of an adult breeder returning to the same area in the colony until their chick reaches breeding age (6 years on Skomer; Lindner 2000); and c is the probability of a chick returning to breed in the same area as it fledged. I also calculated the probability of siblings breeding in the same area using c^2.

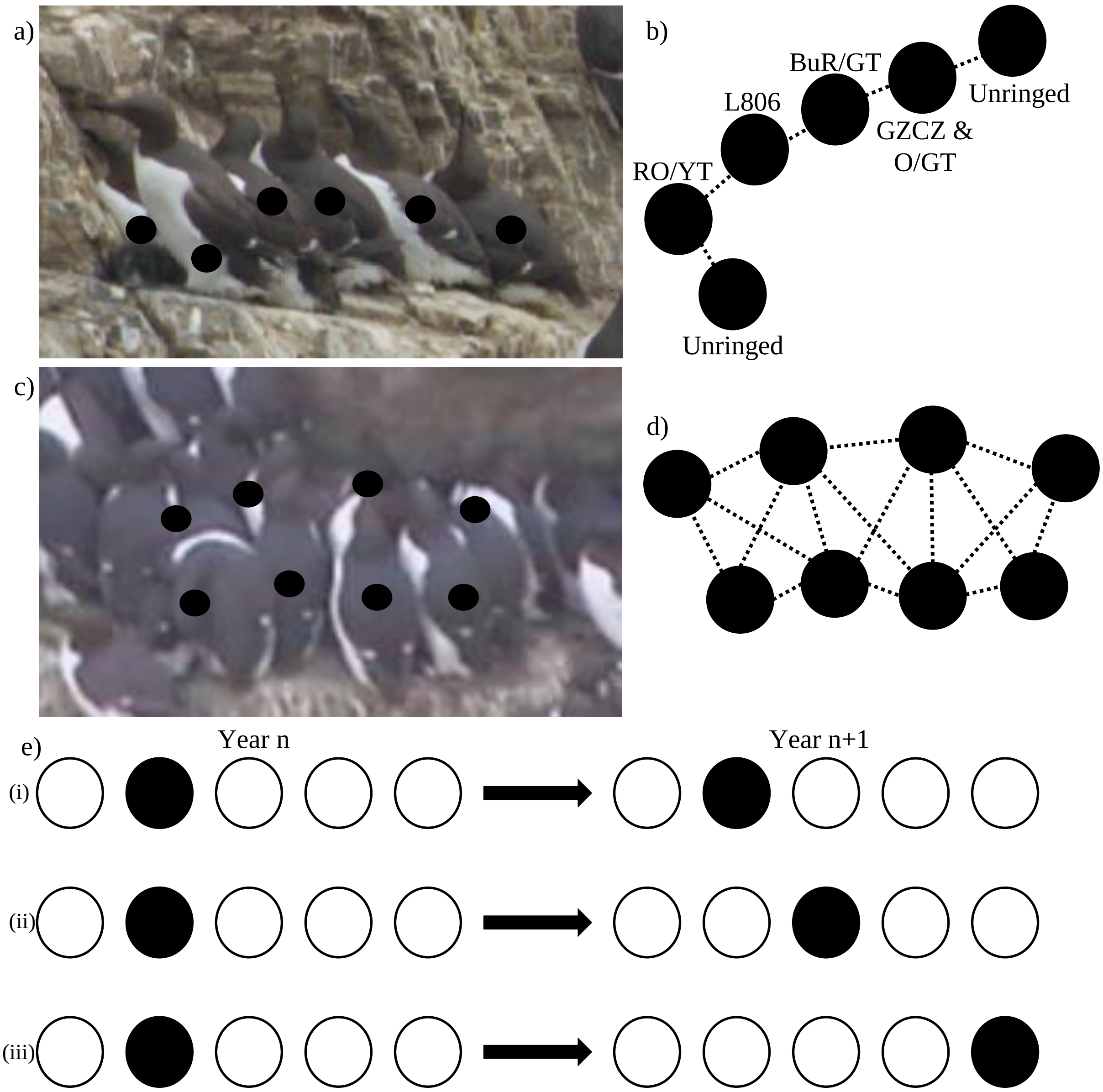


Figure 2.1. (a) Common guillemots *Uria aalge* breeding on a ledge on the Amos, Skomer Island, UK in 2014. Black circles show breeding sites as marked by field researchers each year between 1997 and 2016. One pair member is present at each breeding site in this photograph. Birds breeding at adjacent breeding sites are defined as ‘neighbours’, able to physically interact without moving from incubating the egg; (b) Breeding sites of (a) as viewed from above with identities of each pair member breeding at each breeding site in 2014. Dashed lines represent potential interactions between neighbours; (c) Same as (a), except both members of the pair are present at some breeding sites in this photograph; (d) Breeding sites of (c) as viewed from above. Dashed lines represent potential interactions between neighbours; (e) Schematic diagram of measuring site fidelity, where potential breeding sites are shown as open circles and the presence of a ringed individual is shown as a filled circle. (i) The individual returns to the same breeding site in the following year; (ii) the individual moves to the adjacent site in the following year, and; (iii) the individual moves to a different breeding site on the same ledge.

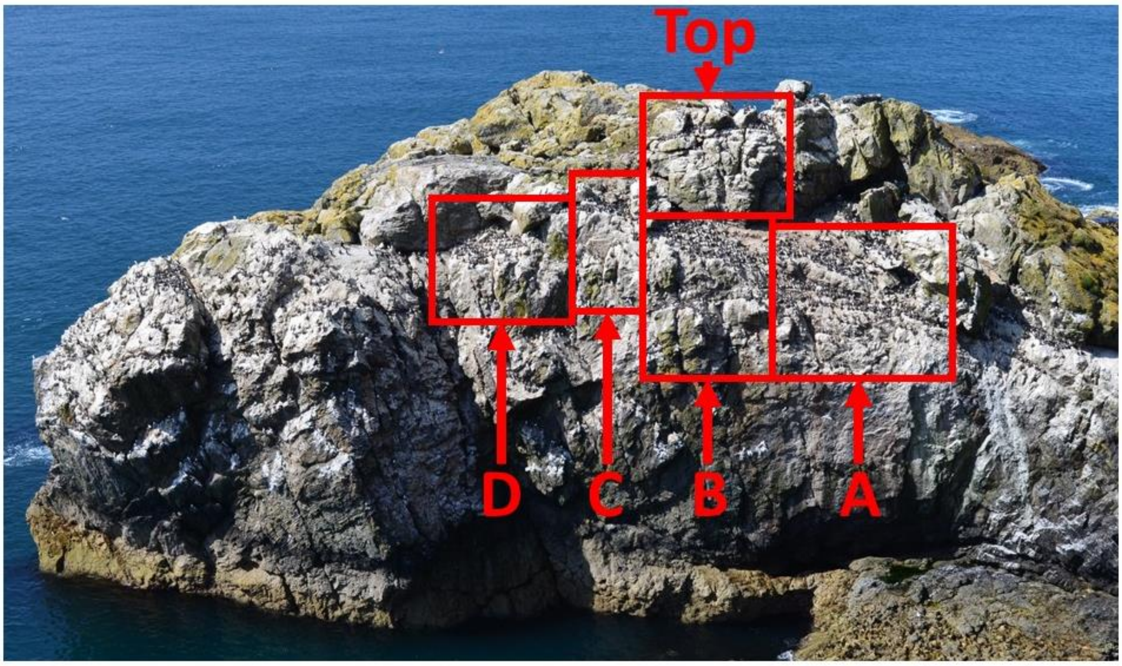


Figure 2.2. The Amos, showing the five areas (A, B, C, D, and Top) which are relatively easily accessible to ring common guillemot chicks, and were used to measure natal philopatry.

Results

The dataset consists of 778 breeding attempts (678 successful) between 1997 and 2015 (excluding 2012), giving an average breeding success (the proportion of pairs rearing a chick to fledging) of 87.1% (76.2% to 97.4% p.a.; table 2.1).

Social stability: site fidelity

Birds returned to breed at the same or adjacent site on 90.8% of occasions, and return rates varied between years (table 2.1). Of the birds that appeared to return to an adjacent breeding site, 26 moved once, 15 moved twice, five birds moved three times, and one bird moved four times. Of the birds that moved breeding site within the same ledge, 12 moved once and five moved twice, and of the birds that moved between different areas within the colony, 19 moved once and four birds moved twice. Eight birds moved away from the colony and returned to the colony the next year: four were seen at other colonies in the Skomer Island population, and four were presumably at other populations.

To investigate whether rates of return were affected by breeding experiences and/or age, the correlations between these variables needed to be taken into account using principal component analyses. The final PCA analysis with three variables of breeding experience and time yielded a one-component solution that explained 91% of the variation in the subset. In principal component one, age, previous number of breeding attempts and previous number of successful breeding attempts loaded positively (table 2.2), such that older individuals had a higher number of both breeding attempts and successful previous breeding attempts and younger individuals had a lower number of both breeding attempts and successful breeding attempts.

Breeding outcome was significantly associated with the likelihood of a bird changing breeding site ($n = 538$ observations of 107 birds, $\beta = 1.68 \pm 0.41$, $\chi^2 = 16.96$, $p < 0.001$, marginal $r^2 = 0.13$, conditional $r^2 = 0.30$): birds that had successfully fledged a chick in the previous year were significantly more likely to return to the same breeding site the following year, whereas failed breeders were more likely to move to a different breeding site in the following year (figure 2.3). Variables associated with PC1 also significantly affected return rates ($\beta = 0.49 \pm 0.23$, $\chi^2 = 4.48$, $p = 0.03$): older and more experienced birds were more likely to return to the same breeding site, whereas younger less experienced birds were more likely to change breeding site in the following year (figure 2.4). The likelihood of changing breeding site was not significantly associated with the interaction between breeding success in the previous year and PC1 ($\beta = -0.37 \pm 0.47$, $\chi^2 = 0.65$, $p = 0.4$) or sex ($\beta = 0.028 \pm 0.43$, $\chi^2 = 0.0042$, $p = 0.9$).

Table 2.1. Movements of 135 adult common guillemots on Skomer Island between 1997 and 2015 and proportion of successful breeding attempts. Breeding site occupancy data in 2012 were insufficient, so movements between 2011 and 2013 are unknown.

			Movement between years					
Year	Total birds in sample	Returned to same breeding site (%)	Moved to adjacent breeding site	Moved to breeding site on the same ledge	Moved to different ledge in the colony	Did not return to the colony	Returned to the colony from elsewhere	Breeding success (in later year)
1997-1998	43	38 (88.4)	3	0	2	0	0	0.76
1998-1999	41	35 (85.4)	4	0	2	0	0	0.78
1999-2000	36	33 (91.7)	1	0	2	0	0	0.84
2000-2001	37	36 (97.3)	0	0	1	0	0	0.88
2001-2002	37	27 (73.0)	2	2	4	2	0	0.91
2002-2003	35	31 (88.6)	0	1	0	2	1	0.94
2003-2004	37	23 (62.2)	5	3	2	0	4	0.90
2004-2005	42	30 (71.4)	7	2	1	2	0	0.91
2005-2006	63	54 (85.7)	5	0	2	0	2	0.83
2006-2007	58	40 (69.0)	14	2	2	0	0	0.80
2007-2008	54	47 (87.0)	5	1	0	1	0	0.97
2008-2009	53	42 (79.2)	9	0	1	0	1	0.93
2009-2010	54	38 (70.4)	9	1	4	1	1	0.78
2010-2011	50	41 (82.0)	2	4	2	1	0	0.97
2013-2014	60	47 (78.3)	7	4	2	0	0	0.88
2014-2015	58	51 (88.0)	2	2	0	0	3	0.86
Total	758	613	75	22	27	9	12	
Percentage	100	80.9	9.9	2.9	3.6	1.2	1.6	0.87

Table 2.2. Standardised loadings from a principal component analysis of three correlated non-independent variables of age and breeding experience (n = 538).

Factor	Standardised Loading: PC1
Age	0.94
Previous successful breeding attempts	0.94
Previous breeding attempts	0.98
Eigenvalue	2.73
Proportion of variation	0.91

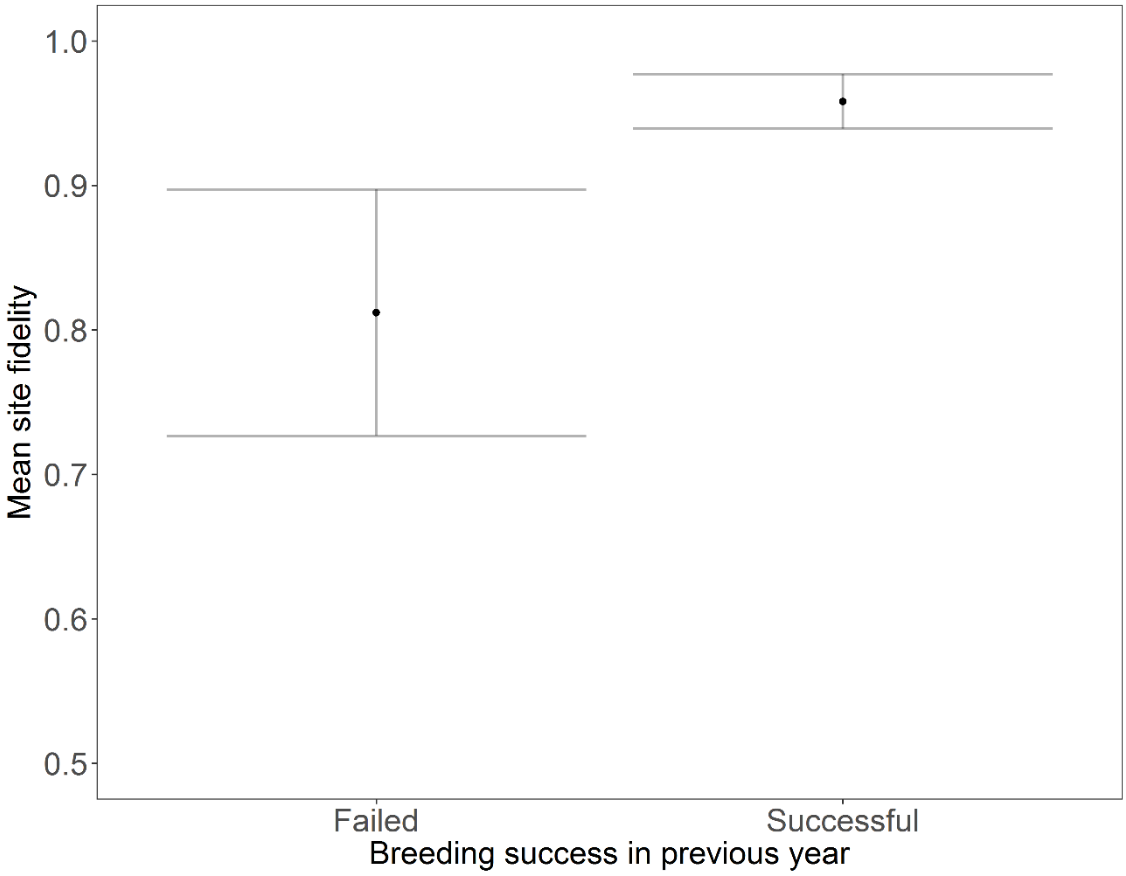


Figure 2.3. Relationship between breeding site fidelity in adult common guillemots and breeding outcome in the previous year (n = 538). Points show mean site fidelity (0 = moved to different breeding site, 1 = returned to same breeding site), lines show 95% confidence intervals.

Social stability: neighbour retention

The median duration of neighbour relationships was 3 years, and the mean neighbour duration was 4.1 ± 3.5 years (figure 2.5). Since guillemots returned to their breeding site or the adjacent site, where they would still interact with the same individuals, 90.8% of the time, I calculated that there was a 82% probability of two birds being neighbouring breeders in consecutive years (0.9077^2), 75% probability of three birds remaining neighbours in consecutive years (0.9077^3), 68% probability of four birds remaining neighbours in consecutive years (0.9077^4), and 62% probability of five birds remaining neighbours in consecutive years (0.9077^5).

Impact of neighbour retention

To investigate whether productivity was affected by familiarity with direct neighbours, while taking into account breeding experiences and age, the correlations between these variables needed to be taken into account using principal component analyses. The final PCA analysis yielded a one-component solution that explained 95% of the variation in the subset. In principal component one, age, previous number of breeding attempts and previous number of successful breeding attempts loaded positively (table 2.3), such that older individuals had a higher number of both breeding attempts and successful breeding attempts and younger individuals had a lower number of both breeding attempts and successful breeding attempts.

The effect of age and experience on breeding outcome differed between birds with and without familiar neighbours (n = 444 breeding attempts by 65 individuals in 92 dyads, $\beta = -1.17 \pm 0.49$, $\chi^2 = 6.83$, df = 1, $p = 0.01$, marginal $r^2 = 0.01$, conditional $r^2 = 0.06$, figure 2.6). Age and experience predicted breeding success for birds with unfamiliar neighbours, but had less of an effect when neighbours were familiar. For birds breeding next to each other for the first time, older and more experienced birds had higher breeding success than younger, less experienced birds. However, for birds breeding next to each other for the second or more time, age and experience did not affect breeding success. However, the proportion of variance explained by these fixed effects was small, which should be taken into consideration when interpreting these results.

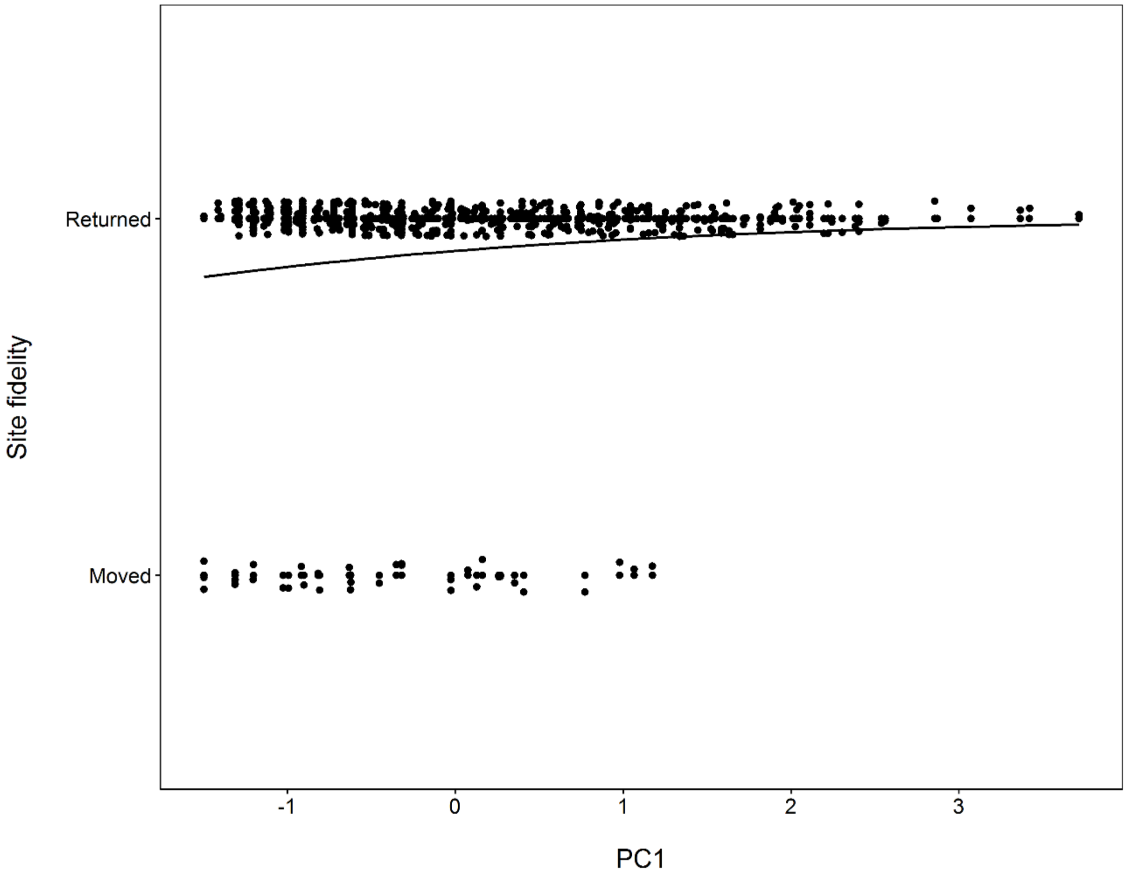


Figure 2.4. Relationship between breeding site fidelity in adult common guillemots and principal component 1, which represents age and breeding experience (n = 538). Points show site fidelity (moved to different breeding site/returned to same breeding site). Curved line shows model prediction.

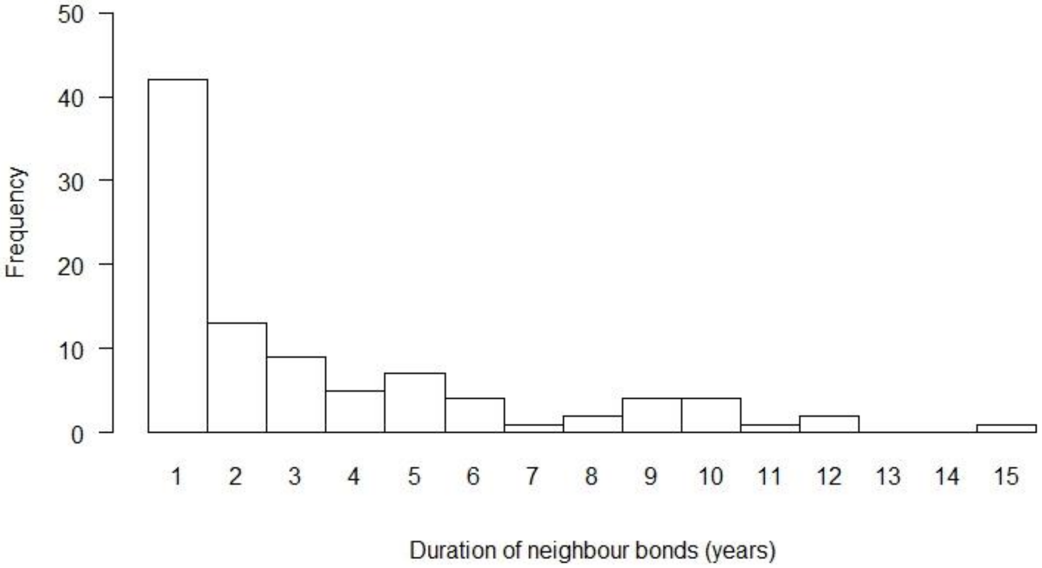


Figure 2.5. Distribution of the final duration of neighbour bonds from 1997 to 2015 (n = 95 pairs).

Table 2.3. Standardised loadings from a principal component analysis of three correlated non-independent variables of age and breeding experience (n = 444).

Factor	Standardised Loading: PC1
Age	0.96
Previous breeding attempts	0.98
Previous successful breeding attempts	0.97
Eigenvalue	2.84
Proportion of variation	0.95

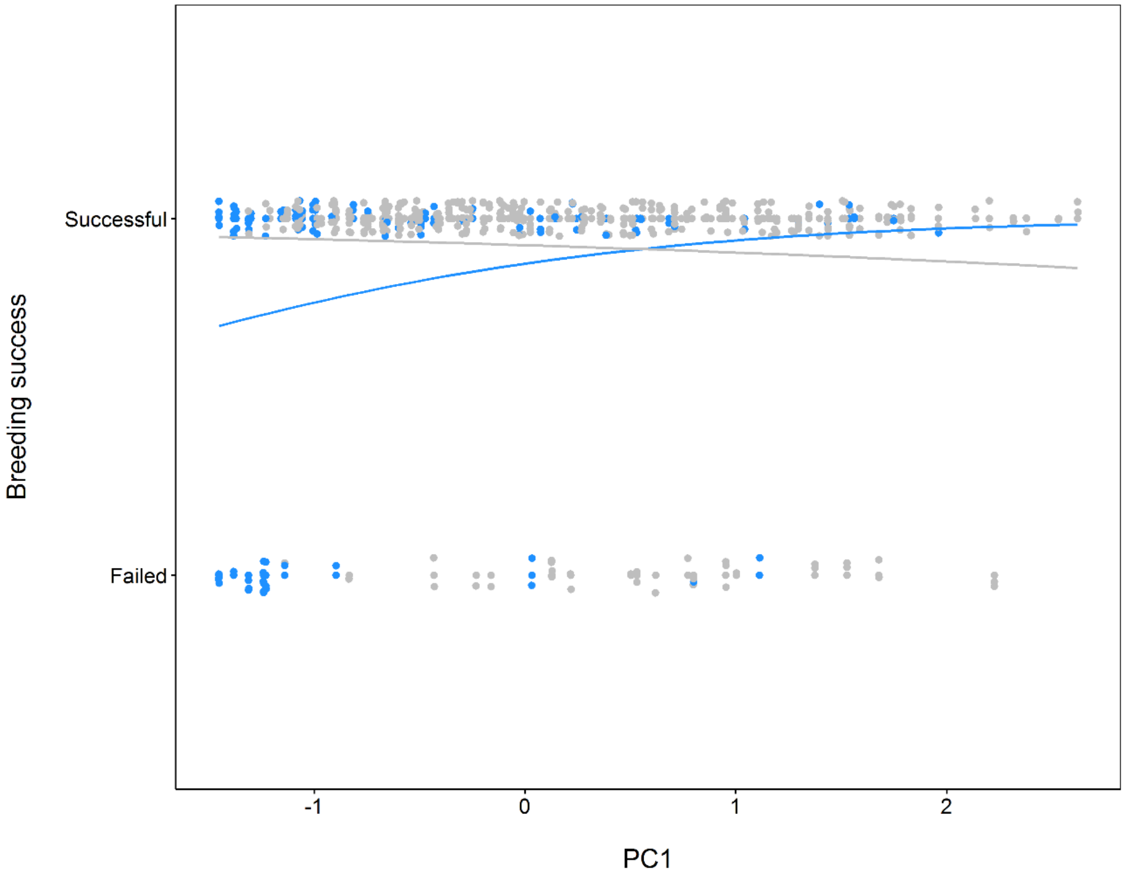


Figure 2.6. Relationship between breeding success and principal component 1 (age and breeding experience) for guillemots with an unfamiliar neighbour (1 year together = blue) and with a familiar neighbour from the previous year (2 or more years together = grey). Points are jittered to show breeding success. Curved lines show model predictions.

Social identity: natal philopatry to estimate relatedness of neighbours

Between 1985 and 2016, 2303 chicks were ringed on Skomer, of which 964 (41.9%) were later recorded breeding. In the Amos colony, 744 chicks (231 male, 226 female, 287 unsexed) were ringed and were later seen breeding, of which 729 (98%) bred on the Amos. Of the ringed chicks that were later seen breeding, 54% were seen breeding in the same area where they were ringed as a chick (table 2.4). Natal philopatry did not differ between sexes: 50% of males and 52% of females returned to breed at their natal group (χ^2 = 0.039, df = 1, p = 0.84; table 2.5).

Using observed values of natal philopatry, I calculated that there was a 30% probability that a chick would breed in the same area at the same time as one of their parents, and a 29% probability that two siblings would breed in the same area at the same time as each other, if the chicks survived to breeding age. Since the probability of a chick returning to its natal population was 98%, and there are 13 possible areas on the Amos to return to, the expected likelihood of a chick returning to breed at the same colony in the same areas as its sibling would be 0.075 (0.98/13) assuming random dispersal within the natal colony. The observed proportion of 0.29 is significantly greater than this (χ^2 = 12.6, df = 1, p = 0.003) suggesting that new recruits into the breeding population chose to breed in the same area where they hatched more often than expected by chance.

Table 2.4. Number of common guillemot chicks ringed in five areas of the Amos on Skomer Island which survived to breeding age, and were seen breeding in the same area where they were ringed.

	Chicks ringed which were later seen breeding:		
Area on the Amos	on Skomer	on the Amos (proportion)	in the same area where ringed as a chick
A	184	182 (0.99)	103 (0.57)
B	27	27 (1.00)	14 (0.52)
C	6	6 (1.00)	1 (0.17)
D	35	34 (0.97)	17 (0.50)
Top	6	5 (0.83)	3 (0.60)
Total	258	254 (0.98)	138 (0.54)

Table 2.5. Number of female and male common guillemot chicks ringed in five areas of the Amos on Skomer Island that survived to breeding age, and were seen breeding in the same area where they were ringed.

Area on the Amos	Female chicks ringed which were later seen breeding:		Male chicks ringed which were later seen breeding:	
	on Skomer	in the same area where ringed as a chick (proportion)	on Skomer	in the same area where ringed as a chick (proportion)
A	51	24 (0.47)	41	21 (0.51)
B	6	4 (0.67)	6	2 (0.33)
C	0	0 (NA)	1	1 (1.00)
D	7	4 (0.57)	6	3 (0.50)
Top	2	2 (1.00)	2	1 (0.50)
Total	66	34 (0.52)	56	28 (0.50)

Discussion

In this study, I have shown that common guillemots on Skomer Island exhibit high site fidelity which allows neighbouring breeders to become familiar with one another over consecutive breeding attempts. A key finding is that familiarity influences breeding success when age and breeding experience are taken into account: age and breeding experience predict breeding success for birds that are unfamiliar with neighbouring conspecifics, but not for birds with familiar neighbours. I also showed, using measures of natal philopatry, that neighbours were unlikely to be related but intra-colony relatedness was likely to be higher than inter-colony relatedness. I will first discuss the factors influencing colony social stability and the implications of such long-term associations, before discussing the consequences of the population genetic structure.

Social stability

My results showed that guillemots on Skomer Island had very high level of breeding site retention (90.8%). This figure is similar to colonies on Isle of May (85.7%), Isle of Canna (99%), Baltic islands (100%), Aberdeenshire (88%) and Skomer in previous years (95%) (Southern et al. 1965; Birkhead 1977; Hedgren 1980; Swann and Ramsay 1983; Harris, Wanless, et al. 1996; Kokko et al. 2004). I found that site fidelity of guillemots on Skomer was related to breeding outcome in the previous year, as well as age and breeding experience. Most pairs (86.7%) of guillemots breeding on Skomer Island reared a chick each year, and the relatively few birds that were unsuccessful tended to be the birds that changed sites. PCA analysis showed that older and more experienced birds were more likely to return to the same site than younger less experienced birds. This is to be expected, since older birds with more breeding experience are also likely to have bred successfully in the previous year (Crespin et al. 2006; Harris et al. 2016).

The ‘win-stay, lose-switch’ model states that, in predictable habitats, individuals should return to the same site if they successfully reproduce, and leave sites after a failed breeding attempt (Switzer 1993). Results in the current study on Skomer Island, as well as studies on the Baltic Sea and Isle of May, support this model (Hedgren 1980; Harris, Wanless, et al. 1996) suggesting that guillemots use their own reproductive performance to assess the quality of the habitat. The physical breeding habitat is highly predictable on Skomer, in as much that rock falls are rare, so supports the proposition that this method of habitat assessment occurs in stable habitats. However, a failed breeding attempt is not sufficient to motivate a site change, nor is it a prerequisite for moving, because some birds did not move site after a failed breeding attempt and others moved after successfully fledging a chick. These exceptions suggest that additional factors play a role in site retention decisions. An individual's choice of nest site may be influenced by multiple factors (Schmidt 2014), and the relative contribution of each factor may vary between individuals. Guillemots responded to both their own breeding performance and the physical site characteristics when abandoning sites on the Isle of May (Kokko et al. 2004), and other species making settling decisions use conspecific presence and/or breeding success to assess their own chances of breeding successfully in a given patch (Danchin et al. 1998; Doligez et al. 1999; Brown et al. 2000; Serrano et al. 2004; Boulinier et al. 2008; reviewed in Valone and Templeton 2002). This use of 'public information' is predicted to occur especially in species like guillemots with high nesting density, high survival and open nests in predictable environments (Doligez et al. 2002; Doligez et al. 2003). In group-living species, particularly colonial birds where the social environment is likely to affect fitness, the social environment should also be taken into consideration when deciding to abandon a site (except in extreme cases where the physical environment has become completely unsuitable). Thus, in a long-lived species, it may be maladaptive to abandon a site after one failed breeding attempt if the physical site, neighbours or partner were of sufficient quality. In such sites, chance events causing failure are more likely to impact new breeders because it is their only experience at that site, whereas established breeders will already have experienced success at those sites. Furthermore, any age effect on breeding success would exacerbate this effect of experience.

Since guillemots were highly likely to return to the same site, retaining the same neighbours in consecutive breeding seasons was also highly likely. Returning to the same site maintains the social environment, whereas abandoning a breeding site inherently changes social relationships with neighbouring breeders. Stable social structure allows for familiarity to build up, which in turn influences breeding success. Breeding success in guillemots increases with age (up to a point, before decreasing again in a quadratic trend) and breeding experience (Crespin et al. 2006; Harris et al. 2016). However, I found that while this trend is maintained for unfamiliar birds, breeding success does not increase with age or breeding experience for familiar birds. It is possible that familiarity with neighbours improves the likelihood of successful breeding such that the 'maximum' breeding success is reached more quickly for familiar compared to unfamiliar birds. This idea is supported by our model (figure 2.6) suggesting that young or inexperienced birds breeding next to a familiar neighbour had a higher likelihood of breeding successfully compared to young inexperienced birds with an unfamiliar neighbour. Once the 'optimum' breeding success is reached (i.e. when the age and breeding experience means that the individual has the maximum likelihood to breed successfully) familiarity may no longer have such an effect on breeding outcome. Any effect of familiarity on breeding outcome appears only via the interaction with age and breeding experience, and even so, the proportion of variance in breeding success explained by this interaction is small. Nevertheless, my results suggest that familiarity with a neighbour benefits breeding success for young or inexperienced guillemots.

Familiarity could benefit reproductive success in guillemots in several ways, by reducing negative interactions and/or increasing beneficial interactions. I will first consider the potential role of familiarity in reducing aggressive behaviour, followed by the potential role of familiarity in beneficial behaviours.

Guillemots are highly territorial, and territory defence is costly: renegotiating the boundary with an unfamiliar newcomer is likely to incur more cost than defending the territory against an established neighbour (Eason and Hannon 1994). This distinction between ‘neighbours’ (familiar individuals) and ‘strangers’ (unfamiliar individuals) underlies the ‘dear enemy phenomenon’ (Fisher 1954), where individuals react less aggressively to known neighbours compared to unknown or distant territorial individuals because they know the competitive abilities of familiar individuals (Briefer et al. 2008; Brunton et al. 2008; Rosell et al. 2008). When the outcome of a contest can be reliably predicted from previous encounters i.e. with familiar neighbours, then the resident will expend less energy on escalating territorial contests. A review of studies on the ‘dear enemy’ phenomenon suggested that for colonial nesters defending a site, owners should respond more aggressively to neighbours than strangers when nearest nest distances are small because neighbours are a greater threat to eggs and chicks (Temeles 1994). However, this is not the case for guillemots, where the relative threat from strangers is greater than the threat from neighbours: a resident could lose their territory to either a neighbour or a stranger, but neighbours bring benefits such as predator protection or alloparenting, and maintain the breeding density crucial for breeding success. Guillemots appear to be an exception to the typical pattern of the ‘dear enemy phenomenon’, because they show higher tolerance to neighbours than strangers (pers. obs.) despite the very small nearest nest distance between breeding guillemots, probably because neighbours pose a lower threat than strangers. Minimising aggression may improve guillemot reproductive success directly, by reducing the risk of an egg being knocked from the ledge during a fight (Birkhead 1978a; Lewis et al. 2007), and indirectly, by avoiding injury and reducing energy expenditure.

Familiarity may also bring fitness benefits through behaviours other than reduced aggression. For example, great tits *Parus major* familiar with neighbours had higher breeding success due to the increased likelihood of reciprocity in mobbing behaviour to deter predators successfully (Grabowska-Zhang et al. 2012). This benefit of predator-deterrence could be relevant to guillemots, which rely on neighbours to help prevent predation by directing their beaks towards avian predators such as gulls or corvids to create a dense protective barrier (Birkhead 1977; Birkhead 1978a). However, since individuals performing predator protection behaviours benefit from such behaviours themselves, it is unlikely that familiarity with neighbours affects participation in anti-predator beahviours. Another way neighbouring guillemots contribute to reducing predation risk is through reproductive synchrony, where greater synchrony helps to swamp predators thereby increasing chances of individuals breeding successfully (Hatchwell 1991). It is possible that familiar neighbours can predict timing of laying more reliably using shared previous experiences, yet there is no evidence of this, and other factors such as the environment and breeding experience are likely to have a far greater contribution to the timing of laying compared to familiarity with neighbours. Guillemots also occasionally alloparent nearby chicks (Tschanz 1979; Birkhead and Nettleship 1984; Wanless and Harris 1985), which may be more likely for familiar neighbours. Since guillemots are highly likely to interact in the future, guillemot social relationships satisfy conditions for direct reciprocity to operate (Trivers 1971; St-Pierre et al. 2009), so familiar neighbours may be more likely to alloparent neighbouring chicks compared to less familiar neighbours because they have had the opportunity to build a social relationship through a series of positive interactions. However, since neighbours can change between breeding seasons, individual recognition and memory of previous interactions would be required for guillemots to build such social relationships. Further research is required to decipher whether neighbouring guillemots can recognise individuals, remember interactions with specific individuals, build social relationships, and whether positive behaviours are exchanged reciprocally.

I measured familiarity as having a neighbour from the previous year, versus having a new neighbour. This measure does not take the number of neighbours into account, nor the number of years birds had been neighbours. The benefits of familiarity may increase with time neighbours have known each other, up to a point, but due to a small sample size and little variation in breeding success I was unable to investigate this. Also, I had information on ringed breeding birds only so I could not know the accurate number of neighbours of each individual. The density and laying times of neighbouring conspecifics influences breeding success through predator protection (Birkhead 1977; Hatchwell 1991), suggesting that the number of neighbours may impact participation in cooperative behaviours, so this would be interesting to take into account. Nevertheless, the measure used captures sufficient information on familiarity to understand its effect on breeding success.

I showed that young inexperienced birds benefit from retaining neighbours but also that these birds were more likely to change breeding sites. Thus, presumably they would avoid changing breeding site if possible to avoid breeding next to unfamiliar neighbours, which would be detrimental to their reproductive success. However, moving site may not be solely a consequence of the individual's decision: a bird may 'decide' to return to the same breeding site, but if it is a desirable site then they may be usurped by another bird, or they could be rejected by their neighbours. The difference between 'initiating' site change and being a 'victim' of site change impacts whether site change is adaptive in guillemots: voluntary site changes increased breeding success, whereas birds forced to move site had lower breeding success after a site change (Kokko et al. 2004). In this way neighbours not only affect breeding success through familiarity and the consequent moderations in behaviours, but also may impact site settlement through rejection or usurpation.

Population genetic structure

My results confirm earlier suggestions that natal philopatry in common guillemots is high (Swann and Ramsay 1983; Nettleship and Birkhead 1985; Halley et al. 1995; Harris, Halley, et al. 1996). Our finding that 47% of chicks returned to their natal area is certainly an overestimate because, although birds which recruited to the focal study areas were very unlikely to be missed, some birds breeding elsewhere may have been overlooked: it is much more difficult to find marked individuals that emigrate from the natal colony than those which are philopatric. Although inter-colony movement is difficult to quantify accurately, previous studies have shown that young guillemots may settle and start breeding away from their natal colony (Halley and Harris 1993; Lyngs 1993; Harris, Halley, et al. 1996). Natal philopatry rates in guillemots on Skomer are comparable to those in other Alcidae species including razorbills *Alca torca* and Atlantic puffins *Fratercula arctica* measured across multiple populations (Breton et al. 2006; Lavers et al. 2007). To obtain an unbiased measure of natal philopatry it would be necessary to search any colonies within a large radius of the study colony with the same intensity of search in each colony as that used in the study colony (1500 km radius estimated by Coulson and Coulson 2008). Such un-biased, large-scale searches have not been achieved in any major study attempting to quantify the extent of philopatry in seabirds, so reported estimates of the degree of philopatry are likely to be excessively high. Nevertheless, I found that, of the birds that returned to the colony, approximately three times more than expected returned to their natal area. This result, while perhaps missing a reliable estimate of the proportion of birds returning (like other studies), does not suffer from the same uncertainty from missing emigrants, and demonstrates that that there is spatial structure to dispersal decisions in guillemots.

Social structure

Alternative methods employed to measure relatedness in guillemot colonies have suggested they may be sub-divided into kin groups. The bridled morph and egg colours of the common guillemot are heritable (Jefferies and Parslow 1976; Nettleship and Birkhead 1985) and spatially clumped in several common guillemot colonies (Birkhead et al. 1980; Gaston and Nettleship 1981; Birkhead 1985), and molecular analysis of allozymes and mitochondrial DNA indicated that Brünnich's guillemots *Uria lomvia* breeding on separate ledges within a colony in Norway comprised of extended family groups (mean coefficient of relationship of ~0.10; Friesen et al. 1996). However, similar genetic analyses of Atlantic colonies of Brünnich's guillemots found genetic homogeneity (Birt-Friesen et al. 1992). This incongruity is likely due to differing rates of immigration in the populations (Friesen et al. 1996), so levels of genetic structuring are likely to vary between colonies due to varying immigration rates. Certainly, genetic analyses would be a useful method to measure accurately relatedness between individuals, but would be extremely difficult to accomplish due to the terrain of guillemot breeding habitats.

Despite the likely overestimations of natal philopatry, this study demonstrates that a considerable proportion of guillemot chicks return to the area of their hatching. Consequently, within-colony relatedness is likely to be higher than between-colony relatedness and the colony is likely to have a degree of population genetic structure. However, it is unlikely that neighbours are related. I showed that there is a 22% chance that siblings will breed in the same area as one another, yet this probability is likely to be considerably lower when we take into account (1) the large capacity of breeding sites available in some study areas, and (2) the low survival rate of chicks. Thus, the probability of an individual having a relative as a neighbour is vanishingly small. This lends further support to the hypothesis that cooperative social behaviours observed in guillemots function through reciprocity or mutual benefit rather than kin selection, and would be an interesting avenue for further research.

I have demonstrated that reproductive success is associated with site fidelity and therefore social stability of the colony, and also that familiarity with neighbours through colony social stability is important for reproductive success for young and inexperienced birds. Since familiarity and reproductive success influence each other there is the potential for positive feedback. The data set represents a relatively short window in guillemot biology, yet my results demonstrate that familiarity on a short timescale can impact fitness. Further investigation on a longer timescale could shed light on the sustainability of populations. My results also suggest a degree of population genetic structure in this guillemot colony. I suggest that since individuals are unlikely to interact with first-order relatives, cooperating in predator protection, alloparenting and other cooperative behaviours are likely to function through reciprocity or mutualistic benefits enabled by the social stability of the colony. Even though I studied only one colony of guillemots, these insights are likely to be widely applicable to other colonies. My results refer to a colony that was increasing (5% per year; Meade et al. 2013) but similar levels of site fidelity were found in a slowly declining population (Isle of May; Harris, Wanless, et al. 1996). It would be interesting to know the extent of site fidelity in a colony that was rapidly increasing or rapidly declining: presumably the factors influencing which birds obtain sites would be very different because the availability and quality of available sites would be altered which would impact the competition involved in obtaining and retaining territory. This study enables the opportunity to investigate how guillemots interact with conspecifics as a function of familiarity.

Chapter 3

Familiarity facilitates extra-pair allopreening between common guillemots *Uria aalge*

Social grooming is widespread across animal taxa, and patterns of social grooming can reflect the strength of relationships between individuals. Social relationships between group members, and their positive contribution to fitness, have been studied extensively in mammals, but the role of social grooming in building relationships between group members in birds is less well understood. By comparing rates of allopreening behaviour between familiar and unfamiliar individuals and examining the reciprocity of this affiliative interaction, I investigated whether common guillemots on Skomer Island, Wales (UK) build social relationships outside the pair bond. To improve our understanding of allopreening outside the pair bond I also examined whether allopreening differed with age, sex, density of individuals and stage of the breeding season. I found that allopreening rates were significantly higher between familiar neighbouring guillemots compared to unfamiliar neighbours, and reciprocation of allopreening was significantly more likely between familiar neighbours. Allopreening rates were higher when breeding partners were absent compared to when partners were present, but did not differ with age, sex, number of neighbours or stage of season. Selective allocation of allopreening to specific individuals, and apparent reciprocity of this affiliative interaction, provide evidence that guillemots build social relationships outside of the breeding pair bond. These findings demonstrate that social behaviour within colonies is more complex than a chance arrangement of breeding pairs, and contribute to the growing understanding of the evolution of social living.

Introduction

Allogrooming, or social grooming, is widespread across animal taxa. This interaction, where an individual grooms another individual, is most common between conspecifics, particularly partners or group members. Such affiliative behaviour reflects the strength of social relationships, so measuring patterns of allogrooming is useful for quantifying the strength of relationships between individuals (Hinde 1979; 1983). Although one function of allogrooming is to maintain hygiene and remove ectoparasites from the recipient (Hart et al. 1992; Tanaka and Takefushi 1993), allogrooming also has functions which provide benefits to the participants in ways other than reducing parasite load: allogrooming in mammals is exchanged for anti-predator mobbing behaviour, agonistic support, conciliation and social tolerance (Henzi and Barrett 1999; Schino 2007; Fraser et al. 2008; Cameron et al. 2009; Kern and Radford 2016). These exchanges, and the associated increase in reproductive success and survival, suggest that allogrooming and the social relationships built from these affiliative interactions are valuable to the participants (Dunbar 1991; Silk et al. 2003; Silk 2007b; Silk et al. 2009; McFarland and Majolo 2013). Studying the patterns of allogrooming interactions has been instrumental in increasing understanding of the social lives of mammals (Smuts 1987; Seyfarth and Cheney 2012).

The social role of the physically equivalent behaviour in birds, allopreening, is less well understood. Allopreening maintains hygiene through effective removal of ectoparasites (Brooke 1985; Clayton et al. 2005; Villa et al. 2016), and has simultaneous social functions (Radford and Du Plessis 2006). Allopreening is most commonly observed between breeding partners, where it is associated with maintaining the pair relationship, contributions to and coordination of offspring care, and post-conflict reconciliation (Spoon et al. 2006; Gill 2012; Ikkatai et al. 2016; Kenny et al. 2017; Takahashi et al. 2017). In some species, allopreening also occurs outside the pair bond between conspecific group members, where these interactions are preferentially allocated to specific individuals depending on the resources available for exchange (Emery et al. 2007; Radford 2008; Radford 2011). As in primates, this affiliative interaction may reflect the strength of a relationship between individuals within the group, yet the specific role of allopreening in building social relationships outside the pair bond has so far been considered in few species (e.g. green woodhoopoes *Phoeniculus purpureus* Radford and Du Plessis 2006; ravens *Corvus corax* Fraser and Bugnyar 2010; rooks *Corvus frugilegus* Emery et al. 2007).

Common guillemots *Uria aalge* are colonial seabirds which typically breed in direct physical contact with neighbouring breeders, which they allopreen, although they do not breed in family groups (Chapter 2), nor breed cooperatively. Neighbouring breeders are likely to be the same between consecutive breeding attempts, because guillemots show high site fidelity and high adult survival (Swann and Ramsay 1983; Hatchwell and Birkhead 1991; Harris et al. 1996; Kokko et al. 2004; Reynolds et al. 2011; Chapter 2). This consistency in the social breeding environment provides the opportunity for neighbouring breeders to build social relationships, which may be facilitated by allopreening interactions. Building relationships may have fitness benefits because neighbouring breeders can positively influence survival of offspring: survivorship of young can be increased through neighbour cooperation in anti-predatory behaviours, synchronous breeding and protection of non-related young (Birkhead and Nettleship 1984; Hatchwell 1991; Ashbrook et al. 2008). Conversely, neighbouring breeders can negatively impact offspring survival through aggressive interactions, which increase the risk of an egg or chick being knocked from the breeding ledge (Birkhead 1977; Lewis et al. 2007). This means that allopreening between neighbouring conspecifics has the potential for mutualistic social functions. Previous work has found that familiarity (Chapter 2) and allopreening (Lewis et al. 2007) between neighbouring common guillemot breeders is positively associated with breeding outcome. These correlations suggest that allopreening may be involved in building and maintaining social relationships outside of the pair-bond. Considering the potential fitness benefits for building social relationships with neighbouring breeders, it is surprising that allopreening interactions in these seabirds have rarely been detailed.

The aim of this study was to understand the role of allopreening interactions between neighbouring breeders (i.e. outside the pair-bond) in common guillemots. First, I aimed to create a profile of allopreening behaviour between neighbouring conspecifics by asking the following questions. (1) Do allopreening rates differ between male and female neighbours? (2) Do allopreening rates differ between guillemots of different ages? (3) Does breeding density affect allopreening between neighbours? (4) Is allopreening preferentially allocated to breeding partners or neighbours? (5) Does allopreening vary between pre-incubation, incubation and chick-rearing stages of the breeding season? Next, I tested the hypothesis that allopreening is involved with social relationships between neighbouring breeders, by comparing allopreening interactions between unfamiliar and familiar neighbours, and measuring reciprocity of allopreening between neighbours. I predicted that if allopreening is associated with relationships, then neighbours which were more familiar would allopreen more, as a higher frequency of affiliative interactions signifies a strong relationship, and allopreening interactions would be directly reciprocated. I measured allopreening interactions between neighbouring guillemots, and found evidence supporting the social function of allopreening in guillemots.

Methods

Study site

A sub-colony of common guillemots on Skomer Island, Wales, known as the Amos, has been closely monitored between 1997 and 2015. A sample of breeding adult guillemots and chicks was ringed with a unique colour ring combination or a coloured identity (Darvic) ring, enabling these individuals to be identified using a telescope from a distance of <100 m in good conditions. Standard protocols were used to collect information on the breeding behaviour of identifiable birds each year. Sex was established by observing copulations, and in some cases, from blood samples, although a few birds could not be classified. Breeding partners were recognised by occasions of bill-arring, extensive allopreening on multiple occasions or swapping incubation duties of an egg (Birkhead 1978a). Age of ringed individuals was defined as the number of calendar years after ringing, if the bird was ringed as a chick (as in Harris et al. 1994). For birds ringed as adults, age at capture was estimated to be the average age of first breeding (as in Crespin et al. 2006). Lindner (2000) found most guillemots on Skomer attempted to breed at six years old, so breeding adults were assumed to be seven years old in the year subsequent to ringing.

Breeding sites (the specific location on the cliff where birds lay and incubate the egg, and care for the chick, ~25 x 25 cm) of colour-ringed guillemots were recorded on large digital photographs of the Amos each year between 1997 and 2015. In 2015, I identified ringed individuals breeding at adjacent breeding sites, and using plotted breeding locations from previous years, I categorised these neighbour ‘dyads’ into two categories: those breeding at adjacent sites for the first or second year (‘short’ neighbour tenures, or ‘unfamiliar’ neighbours), and those breeding at adjacent sites for five or more consecutive years (‘long’ neighbour tenures, or ‘familiar’ neighbours). This categorisation of neighbour tenures was necessary for two reasons: (1) targeting dyads of specific neighbour tenure was the most efficient way to use the time available during the short breeding season, and (2) distinct differences in neighbour tenure mean that any effect of familiarity will be easier to detect. For further definitions, see table 3.1.

Observational data

Dyads in long and short neighbour tenures were videoed opportunistically between 05:00 and 09:30, and between 15:00 and 19:30 between April and July 2015, weather permitting. These sampling times were chosen because individual movements within the colony (joining or leaving the colony) and incubation changeovers were greatest between these times, which maximised the chance of observing the identification rings of chosen dyads within the dense colony. Dyads were videoed for 20 mins using a Panasonic SDR-H80 camcorder mounted in a hide 50 m from the study colony.

Individual behaviours were extracted from the videos, including all allopreening and aggressive interactions each ringed individual was involved in. Behaviours were recorded in bouts, defined as a single behaviour from one individuals directed to another individual, and were considered to be ended when there was a lapse of more than 2 s of the behaviour or when the participants began to engage in a different behaviour. Within a dyad, the bird performing the allopreening was the ‘actor’, and the bird receiving the allopreening was the ‘recipient’. The timings of all allopreening behaviours donated and received by members of chosen dyads were extracted from the video footage. This study was concerned with interactions between neighbours only, and did not include behaviours between individuals within breeding pairs. Aggressive interactions were rare, so were not used in any statistical analyses. The presence/absence of breeding partners was recorded, ascertained by pair behaviours described previously. The number of neighbours (adjacent breeders close enough to be involved in allopreening) was also recorded. Only videos where the social environment remained constant throughout the observation were used in analyses i.e. no birds arrived or left.

Table 3.1. Definitions of key terms used in the text.

Term	Definition
Allopreen	Individual bird uses its bill to run through the feathers of another bird. Can be ‘donated’ or ‘received’
Aggression	Individual bird uses its bill to jab, lunge or peck at another bird
Actor	Individual bird initiating/donating allopreening
Recipient	Individual bird being allopreened
Neighbour	Adjacent breeder, breeding sufficiently close to be involved in physical interactions (allopreening and aggression)
Dyad	Two neighbours
Short neighbour tenure	Two individuals which are neighbours for the first time, or two consecutive years
Long neighbour tenure	Two individuals which are neighbours for the fifth consecutive year or more

Statistical analyses

Unless otherwise stated, the response variables in each model were either the amount of time donating or receiving allopreening within a 20 min observation period. Many observations did not include allopreening which caused our data to be over-dispersed (variance > mean) so, unless otherwise stated, I used zero-inflated mixed models with the glmmADMB package to model the data (Skaug et al. 2006). Zero-inflated models attempt to account for excess zeros by estimating two equations simultaneously: true zeros, and zeros due to observation method (Zuur et al. 2005). For each model, I used AIC values to compare the zero-inflated models with negative binomial models without zero-inflation, to verify that zero-inflated models were the most suitable (Zuur et al. 2005). In all cases, I obtained p-values using likelihood ratio tests to compare models with and without the variable of interest. The model estimates (β) are stated ± estimated standard error, and raw means are given ± standard deviation.

Individual and social environment effects

I first tested whether allopreening behaviour varied between the sexes. Since a subset of the sample had been sexed (33 birds, totalling 260 observations) and I wanted to maximise the sample size for other variables of interest, sex was tested in a separate model from other variables. I then used a separate model to test for an association between allopreening donated and the actor’s age (4 level factor: <10, 11-15, 16-20, 21-25 years old), the stage of the breeding season (pre-laying, incubation, chick-rearing), presence of the actor’s partner (2-level factor: present/absent) and the number of neighbours (integer: 1, 2, 3, or more than 3). Age was split into four categories because where there were few, or one bird, of a certain age, there was no variation in allopreening for the model to estimate. To account for multiple observations of the same birds (38 individuals, totalling 304 observations) actor ID was included as a random effect. Next, I tested whether allopreening received was associated with the receiver’s age, stage of season, presence of the receiver’s partner and the number of neighbours surrounding the receiver, with receiver ID as a random variable. I did not have an *a priori* biological reason to predict allopreening behaviour to differ as a function of combinations of variables, and as such, interactions were not included in the models. These maximal models were simplified by backwards stepwise regression, removing non-significant ($p > 0.05$) main effects in turn until only significant ($p < 0.05$) or no independent variables remained (minimum adequate model). Likelihood ratio tests were used to compare models with and without the term of interest, and to obtain probabilities, p-values (Bolker et al. 2009) and the estimates (β) ± estimated standard error of fixed factors are presented for each term: for nonsignificant terms, these were calculated from the maximal model, whereas for significant terms, these were calculated from the minimum adequate model. When a significant effect was found for categorical variables, I performed post-hoc pairwise comparisons, using Tukey tests for multiple comparisons of means.

Neighbour tenure and reciprocity

Before testing whether allopreening was involved in social relationships, I first needed to investigate the potential for collinearity between age and neighbour tenure: it was impossible for first time breeders to have a long neighbour tenure, so young breeders could be disproportionately represented in short neighbour tenures. Likewise, older breeders could be more likely to be in long neighbour tenures, although older birds can have short neighbour tenures if they or surrounding birds move or are replaced. I therefore tested if an individual’s age (predictor variable: continuous) was associated with the duration of neighbour tenures (response variable: short/long). If no such association was found, this would indicate that any effect involving neighbour tenure found would not be attributed to age. I used a generalised mixed model (lme4 package, Bates et al. 2015) with binomial family and log link function, and to account for individuals involved in multiple neighbour dyads, individual ID was included as a random effect.

To investigate whether allopreening increases with the length of relationships, I tested whether allopreening interactions were associated with neighbour tenure. The total amount of time dyads spent engaged in allopreening in each observation session was the response variable, and the duration of the neighbour tenure (long/short) was the categorical predictor variable. Further, I tested for evidence of short-term direct reciprocity of allopreening by testing whether total allopreening directed at a particular neighbour was associated with total allopreening received from the particular neighbour, for each observation of each dyad. To test whether reciprocity of allopreening varied with familiarity of neighbours, duration of neighbour tenure was included as a categorical interaction term. These models included dyad ID as a random variable to account for multiple observations of the same dyads (n = 112 observations on 28 birds in 22 neighbour dyads: 12 ‘long’ neighbour dyads, and 10 ‘short’ neighbour dyads).

Results

I observed 339 allopreening events between neighbouring breeders (mean bout duration = 18.4 ± 31.6 s, median = 10 s, range = 1 – 455 s).

Individual and social environment effects

The total time individuals spent donating or receiving allopreening did not differ between males and females (donating allopreening: males = 33.13 ± 66.77 secs, females = 28.64 ± 80.62 secs, $\beta = 0.14 \pm 0.33$, $z = 0.42$, $p = 0.7$; receiving allopreening: males = 20.10 ± 52.69, females = 20.45 ± 48.61, $\beta = -0.48 \pm 0.57$, $z = -0.84$, $p = 0.4$; n = 260 observations from 33 birds). Sexes were therefore combined for the following analyses on individual and social effects.

The total time individuals spent donating allopreening was not associated with the age category of the actor, the stage of the breeding season, nor the number of neighbours surrounding the actor (median number of neighbours = 2; table 3.2). Donation of allopreening behaviour was significantly associated with partner presence, where birds were significantly more likely to allopreen a neighbour when their partner was absent (table 3.2, figure 3.1a). Similarly, receipt of allopreening from a neighbour was not associated with the age of the receiver, nor the number of neighbours surrounding the receiver (table 3.3). The stage of breeding significantly affected allopreening received (table 3.3), although post-hoc Tukey tests revealed a marginal difference between allopreening received during the pre-laying and chick rearing periods ($z = 2.042$, $p = 0.09$). Birds were significantly more likely to receive allopreening when their partner was absent (table 3.3, figure 3.1b).

Neighbour tenure and reciprocity

Older and younger birds were represented in both long and short neighbour dyads: younger birds tended to be in short neighbour tenures, and older birds tended to be in long neighbour tenures, but neighbour tenure was not significantly associated with age (mean age of birds involved in: long neighbour tenures = 17.79 ± 3.77 years old; short neighbour tenures = 14.09 ± 7.54 years old; $\beta = -0.13 \pm 0.08$, $\chi^2 = 3.17$, df = 1, $p = 0.07$, n = 30).

Long neighbour dyads allopreened significantly more than short neighbour dyads (long neighbour dyads = 37.40 ± 81.29 secs, n = 12; short neighbour dyads = 11.14 ± 35.48 secs, n = 10; $\beta = 3.87 \pm 1.56$, $\chi^2 = 3.96$, df = 1, p = 0.047, n = 112; figure 3.2). There was evidence of reciprocity between neighbours, where individuals donated more allopreening to those individuals from whom they had received allopreening, although only when taking familiarity into account (interaction term: $\beta = 0.13 \pm 0.04$, $\chi^2 = 8.34$, df = 1, p = 0.004; figure 3.3). A post-hoc Tukey test revealed that this small but significant positive relationship between durations of allopreening donated and received was found in dyads of long neighbour tenure only (z = -2.61, p = 0.009), although this effect may be due to the categorical nature of neighbour tenure only. Furthermore, the model predicted line for short neighbour dyads appeared to be strongly influenced by one data point; indeed, when this data point was removed, the model predicted line for short neighbour dyads appeared to fit the data much better (appendix figure A1).

Table 3.2. Mean ± standard deviation, and test statistics from zero-inflated mixed models, for the total amount of time (seconds) common guillemot actors spent donating allopreening to neighbours in relation to individual and social variables. For categorical variables, the first category is the reference category. Values in bold show significant differences in allopreening donated.

Variable		Mean ± SD	N	Estimate (β)	χ^2	P
Number of neighbours	1	36.12 ± 65.33	43			
	2	27.15 ± 79.96	137	−0.148 ± 0.206	0.518	0.47
	3	26.57 ± 75.99	76			
	4+	37.58 ± 77.96	48			
Stage of season	Pre-laying	21.02 ± 79.33	69			
	Incubation	23.82 ± 63.04	167	-0.161 ± 0.392	2.92	0.23
	Nestling	53.94 ± 97.38	68	0.412 ± 0.409		
Age	6-10	27.54 ± 91.27	69			
	11-15	47.93 ± 95.61	54	0.114 ± 0.653	4.43	0.22
	16-20	33.11 ± 72.41	127	-0.383 ± 0.557		
	21-25	7.46 ± 17.35	54	-1.362 ± 0.681		
Partner presence	Absent	35.25 ± 76.88	232	**-2.034 ± 0.495**	**8.6**	**0.003**
	Present	12.75 ± 7.23	72			

Table 3.3. Mean ± standard deviation, and test statistics from zero-inflated mixed models, for the total amount of time (seconds) common guillemot recipients spent receiving allopreening from neighbours in relation to individual and social variables. For categorical variables, the first category is the reference category. Values in bold show significant differences in allopreening received.

Variable		Mean ± SD	N	Estimate (β)	χ^2	P
Number of neighbours	1	19.77 ± 48.54	43	-0.073 ± 0.198	0.14	0.71
	2	21.17 ± 52.33	137			
	3	24.08 ± 61.59	76			
	4+	24.96 ± 64.55	49			
Stage of season	Pre-laying	9.51 ± 38.26	68		**6.66**	**0.04**
	Incubation	18.66 ± 45.63	167	0.261 ± 0.415		
	Nestling	44.43 ± 83.16	70	0.877 ± 0.430		
Age	6-10	18.91 ± 56.79	69		0.87	0.83
	11-15	26.61 ± 63.11	54	0.376 ± 0.419		
	16-20	21.08 ± 52.76	129	0.167 ± 0.356		
	21-25	25.32 ± 56.78	53	0.124 ± 0.403		
Partner presence	Absent	22.79 ±57.35	291	**-1.416 ± 0.484**	**6.614**	**0.01**
	Present	12.07 ± 10.55	14			

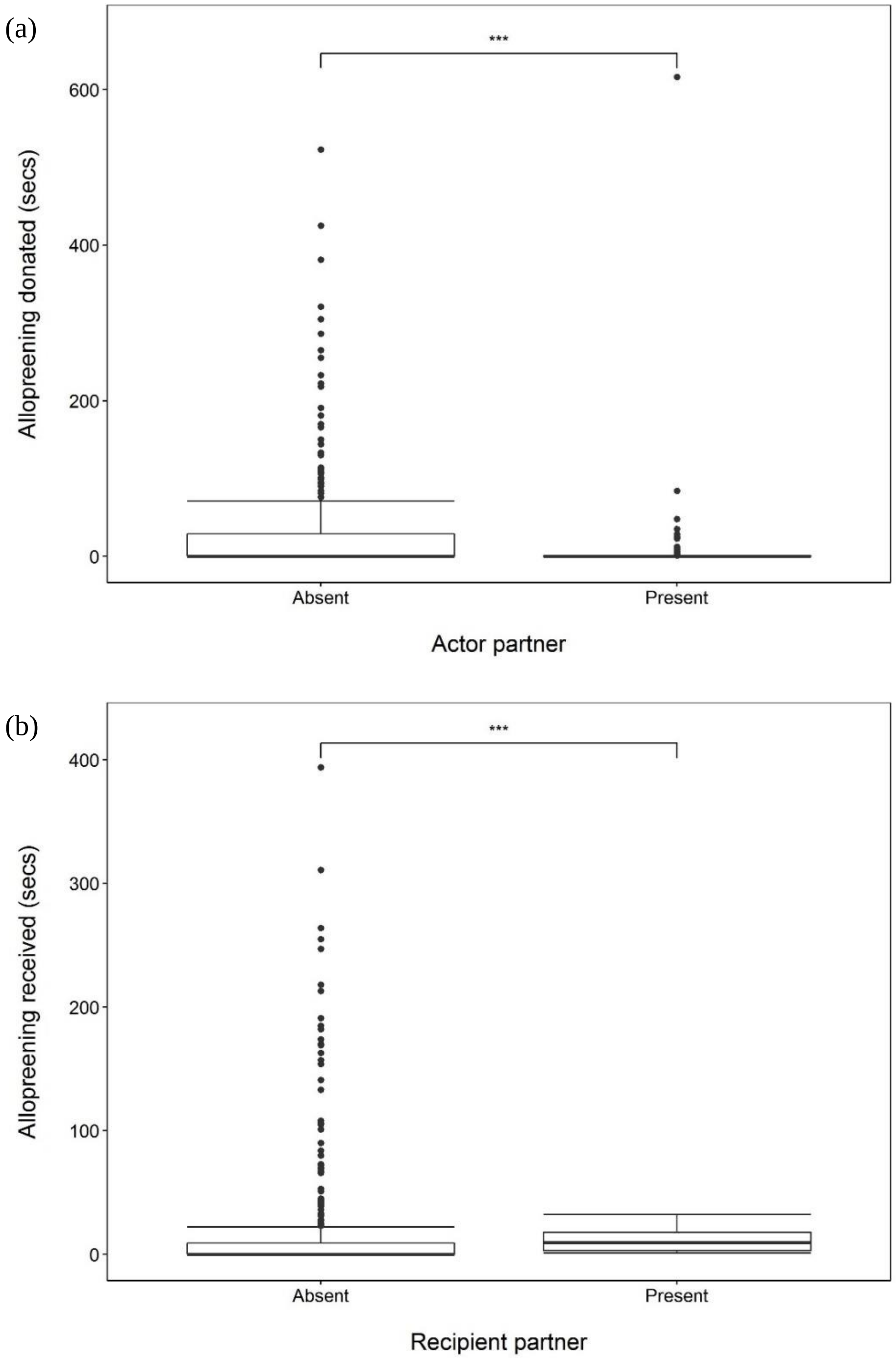


Figure 3.1. Total allopreening (a) donated from common guillemot actors to neighbour recipients, where the breeding partner of the actor was absent or present and (b) received from common guillemot actors to neighbour recipients, where the breeding partner of the recipient was absent or present (n = 304 with 38 individuals). Box plots show the median and the interquartile range from the 25th to the 75th percentiles. Whiskers above and below the box indicate the 10th and 90th percentiles, circles denote outliers. *** P < 0.01

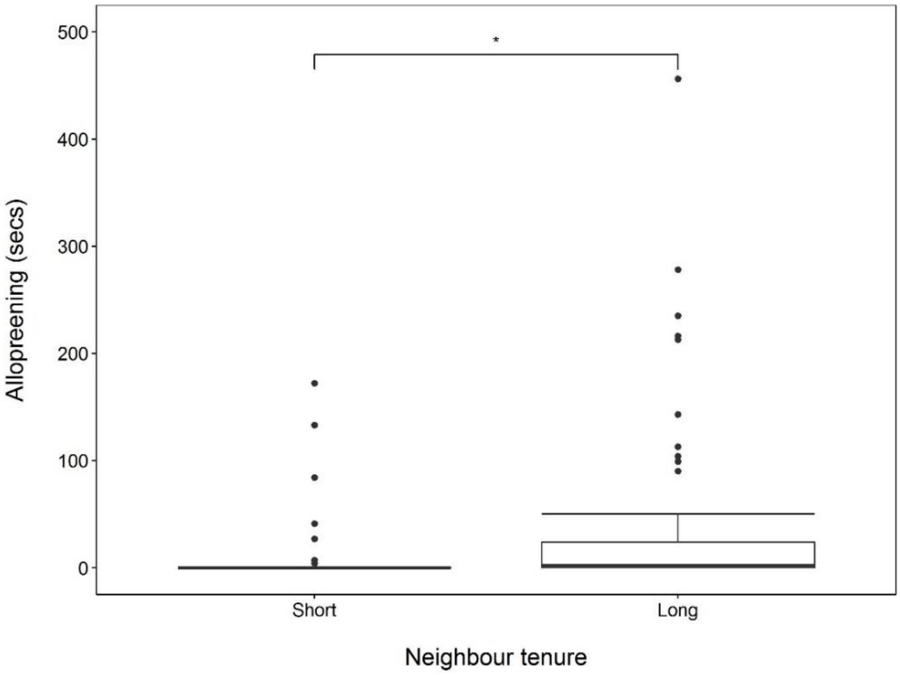


Figure 3.2. Total allopreening observed within common guillemot dyads with short (1 or 2 year) and long (5 or more year) neighbour tenures (n = 112 observations of 22 dyads). Box plots show the median and the interquartile range from the 25th to the 75th percentiles. Whiskers above and below the box indicate the 10th and 90th percentiles, circles denote outliers. * $P < 0.05$

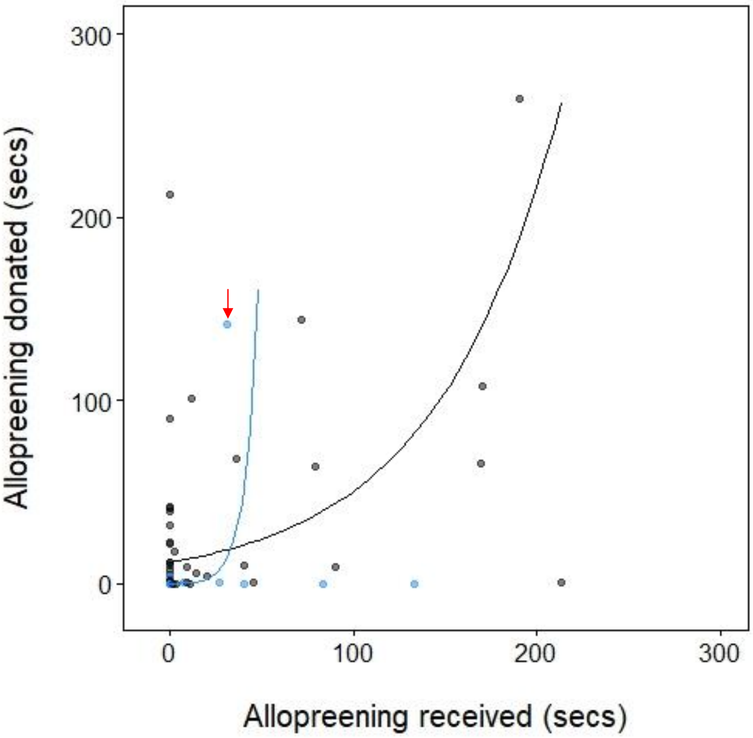


Figure 3.3. Relationship between allopreening donated and received within dyads of common guillemots in short neighbour tenures (blue: n = 42 observations of 10 dyads) and long neighbour tenures (black: n = 70 observations of 12 dyads). The intensity of colour indicates point density. Lines show model predictions. Red arrow indicates data point with disproportionately strong influence over model predicted line.

Discussion

The primary findings of this chapter are that familiar neighbouring common guillemots (individuals which have bred at adjacent breeding sites for over four years) allopreen at higher rates and are more likely to directly reciprocate allopreening compared to unfamiliar conspecific neighbours (those which have bred at adjacent breeding sites for one or two years). Variation in allopreening was not attributed to age, breeding density or stage of the breeding season. Thus, my findings demonstrate that guillemots form relationships with familiar neighbouring conspecifics, and indicate that guillemot colonies are more than simply an aggregation of pairs.

I found that allopreening rates between familiar neighbours (which had been breeding next to each other for longer) were greater than those between unfamiliar neighbours (which had been breeding next to each other for fewer years). Frequencies of affiliative interactions are used to quantify the strength of relationships (Hinde 1979; 1983), and as such, this study demonstrates that guillemots form strong relationships with familiar adjacent conspecifics, and weaker relationships with less familiar neighbours. This contrasts with findings by Lewis et al. (2007) who found that the duration of the neighbour bond was not associated with allopreening rates. This difference between our results may be due to the contrasting methods of analysis: Lewis et al. (2007) used the number of years birds had been neighbours as a continuous variable with a small sample size of neighbour dyads (n = 10), whereas the current study characterised neighbour dyads into distinct categories separated by several years (neighbours for 1 or 2 years vs 5 or more years) using a larger sample size (n = 22). Any effect present would be easier to detect with this larger sample size and with distinct categories compared to with a smaller sample size with a continuous variable. Non-random affiliative extra-pair interactions have been observed in several species (e.g. rooks, Boucherie et al. 2016; ravens, Fraser and Bugnyar 2010; zebra finches *Taeniopygia guttata*, Elie et al. 2011), yet this is the first quantitative evidence to suggest that common guillemots form social bonds with individuals beyond the breeding pair relationship.

Similar to Lewis et al. (2007), I found support for direct reciprocity of allopreening between guillemot neighbours, because an individual was more likely to be preened by a given individual when it preened this individual. However, I found that reciprocity was observed only within familiar neighbour dyads, and there was no reciprocity within unfamiliar neighbour dyads, which suggests that this apparent reciprocity could in fact be a residual effect of familiarity. Since I found that familiar dyads allopreen more than unfamiliar dyads, then these higher rates of allopreening inherently mean that there will be more reciprocity of allopreening in familiar dyads compared to unfamiliar dyads. Teasing apart the effect of familiarity on allopreening from reciprocity of allopreening would require a larger sample size in order to study the effects of familiarity on a continuous scale, rather than a categorical scale. Nevertheless, the higher rates of allopreening between familiar conspecifics, and hence reciprocity of allopreening, supports the view that social grooming increases the 'trust' between individuals which in turn facilitates the social bond between the individuals; the lack of allopreening and hence reciprocity between unfamiliar neighbours suggests a lack of 'trust' between the individuals, and lack of a social bond (Fedurek and Dunbar 2009; Engelmann et al. 2015; Engelmann and Herrmann 2015). Under direct reciprocity, donor individuals benefit from the receiver reciprocating in the near future, which may explain how cooperative behaviours (such as social tolerance) can evolve between unrelated individuals (Trivers 1971). Reciprocal allogrooming/preening has been observed in several other bird species and primates (Seyfarth and Cheney 1984; de Kort et al. 2006; Emery et al. 2007; Schino and Aureli 2008a; Schino and Aureli 2010; Gill 2012; Roulin et al. 2016). Traditionally, direct reciprocity was thought to require a high level of cognitive ability to keep track of interactions with specific individuals and direct behaviours to the correct individual (Stevens and Hauser 2004). Guillemot colonies can include hundreds of thousands of individuals, but guillemots positively physically interact with immediate neighbours only during the breeding season, so would only require the cognitive capacity to 'remember' affiliative interactions with the few immediate neighbouring conspecifics. The direct reciprocity of allopreening observed only between familiar neighbours may suggest that guillemots have sufficient cognitive ability to keep track of interactions with multiple individuals, although this would require further research.

I tested only for direct reciprocity, but another form of reciprocity may occur. Interchange, where allopreening is exchanged for other resources or commodities (Hemelrijk 1990), has been observed in green woodhoopoes, where allopreening is exchanged for group defence (Radford 2008; Radford 2011) and rooks, where allopreening is exchanged for reduced aggression (or increased social tolerance) (Emery et al. 2007). A grooming trade model inspired by biological market theory (Noë and Hammerstein 1995; Barrett et al. 1999) predicts that interchange would occur only in social groups where individuals have markedly different resource-holding potential (RHP) and as such the group has a strong dominance hierarchy; in social groups with relaxed dominance relationships and the RHP of individuals is similar, the model predicts that direct reciprocity would be more likely than interchange (Leinfelder et al. 2001). Since guillemot colonies do not show an obvious dominance hierarchy and individuals do not vary in behavioural commodities to trade for benefits of allopreening, this model would predict that allopreening in guillemots is unlikely to be exchanged for other resources. For example, exchange of allopreening for group defence in guillemots, in terms of participation of antipredator behaviours, is unlikely because participation in anti-predatory behaviour is a mutual benefit, rather than altruistic; it is in the individuals' best interest to remain guarding their egg when faced with a predator, and the efficacy of guarding their egg is increased when neighbouring breeders do the same.

Taken together, findings of the current study indicate that guillemots form social relationships with neighbouring conspecifics. One potential benefit of establishing close social bonds is to promote group cohesion as seen in primates where allogrooming rates are associated with social group size (Dunbar 1991; Lehmann et al. 2007). Guillemot colonies are large with high competition for territory, so there is a high risk of aggression (Kokko et al. 2004), and since aggression increases the risk of losing an egg or chick, behaviours to reduce rates of aggression are likely to be important in guillemot colonies (Birkhead 1977; Lewis et al. 2007). Aggression is negatively correlated with allopreening in several species (e.g. guillemots, Lewis et al. 2007, cockatiels *Nymphicus hollandicus* Spoon et al. 2004, rooks Emery et al. 2007), so even though I could not statistically determine a relationship between aggression and allopreening in the current study due to the rarity of aggressive interactions, it is reasonable to assume that allopreening is correlated with reduced aggression in individuals studied here. If allopreening was simply exchanged for social tolerance on a short-term basis, then I would expect equal rates of allopreening between all neighbouring breeders in order to minimise aggression with all surrounding breeders. The non-random distribution of allopreening, however, suggests that the correlation between allopreening and reduced aggression is a more long-term effect; a consequence and adaptive benefit of the social bonds they form. Indeed, the strength of social bonds is also measured by rates of aggression, where reduced aggression is taken as a sign of strong social bonds (Cords and Aureli 2000; Fraser and Bugnyar 2010). Potentially, then, low rates of aggression may encourage allopreening behaviour, as a different direction of causation. Alternatively, aggression between individuals with a strong social bond incurs greater anxiety than aggression between individuals with weaker social ties (Aureli 1997; Romero et al. 2009), suggesting that a major cost of aggression is the disruptive effect on social relationships (De La O et al. 2013), and therefore is another incentive to avoid aggression with familiar individuals. Either way, the current study furthers understanding of this correlation: the *selective allocation* of allopreening found here suggests that reduced aggression is part of a long-term benefit of forming social relationships with surrounding breeders.

Another potential benefit of building strong relationships outside of the pair bond could be to scope prospective partners and to facilitate mate-switching (Elie et al. 2011; Boucherie et al. 2016). If this was the case, I would expect allopreening rates to be higher in mixed-sex dyads compared to same-sex dyads. Due to the small number of known same-sex dyads in my sample, rates of allopreening in mixed-sex and same-sex dyads could not be compared. However, the strong extra-pair affiliations between familiar individuals is unlikely to be for mate-switching in guillemots because I found no sex differences in rates of allopreening, and because an equal proportion of new pairs formed were between known neighbours as between strangers (pers. obs.). In addition, even though extra-pair copulations tend to be between neighbours, both the frequency of extra-pair copulations (<10% of all copulations; Hatchwell 1988) and the rate of extra-pair paternity in this colony are low (<8%; Birkhead et al. 2001), so allopreening preferred individuals is unlikely to function to encourage extra-pair matings.

Thus far I have considered allopreening only in terms of building relationships with familiar individuals. It is possible, however, that high rates of allopreening are instead associated with familiarity with the breeding site. In ‘short’ neighbour tenures, at least one of the dyad members is relatively new to their breeding site, so the lower rates of allopreening between unfamiliar birds may instead be a behavioural response to the change in site by the ‘mover’ bird. Separating the effects of familiarity with (1) individuals and (2) the breeding site, would require a sufficient number of instances where familiar neighbours move to new adjacent breeding sites for comparison with familiar individuals on familiar sites. This rarely happens in guillemot colonies, so the possibility that allopreening is a response to site changing cannot be ruled out. However, it is likely that the identity of neighbours plays some role in allocation of allopreening behaviour because neighbours are an inevitable consequence of high breeding density.

I found that allopreening rates between neighbouring breeders were highest when breeding partners were absent, suggesting that the breeding pair relationship takes precedence over neighbour relationships. In addition, allopreening rates between partners were markedly higher than allopreening rates between neighbours (Birkhead 1978a), providing further evidence that the bond between breeding partners is more important or valuable than bonds between neighbouring breeders. This difference would be expected due to the relative roles that partners and neighbours play in individual fitness: breeding partners are involved in all aspects of chick rearing, with both males and females contributing to offspring care, whereas neighbouring breeders provide a more indirect contribution to individual fitness through alloparenting and cooperation in predator protection (Birkhead 1978a; Birkhead and Nettleship 1984; Hatchwell 1991). Allopreening between breeding partners and neighbours therefore is likely to have different social functions, in relation to the relative roles these relationships have in determining individual fitness (see table 3.4 for a comparison of allopreening between partners and neighbours).

Table 3.4. Comparison of variables associated with allopreening behaviour between neighbours and partners. References: * current study; ** personal observation; † Lewis et al. (2007); †† Birkhead (1976).

Variable	Allopreening between partners	Allopreening between neighbours
Sex	Males allopreen more than females †	No difference *†
Age	No difference †	No difference *†
Presence of partners	NA	More allopreening donated and received when partners are absent compared to when partners are present *
Number of neighbours	Unknown	No difference *
Stage of season	More allopreening during incubation compared to pre-laying or nestling stages †† (Incubating partners donate less and receive more allopreening compared to non-incubating** / incoming† partner)	No difference *
Reciprocity	Absent †	Present *†
Duration of bond	No difference †	More allopreening between familiar neighbours than unfamiliar neighbours * (No difference †)
Aggression	Unknown	Associated with reduced aggression between neighbours †
Breeding success	Associated with higher average breeding success †	Associated with higher breeding success in current breeding attempt †

This study contributes to the growing body of evidence for a prominent social role of allopreening (e.g. Emery et al. 2007; Radford 2008; Gill 2012), alongside the strong evidence for its hygienic role (e.g. Clayton et al. 2005; Villa et al. 2016). I argue that these two roles, social and hygienic, are not mutually exclusive: the benefits associated with parasite removal may be driving the evolution of social bonds. This view has been suggested for allogrooming in primates, where there is support for a role of social grooming in maintaining both social relationships and hygiene (Sánchez-Villagra et al. 1998; Zamma 2002; Akinyi et al. 2013; Grueter et al. 2013). The role of allopreening may depend on the body area involved: for green woodhoopoes allopreening directed at the body has a social function and allopreening directed to the head and neck area has a hygienic function (Radford and Du Plessis 2006). However, it appears that the role of allopreening in guillemots does not depend on the body area involved as all allopreening is directed at the head and neck area (pers. obs.), but is nevertheless associated with social relationships. The mechanism behind the social role of allopreening, and the potential for mutual reinforcement of the social and hygienic roles, remain as yet untested. One possibility is that individuals preferentially remove parasites from familiar neighbouring conspecifics, in order to remove parasites from the individuals they spend longest breeding next to and to reduce the risk of parasite transmission, or because familiar individuals can be trusted to reciprocate the removal of parasites. Additionally, allopreening could have originally evolved to reduce the risk of parasite transmission by removing parasites from nearby conspecifics, and, by chance, this physical interaction induces downstream physiological effects which encourage further positive interactions between participants. One possible downstream physiological effect is the reduction of stress, or tension, which could encourage participants to spend more time together, exchange other beneficial commodities of behaviours, and reduce the likelihood of aggression (Terry 1970). Support for the tension-reduction hypothesis of social grooming has been found in mammals (Schino et al. 1988; Boccia et al. 1989; Feh and de Mazière 1993; Aureli et al. 1999; Wittig et al. 2008; Madden and Clutton-Brock 2009; Aureli and Yates 2010), but the possibility of the tension-reduction mechanism of allopreening occurring in birds has been tested only using self-preening as a proxy for stress (Radford 2012) and thus requires further research.

In conclusion, I have shown that familiar neighbouring guillemots perform more affiliative behaviours, and are more likely to reciprocate such positive interactions, than unfamiliar neighbouring breeders, demonstrating for the first time that guillemots build strong social relationships outside the pair bond. This ability to form relationships with specific social partners demonstrates that colonies are more than an aggregation of pairs. Since social interactions and the consequent social relationships are likely to play a significant role in individual fitness, these factors should be taken into account when assessing breeding success in group living species, especially long-lived colonial birds.

Chapter 4

Allopreening in birds is associated with parental cooperation over offspring care and stable pair bonds across years

Individuals of many species form bonds with their breeding partners, yet the mechanisms maintaining these bonds are poorly understood. In birds, allopreening is a conspicuous feature of interactions between breeding partners and has been hypothesised to play a role in strengthening and maintaining pair bonds within and across breeding attempts. Many avian species, however, do not allopreen and the relationship between allopreening and pair-bonding across species remains unexplored. In a comparative analysis of allopreening and pair bond behaviour, we found that allopreening between breeding partners was more common among species where parents cooperate to rear offspring. The occurrence of allopreening was also associated with an increased likelihood that partners would remain together over successive breeding seasons. However, there was no strong evidence for an association between allopreening and sexual fidelity within seasons or time spent together outside the breeding season. Allopreening between partners was also no more common in colonial or cooperatively-breeding species than in solitary species. Analyses of evolutionary transitions indicated that allopreening evolved from an ancestral state of either high parental cooperation or high partner retention, and we discuss possible explanations for this. Overall, our results are consistent with an important role for allopreening in the maintenance of avian pair bonds.

This manuscript has been published in *Behavioral Ecology* (volume 28, issue 4, 1 August 2017, pages 1142–1148). I have included the supplementary material in this thesis to provide the complete study; otherwise, the versions are the same.

Introduction

Types of social relationship between males and females vary from promiscuous species with no bond to long term social monogamy, yet behaviours associated with these different types of relationship remain poorly understood. In birds, one behaviour that may play an important role in maintaining a social relationship between partners is allopreening (mutual preening), whereby the bill is used to preen the partner's feathers. In primates, the analogous behaviour, allogrooming, is exchanged reciprocally between group members or traded for other commodities which strengthens relationships (Seyfarth and Cheney 1984; Henzi and Barrett 1999; Tiddi et al. 2012) and ultimately increases participant fitness (Dunbar 1991; Silk et al. 2009; Silk et al. 2010; McFarland and Majolo 2013) by reducing stress and removing ectoparasites (Boccia et al. 1989; Tanaka and Takefushi 1993; Aureli et al. 1999; Wittig et al. 2008). In contrast, the social function of allopreening in birds is considerably less well understood. This is particularly surprising given the striking variation across bird species in the occurrence of allopreening: in some species, allopreening is a highly conspicuous feature of breeding partner interactions; in others this behaviour is entirely absent.

Allopreening can aid ectoparasite removal (Brooke 1985; Villa et al. 2016). However, if hygiene is the primary function of allopreening, why does this behaviour occur in certain species only? One possibility is that gregarious species, in which frequent physical contact among individuals facilitates parasite transmission, are more prone to ectoparasites (Boyd 1951). Alternatively, the removal of ectoparasites by allopreening may provide long-term fitness benefits by maintaining the health of both breeding partners in species with long-term pair bonds (Black 1996).

A third explanation for the uneven distribution of allopreening across species is that allopreening serves a different social function. An early review by Harrison (1965) argued that allopreening strengthens the bond between breeding partners, but examined only a small number of species and did not determine the statistical association between pair bond strength and allopreening across species. The notion that allopreening reinforces pair bonds has gained widespread acceptance (e.g. Harrison and Harrison 1997; Dagg 2011; Mandal 2015), but to date this hypothesis has been examined in only a handful of species. In buff-breasted wrens *Cantorchilus leucotis* and cockatiels *Nymphicus hollandicus*, allopreening is associated with partner retention across breeding seasons and coordination over incubation respectively (Spoon et al. 2006; Gill 2012), but in a third species, the common guillemot *Uria aalge*, allopreening appears to play no role in pair bond maintenance (Lewis et al. 2007). Outside the pair bond, evidence for a social function of allopreening comes from studies of cooperatively breeding green woodhoopoes *Phoeniculus purpueus*, which have been reported to increase allopreening among group members following territorial conflicts with neighbouring groups (Radford 2008; Radford 2011). However, the lack of detailed observations for most species denies us a broad understanding of variation in allopreening across birds, and in particular, how it might influence the establishment and reinforcement of social relationships between breeding partners.

Here, we carry out a comparative analysis of allopreening within breeding bird pairs, testing the hypothesis that across species the presence of allopreening is associated with strong pair bonds. Specifically, we explored the association between allopreening and four measures of pair bond strength: (1) parental cooperation in offspring care duties; (2) retention of breeding partners in consecutive breeding attempts; (3) sexual fidelity within seasons, and (4) time spent together outside the breeding season.

Methods

Data collection

We searched published sources for information on the following aspects of avian pair bonds: parental cooperation over offspring care (using scores from Remeš et al. 2015), duration of offspring care (days until independence), annual divorce rate (number of divorced pairs divided by the total number of pairs where both partners survived from one year to the next), extra-pair paternity (EPP; percentage of broods containing extra-pair offspring) and duration of the pair bond throughout the year (continuous or part-time relationship). We also recorded whether species typically exhibited solitary breeding or colonial- or cooperative-breeding, to test whether allopreening was more common between pairs breeding in groups, as has been suggested by previous authors (Harrison 1965; Spottiswoode 2008).

Investment in offspring care

Parental cooperation, defined here as the extent of biparental care, varies along a continuum from approximately equal investment by the male and female to obligate uniparental care (Clutton-Brock 1991). We used parental cooperation scores calculated by Remeš et al. (2015), which reflect the relative contribution by each pair member across eight activities: nest building, incubation, nest guarding, chick brooding, chick feeding, chick guarding, post-fledging feeding of chicks, and post-fledging guarding of chicks. The resulting parental cooperation score ranged from minimum parental cooperation (-1.5, where all activities are carried out by one pair member i.e. uniparental care) to maximum parental cooperation (+1.5, where all parental duties are shared approximately equally between the parents). For detail on score calculation methods see Remeš et al. (2015).

In species where both parents provide some form of care to offspring, pair bond strength may reflect not only the level of cooperation between parents but also the duration of care required to produce independent offspring. We collated information on the duration of incubation and the duration from hatching to independence (in days). Incubation period and age of independence were positively correlated (Pearson product moment correlation: $r = 0.5$, $t = 6.81$, $df = 136$, $p<0.001$), so we added these together to create a new variable, ‘total offspring care’, to encompass the total time offspring are cared for by parents.

Divorce rate

Annual divorce rate was measured as the number of divorced pairs (cases where both partners are known to be alive but have not re-paired) divided by the total number of pairs where both partners survived from one year to the next. This definition of divorce measures the likelihood of an individual of a species choosing to repair with the same partner when the partner has survived. A previous analysis found that the primary determinant of divorce rate was mortality rate: where mortality rates are high, individuals have a low probability of encountering partners from previous breeding seasons and as a result are more likely to breed with a different partner in consecutive breeding seasons (Jeschke and Kokko 2008). To account for this, we also collected information on mortality rates for all species for which divorce rates were available. If there was more than one estimate of divorce rate for a given species, the mean of the reported rates was used.

Sexual fidelity to social partner

Pair bond infidelity within breeding seasons was estimated as the frequency of extra-pair paternity (EPP), measured as the percentage of broods containing extra-pair offspring. Where several estimates were available for a species, for example from different years or populations, the mean value was used.

Time together

Species that spend all year together were classified as having ‘continuous’ partnerships, while those that come together for breeding only were classified as having ‘part-time’ partnerships.

Colonial and cooperative breeding

To test whether allopreening is more common in species where breeding occurs in groups rather than in solitary pairs, we compared allopreening behaviour between (1) species that typically breed in large, dense colonies and those that do not, and (2) species that breed in cooperative groups of more than two individuals and those that breed in single pairs.

Presence/absence of allopreening

For species where information on one or more aspect of pair bond strength was available, we searched for data on presence/absence of allopreening. We used this binary measure of allopreening because rates of allopreening are available for a few species only. We defined allopreening as the use of one bird’s bill to preen or groom a second individual’s feathers (Harrison 1965; Radford and Du Plessis 2006). Allopreening behaviour is therefore mechanistically distinct from other superficially similar behaviours, such as the ‘ruff-sniff’ display in crested auklets *Aethia cristatella* (Gaston and Jones 1998; H. Douglas pers. comm.) and the ‘false preening’ behaviour of mute swans *Cygnus olor* (Boase 1959), and which were not considered in this study. Furthermore, since the focus of our study was on the relationship between allopreening and aspects of the pair bond between breeding partners, we did not consider cases of allopreening among nestlings (e.g. barn owl *Tyto alba*, Roulin et al. 2016), between parents and nestlings (e.g. wood stork *Mycteria Americana*, Clark 1980) or between adults other than the breeding pair (e.g. green woodhoopoe *Phoeniculus purpureus*, Radford and Du Plessis 2006; guillemot *Uria aalge*, Birkhead 1978a). We did not identify any species where allopreening was absent between breeders but occurred between other adult group members. For a number of species where allopreening was reported as occurring, it was not possible to determine whether this was based on observations of breeding pairs or of other individuals, potentially outside the breeding season. For these species, we assumed that allopreening occurs between breeding partners.

We performed extensive online searches using Web of Science and Google Scholar (search terms: “*allo*preen**”, “*mutual preen**”, “*allo*groom**” and “*mutual groom**”, in combination with the species’ binomial nomenclature and common name(s)). Additionally, we also collated information from published sources held at the Alexander Library of Ornithology (Bodleian Libraries, University of Oxford, UK). Finally, where information on the presence or absence of allopreening was lacking, we contacted researchers involved in long-term, detailed behavioural studies of the species in question. Our literature search indicated that, for a given species, the presence of allopreening was more likely to be reported than its absence. We therefore assumed that allopreening did not occur if no reference was made to allopreening within otherwise detailed accounts of pair-bonding behaviour. Where there was any uncertainty about whether or not a species allopreens (for example, due to difficulties observing pair-bonding behaviour in cavity-nesting species), these species were excluded from our data set. We also excluded any species where information on the presence or absence of allopreening was only available from captive populations, as behaviours in captivity may not reflect those occurring under natural conditions (e.g. Lambrechts et al. 1999; Garner 2005). We gathered information on the occurrence of allopreening in a total of 503 species from 116 families. Differences in sample sizes between analyses reflect differences in the availability of estimates for variables among species.

Phylogenetic relationships

To account for evolutionary non-independence, 100 phylogenetic trees were extracted randomly from the 10 000 alternative avian phylogenies from the most recent comprehensive avian phylogeny (Hackett constraint, Jetz et al. 2012). In one case we had data on two subspecies, *Phalacrocorax atriceps melanogenis* and *P. a. bransfieldensis*, but the phylogenetic trees contained *P. atriceps* only. We assumed that the two subspecies are a sister pair, so both were added to the trees with arbitrarily short branch lengths as sister species. Rather than basing our analyses on a single phylogenetic tree and assuming this tree was known without error, we instead used a distribution of 100 trees and fitted each of our models to each of these trees using the ‘mulTree’ package (Guillerme and Healy 2014) (in R version 3.2.2, R Core Team 2013) which carries out analyses using Markov chain Monte Carlo estimation (Hadfield and Nakagawa 2010) and summarises the resulting 100 parameter estimates. The influence of evolutionary history was established for each variable by testing for the presence of a phylogenetic signal using the ‘pgls’ function in the caper package (Orme et al. 2013) which estimated Pagel’s lambda (Pagel 1999).

Data analysis

We ran separate MCMC models to determine the relationship between allopreening (present/absent) and the following predictors: parental cooperation score, duration of offspring care, divorce rate (with mortality rate as a covariate), extra-pair paternity, partnership duration (continuous or part-time), colonial breeding (yes/no) and cooperative breeding (yes/no). In addition, to confirm the effects obtained from the separate models, we also ran a full model containing all predictors on a subset of 37 species for which information on all variables was available.

Models were run for 51000 iterations with a burn-in of 1000 iterations and a thinning interval of 50. We used a weakly informative prior with expanded parameters (V = 1, nu = 1000, alpha.mu = 0, alpha.V = 1) to improve mixing and decrease autocorrelation among iterations, and variance was fixed at one because the response variable was binary (Hadfield and Nakagawa 2010). We checked the convergence of models by visually inspecting trace plots of MCMC chains and by examining autocorrelation between posterior samples. The parameter estimates we report are the posterior mode and 95% confidence intervals (lower CI – upper CI). Parameter estimates were considered statistically significant when 95% confidence intervals did not include 0.

Evolutionary transition analyses

Based on the results of the above analyses, we tested for correlated evolution between allopreening and (1) divorce and (2) parental cooperation using the BAYESTRAITS DISCRETE module with MCMC sampling (Pagel 1994). As BAYESTRAITS requires binary characters, we assigned species that were equal to or greater than the median level of divorce as “high divorce rate” (n = 87) and those that were less as “low divorce rate”, (n = 87) and likewise for parental cooperation scores (“high parental cooperation” n = 209; “low parental cooperation” n = 209), following Cornwallis et al. (2010) and Downing et al. (2015). To test the sensitivity of this categorisation, we repeated the analyses with species divided by 10% above and below the median: species that were equal to or greater than 10% above the median level of divorce were categorised as “high divorce rate” (n = 83) and those that were less as “low divorce rate” (n = 91); we then assigned species that were equal to or greater than 10% below the median as “high divorce rate” (n = 90) and those that were less as “low divorce rate” (n = 84); and likewise for parental cooperation scores (10% above the median: “high parental cooperation” n = 139; “low parental cooperation” n = 279; 10% below the median: “high parental cooperation” n = 283; “low parental cooperation” n = 135).

Transition rates were assessed by running a Reverse Jump model, which integrates results over a model space, weighting naturally by probabilities (Pagel and Meade 2006). Models were run for 10100000 iterations, sampling once every 1000th iteration, with a burn-in of 100000 iterations. We used hyper-priors which selected parameter values from exponential prior distributions with mean values between 1 and 100, which created a flat prior density. We checked the convergence of models by visually inspecting trace plots of MCMC chains and by examining autocorrelation between posterior samples, and took posterior distributions where the harmonic mean stabilised. We combined the posterior distribution of three independent runs from each model to ensure that transition rate estimates were stable and accurate, and accounted for phylogenetic uncertainty by including the same 100 trees used in the above analyses. We compared model support using Bayes factors estimated from a stepping stone sampling procedure (Xie et al. 2011). The marginal likelihoods of the models were calculated using a stepping stone sampler in which 100 stones were drawn from a beta distribution (with alpha = 0.4 and beta = 1). Each stone was sampled for 10000 iterations. We treated Bayes factors > 2 as evidence favouring the dependent model.

The models we report were visited in >85% of iterations in the post-burnin MCMC chain, which suggests that if these models were the best, then the parameters would by default be perfectly correlated. We therefore verified that these models were the best by comparing (1) a full unrestricted model with an exponential hyper prior, and (2) a full model with the relevant parameters restricted to zero and an exponential hyper prior. We ran these test models three times to account for variation between runs, for 1010000 iterations sampling every 1000th iteration after a burn-in of 10000 iterations, and compared each model using Bayes factors calculated from the stepping stone method (Xie et al. 2011). For both models, Bayes factors were > 9, demonstrating that the model reached by the Reverse Jump method was the best one.

Results

We found the presence of allopreening to be typically conserved within avian orders but variable between orders, as demonstrated by the strong phylogenetic signal (Pagel’s $\lambda = 0.83$; figure 4.1). For example, allopreening occurs widely within both the Procellariiformes (albatrosses and petrels) and Psittaciformes (parrots) but is almost entirely absent from the Anseriformes (ducks and geese). In several orders, however, there is substantial variation in allopreening between genera, for example within the Sphenisciformes (penguins) and Accipitriformes (hawks, eagles and allies).

Controlling for phylogeny, we found that allopreening was associated with greater cooperation between parents over offspring care (n = 418 species, table 4.1, figure 4.2a). This association remained significant when tested in the full model (n = 37 species, appendix table A1). Parental cooperation did not vary with the duration of offspring care (r = 0.004, t = 0.04, df = 112, p = 0.96) and there was no association between allopreening and offspring care duration (posterior mode = 0.004, 95% CIs = -0.009 – 0.02, n = 184).

We found that divorce rates were significantly lower in allopreening species than in non-allopreening species (median = 9.7% vs. 19.5%, n = 174, table 4.2, figure 4.2b). There was no association between the likelihood of divorce and cooperation score (posterior mode = -0.03, 95% CIs = -0.14 – 0.08, n = 92), indicating that allopreening varies independently with both divorce and parental cooperation. Despite mortality being a significant correlate of divorce (Jeschke and Kokko 2008), annual mortality rate did not significantly predict allopreening when included as a covariate in the divorce model (table 4.2) indicating that the relationship between allopreening and divorce is not driven by mortality. When analysing divorce together with other pair bond measures in the full model, the association between allopreening and divorce was no longer significant (n = 37 species, appendix table A1). This was likely due to the reduction in sample size, and hence power, of the full model, rather than the influence of other predictors: when the effect of divorce was analysed separately on the same subset of species, the relationship with allopreening was again nonsignificant (posterior mode = -0.59, 95% CIs = -6.49 – 4.88, n = 37).

Although allopreening species were more likely to retain partners across breeding seasons, we found no evidence for an association between allopreening and sexual fidelity to social partners within breeding seasons, measured as the rate of EPP (posterior mode = -0.011, 95% CIs = -0.065 – 0.042, n = 74). However, when EPP was included as a predictor in the full model, we detected a weak but significant effect, with allopreening species showing higher rates of EPP than non-allopreening species (n = 37 species, appendix table A1). The reason for this discrepancy is unclear. One explanation could be that a relationship between EPP and allopreening does indeed exist, but that it is weak and only evident when accounting for variance in allopreening explained by other variables. Consistent with this, when the effect of EPP was analysed separately on the same subset of species, the relationship with allopreening was nonsignificant (posterior mode = 0.037, 95% CIs = -0.021 – 0.096, n = 37). Alternatively, the presence of an effect of EPP in the reduced subset of 37 species but not in the full set of 74 species for which EPP data were available may be spurious and reflect an unidentified bias in the reduced set of species analysed in the full model.

Within-pair allopreening

Breeding partners in many species maintain bonds during the breeding season only, but some species also remain together throughout the nonbreeding season. The latter had significantly lower divorce rates (median = 5.60% vs. 23.25%, posterior mode = -9.30, 95% CIs = -14.75 – -4.90, n = 137) but were not more likely to allopreen than the former (posterior mode = 1.013, 95% CIs = -0.63 – 1.57, n = 137). Finally, we also found no association between allopreening between breeding partners and group sociality. Specifically, allopreening between breeding partners was not more common in colonially- (posterior mode = 0.92, 95% CIs = -0.72 – 2.59, n = 166) or cooperatively- (posterior mode = -0.86, 95% CIs = -2.30 – 0.56, n = 358) breeding species than in solitary-breeding species.

In analyses of evolutionary transitions, a model that assumed correlated evolution of allopreening and parental cooperation provided a better fit to the data than a model assuming independent evolution (likelihood = -427.46 vs. -437.07, Bayes factor = 25, df = 4, p < 0.001, n = 418). In these analyses, estimates of the rates of evolutionary transitions were somewhat dependent upon the method of classifying high and low parental cooperation. When categorising high and low parental cooperation as higher or lower than the median cooperation score across species, the estimated rate of transition to gain allopreening was close to zero for ancestors with little or no parental cooperation over offspring care, while all other transitions were equally likely (appendix figure A1, A2, table A2). Similar results were obtained when categorising high and low cooperation as greater or lesser than 10% below the median, but not when categorising high and low cooperation as greater or lesser than 10% above the median. Nonetheless, among the 70 species that switched between the ‘low’ and ‘high’ parental cooperation categories in these two models, most of those with higher parental cooperation scores allopreen and most of those with lower parental cooperation scores do not allopreen.

For partner retention, a model assuming correlated evolution of allopreening and divorce provided a better fit to the data than a model assuming independent evolution (likelihood = -208.97 vs. -213.99, Bayes factor = 10, df = 4, p < 0.04, n = 174). Transition rates were robust to the method of categorising high and low divorce rates (appendix table A3). The rate of transition to gain allopreening behaviour was close to zero for ancestors with high divorce rates and the rate of transition to lose allopreening behaviour was close to zero for ancestors with low divorce rates. All other transitions were equally likely (appendix figure A1, A3, table A3). Overall, these results suggest that allopreening evolved either from a state of high parental cooperation or high partner retention.

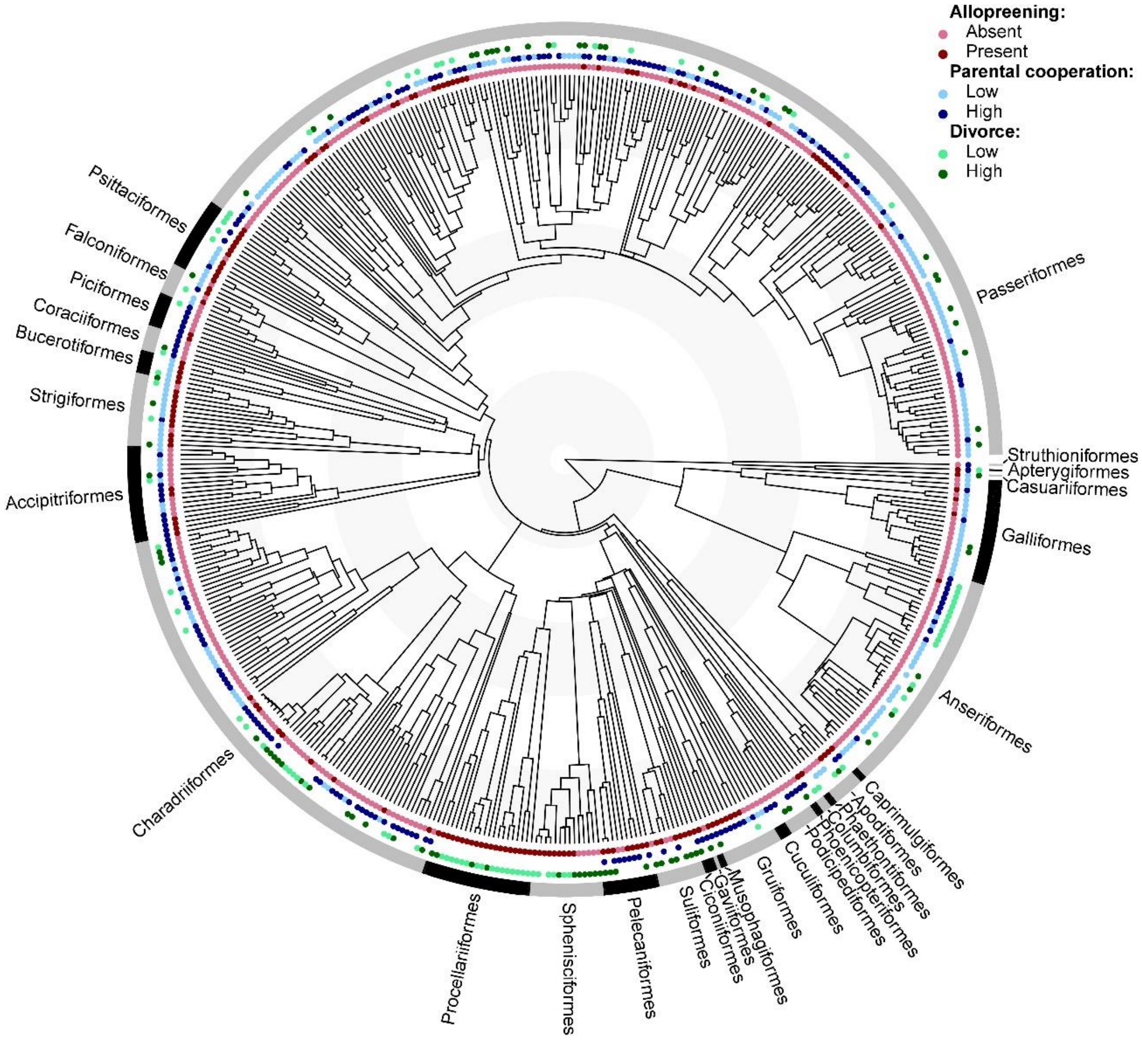


Figure 4.1. The phylogenetic distribution of allopreening, divorce and parental cooperation in birds (n = 503). ‘High’ and ‘low’ divorce and parental cooperation are categorised as higher as or lower than the median rate/score.

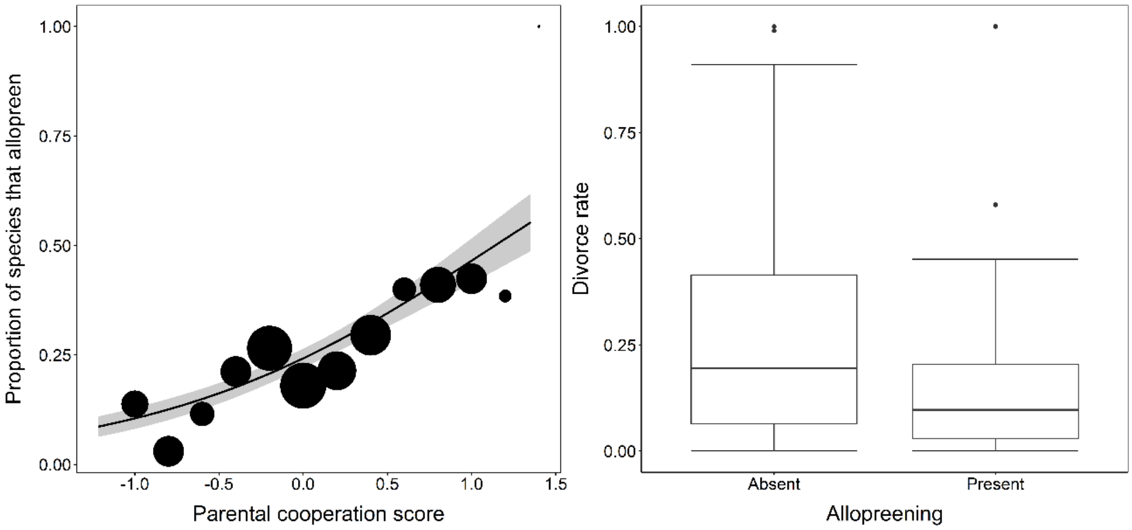


Figure 4.2. (a) Allopreening is more common among species where parents cooperate over offspring care (data from 106 allopreening and 312 non-allopreening species). Higher parental cooperation scores represent more equal contribution from both pair members to offspring care duties; lower parental cooperation scores indicate unequal contributions from pair members to offspring care duties. Point sizes represent the number of species that were assigned a given parental cooperation score (from Remeš et al. 2015). The grey area shows 95% confidence intervals. (b) Allopreening species have lower divorce rates than non-allopreening species (n = 174). Central lines represent median values, the top and bottom lines of the box represent the first and third quartiles and vertical lines represent approximately two standard deviations around the interquartile range (circles denote outliers).

Table 4.1. Allopreening is significantly associated with parental cooperation in 418 avian species. (Estimates are modal estimates from 100 models. Lower CI = lower 95% confidence interval. Upper CI = upper 95% confidence interval. Posterior distribution = distribution of estimates. Parameter estimates were considered statistically significant when 95% confidence intervals did not include 0. Residual variance was set to 1.)

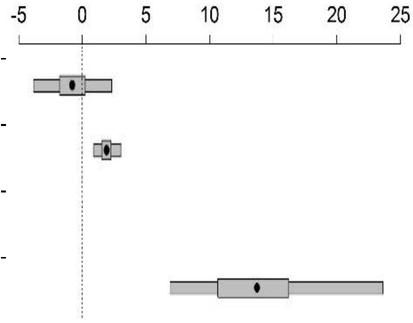
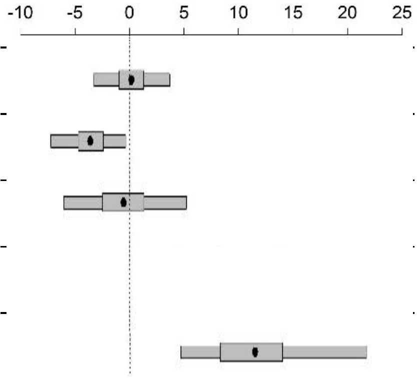
	Estimate (β)	Lower CI	Upper CI	Posterior distribution
Fixed terms				
Intercept	-0.78	-3.83	2.33	
Parental cooperation	1.92	0.90	3.05	
Random terms				
Phylogenetic variance	13.74	6.89	23.62	

Table 4.2. Allopreening is significantly associated with divorce rates in 174 avian species. (Estimates are modal estimates from 100 models. Column heads explained same as given in table 4.1. Residual variance was set to 1.)

	Estimate (β)	Lower CI	Upper CI	Posterior distribution
Fixed terms				
Intercept	0.18	-3.26	3.69	
Divorce	-3.58	-7.20	-0.35	
Mortality	-0.54	-6.05	5.23	
Random terms				
Phylogenetic variance	11.48	4.68	21.68	

Discussion

Controlling for phylogeny, we found that the presence of allopreening was significantly associated with cooperation by parents over offspring care. We also found support for a relationship between allopreening and partner retention across years, with allopreening species exhibiting lower rates of divorce between breeding seasons. Within breeding seasons, there was also some suggestion of an association between allopreening and sexual fidelity, but the apparent effect we observed was weak and inconsistent between analyses, preventing us from drawing clear conclusions. Of course, the results of our comparative analysis are correlative and do not directly address causal links between pair bond strength and allopreening, nor do they rule out the possibility that other, unidentified factors are responsible for driving the observed associations between allopreening and pair bond strength. However, the results of our analyses of evolutionary transitions indicate that allopreening most likely evolved when divorce rates were low or cooperation over offspring care was high, lending support to the idea that allopreening may have evolved as a mechanism to maintain social relationships in species where reproductive success depends upon strong pair bonds between breeding partners.

Parental cooperation was not correlated with divorce rate in our study. This is in contrast with a number of within-species studies that have shown (1) re-mating with the same partner promotes coordination of breeding activities (Handel and Gill 2000; Griggio and Hoi 2011; Sánchez-Macouzet et al. 2014; Leu et al. 2015) and (2) divorce is more common when partners fail to provide adequate parental care (Moody et al. 2005). Although joint parental investment in offspring care might be expected to coevolve with stable pair bonding across breeding attempts, theoretical modelling has shown this will depend on the costs to partners of forming such a bond (Song and Feldman 2013). For example, waiting for a late-arriving partner at the start of a breeding season may result in lost breeding opportunities, while increased disease transmission or competition from resources may disfavour breeding partners remaining in close contact in the non-breeding season. Alternatively, our analyses may have lacked power to detect a relationship between divorce and parental cooperation among the relatively small number of species for which data on both variables were available.

Our analyses indicate that relative contributions to parental care and divorce rates coevolved with allopreening, and that allopreening evolved either from a state of high parental cooperation or low divorce. This finding poses the question: if, as our results suggest, allopreening evolved to strengthen the pair bond, why would allopreening be selected for in species where the pair bond was already strong? One possibility is that where it is adaptive to share offspring care duties or to re-pair with the same partner, it may be adaptive to care for the partner's health by engaging in preening to remove ectoparasites. Alternatively, allopreening may serve to reinforce pair bonds by facilitating cooperation between partners or long-term recognition. In birds and mammals, the pituitary hormone oxytocin appears to play important roles in both contexts (Williams et al. 1994; Ross and Young 2009; Insel 2010; Klatt and Goodson 2013; Romero et al. 2014), and a number of other hormones, including testosterone (Hirschenhauser 2012), vasopressin (Lim and Young 2006) and endorphins (Keverne et al. 1989; Dunbar 2010), have also been implicated in the development of pair bonds. Although our study is correlative and does not address the underlying mechanisms linking allopreening with pair bond behaviour, one possibility is that allopreening between partners stimulates the release of hormones such as oxytocin, which in turn initiates pair bond formation and facilitates learning of breeding partner identity. Consistent with this idea, research on primates has shown that affiliative interactions among close social partners are associated with an increase in levels of peripheral oxytocin (Crockford et al. 2013) and the release of endorphins (Keverne et al. 1989). Studies of primates have also shown that both affiliative contact between individuals and the subsequent increases in levels of oxytocin and endorphins are effective in reducing stress (Boccia et al. 1989; Sapolsky et al. 1997; Aureli et al. 1999; Carter et al. 1999; Taylor 2006; Wittig et al. 2008; Aureli and Yates 2010), which is likely to play an important role in reinforcing pair bonds. Allopreening may serve a similar function in birds, though more research on the physiological changes that occur in response to allopreening and their downstream effects is required to test this idea.

Although we identified significant associations between allopreening and partner retention and parental cooperation, there were exceptions to the general trends: for example, riflemen *Acanthisitta chloris* pairs do not allopreen yet have high mate retention, and greater painted-snipe *Rostratula benghalensis* preen their partners but show uniparental care. Thus, allopreening is neither necessary nor sufficient for either equal parental investment or high mate retention. In the absence of allopreening, other pair behaviours, such as courtship feeding or duets, may have similar or complementary effects on parental care strategies or mate retention (e.g. Lack 1940; Boucaud et al. 2016). Interestingly, we found that allopreening was not more likely among species that maintain pair bonds throughout the non-breeding season than those that come together during the breeding season only. This does not necessarily contradict the idea that allopreening is important in pair bond maintenance, however. Pair bond reinforcement through allopreening and other behaviours may be more important in the breeding season, when the ability to provide effective parental care may depend upon close coordination of breeders' activities and hence may be compromised by exploitation of one parent by the other (e.g. through brood desertion) (Houston et al. 2005). Another possibility is that allopreening has downstream effects that persist beyond breeding and contribute to the maintenance of pair bonds in the non-breeding season; indeed, accumulated effects of past interactions are known to be important in shaping future relationships (Hinde 1979). Testing this hypothesis, however, will require more detailed knowledge of the physiological effects of allopreening (see above).

Previous studies have suggested that allopreening may play an important role in social species (Cote and Poulin 1995; Spottiswoode 2008). In many colonially-breeding species, large numbers of individuals nest in close proximity, with each pair occupying a very small breeding territory. Harrison (1965) reported that species breeding under such conditions were more likely to allopreen and argued that allopreening evolved to reduce aggression within and between breeding partners that arises as a consequence of enforced proximity (Harrison 1965). Observations of common guillemots *Uria aalge* provide support for this idea, with high rates of aggression among neighbouring birds associated with low rates of allopreening (Birkhead 1978a; Lewis et al. 2007). In the present study, however, we found no association between allopreening and colonial breeding. The discrepancy between our results and those of Harrison (1965) is likely due to the fact that our analyses controlled for phylogeny; when phylogeny is not accounted for, we similarly find a positive association between colonial breeding and allopreening (GLM: $z = 2.70$, $p < 0.01$, $n = 166$).

An association between social breeding and allopreening has also been suggested, based on the hygienic benefits that allopreening provides (Brooke 1985; Villa et al. 2016). Focusing on cooperatively-breeding species, Spottiswoode (2008) suggested that allopreening may have evolved in response to the increased risk of parasite transmission that results from close contact among group members (an argument that also holds for non-cooperative species breeding in dense colonies). However, while there is evidence that cooperatively-breeding bird species invest more in immune defences, potentially in response to increased risk of disease transmission (Spottiswoode 2008), we found no evidence that such species are more likely to allopreen than solitary-breeding species. Though we focused on the occurrence of allopreening between breeding pairs, our literature search did not identify any species where allopreening was absent between breeders but occurred among other adult group members. Thus, the occurrence of allopreening between breeders provides an accurate guide to the presence or absence of allopreening within the group as a whole.

Across bird species, allopreening is associated with parental cooperation over offspring care and partner retention across breeding attempts. The interactions that establish and maintain pair bonds in birds have previously received little attention and we hope our results will stimulate further research into the mechanisms by which allopreening influences the avian pair bond, for example through parasite removal or stress reduction. The present study focused only on the presence or absence of allopreening, but there is also likely to be variation in the amount of within-pair allopreening between species. However, data on intraspecific variation in allopreening currently exist for only a handful of species. Quantifying variation in the amount of allopreening within a greater number of species and relating this to variation in parental care and partner retention would therefore be valuable for further elucidating the adaptive significance of allopreening.

Chapter 5

Novel method designed to measure heart rate in remote populations of group-living birds

Physiological responses to stress prime animals to react adaptively to stressful stimuli, although repeated stimulation of the stress response may be detrimental to fitness, particularly at critical times of the life cycle (e.g. reproduction). Monitoring stress in animals can provide vital information to help predict population responses to environmental and social changes. However, measuring stress levels of individuals in real time is problematic because current methods require expensive specialist equipment, expertise and capture, and may not be feasible in remote locations. We designed a simple method to measure stress in avian species in remote conditions: we developed a heart rate monitor inside an artificial egg (which we refer to as a 'GuilleMonitor') to measure the heart rates of incubating birds *in situ*, where heart rate changes could be matched to specific behaviours and events. Comparison tests demonstrated that the GuilleMonitor measured heart rates accurately in humans when placed on the finger, but did not measure heart rates accurately in chickens *Gallus domesticus* when placed on the brood patch. Most likely, this is because blood flow in the brood patch can be regulated independently from the heartbeat, and the visible light used in the pulse sensor was more suitable for human skin than avian skin. To test the potential for using this method *in situ*, GuilleMonitors were introduced at common guillemot *Uria aalge* and razorbill *Alca torda* colonies on Skomer Island, Wales: all GuilleMonitors placed were incubated and all GuilleMonitors retrieved had recorded signals. However, these signals were unlikely to reflect real heart rates. Developments of this prototype should incorporate a pulse sensor that uses non-visible light wavelengths, which could enable this design to monitor stress responses in many avian species with a variety of breeding/nesting behaviours (burrowing, cliff-nesting, tree-nesting etc.) at a critical time of the life cycle.

Introduction

Physiological stress has been defined as ‘the multidimensional physiological response to predictable and unpredictable environmental stimuli that challenge internal stability or homeostasis’ (Dantzer et al. 2014). Physiological responses to stressful stimuli comprise a suite of behavioural and physiological coping mechanisms which prime the animal to be able to respond quickly and adaptively to an array of social and physiological challenges (Romero 2004). This ‘acute stress response’ is adaptive, yet persistent stimulation of the acute stress response by repeated exposure to stressors leads to chronic stress, which may be detrimental to reproduction and survival (Koolhaas et al. 1997; Müllner et al. 2004; Crespi et al. 2013; Strasser and Heath 2013; Thierry et al. 2013). One of the primary sources of information that can induce a physiological stress response is the social environment (Creel et al. 2013). Therefore, animals living in groups may be more prone to chronic stress than solitary living animals because they have a higher frequency of interactions with conspecifics, so use behavioural mechanisms to reduce the unpredictability of social interactions and avoid chronic stress (Creel et al. 2013). For example, in many group living primates, grooming other members of their social group (allogrooming) plays a role in building and maintaining social relationships, and is associated with reduced stress in participants (Boccia et al. 1989; Dunbar 1991; Aureli et al. 1999; Lehmann et al. 2007). Similar behaviour in birds, allopreening, in which the bill is used to preen a conspecific’s feathers, has been hypothesised to reduce stress in participants (Lewis et al. 2007; Henson et al. 2012). This hypothesis has been tested using self-preening as a proxy for stress (Radford 2012) but has not been tested explicitly using physiological markers of stress.

Monitoring stress, in order to test hypotheses regarding stress in birds requires careful, accurate and reliable measurements, taken with minimal disturbance to the individual. In birds, a widely used physiological marker of stress is an increase in levels of glucocorticoid hormones (GCs) such as cortisol and corticosterone (McEwen and Wingfield 2003; Romero et al. 2009). GCs can be measured invasively from blood samples (Romero and Reed 2005), or non-invasively from feather or faecal samples (Bortolotti et al. 2008; Harper and Austad 2012). While these methods are useful to glean the overall stress level in an individual over a specific period of time, these methods cannot be used at multiple time points so cannot be used to investigate the strength or duration of a stress response, or attribute a stress response to specific environmental stimuli or behaviour. Another measureable physiological response to stress is vasoconstriction, which channels blood from the periphery to the core causing stress-induced hyperthermia (SIH) (Oka et al. 2001) and cooling of the skin (Busnardo et al. 2010). The decrease in skin temperature in response to stress can be measured using non-invasive infrared thermography (Jerem et al. 2015), but this method is currently restricted to use in carefully controlled environments: accurate measurements of skin temperature using this method require influences from infrared radiation to remain constant (e.g. water vapour, wind, distance between the individual and the thermographic camera) so cannot be used on individuals moving *in situ*. A commonly used proxy for stress is heart rate, which has been accurately measured using electrocardiogram (ECG) sensors which record electrical signals produced by the heart, or a microphone in an artificial egg to record the audio of the heart beating (table 5.1).

Despite the multiple methods of measuring stress in birds, particularly by measuring heart rate responses to stressful stimuli, most methods described thus far are unsuitable for measuring stress responses to specific behaviours *in situ* in wild populations of group living birds: heart rate measurements by ECG can be used *in situ* and matched to specific behaviours, but cannot be used on individuals which cannot be reliably caught to have the apparatus removed; microphones in artificial eggs can be used *in situ* and do not require individuals to be captured, but cannot be used in areas of high background noise, such as in group living species where conspecific calls are frequent (table 5.1). Pulse oximetry, which uses light to measure the change in blood vessel volume as blood is pumped through by the heart, can be used on vascularised tissue such as the brood patch of incubating birds; an artificial egg containing a pulse oximeter could have the same advantages as a microphone in an artificial egg without the negative effect of background noise. Using pulse oximetry to measure heart rate through the brood patch, therefore, has the greatest potential for use in measuring stress responses to specific behaviours *in situ* in wild populations of group living birds, yet, to our knowledge, has not been employed in an artificial egg since its invention and first deployments in the mid-1990s by Nimon et al. (1994, 1995, 1996). This is surprising given that, in using an artificial egg, stress can be monitored during one of the most important periods of avian reproduction: incubation. While this method is potentially suitable, there are three clear issues which need to be resolved if this is to be a viable method: (1) artificial eggs made by Nimon et al. (1994, 1995, 1996) used a pen chart recorder to record the reflected light, so could be updated to modern methods which are likely to be more accurate and reliable; (2) the circuitry in the artificial egg was connected to the recorder and battery by a long cable, which could cause great disturbances in some species and be impossible to implement in some remote locations, and; (3) perhaps most importantly, this method was not tested for accuracy. Pulse oximetry has since been shown to be accurate in birds when used on the tongue (Schmitt et al. 1998), but the accuracy of pulse oximetry on the brood patch remains unknown.

Table 5.1. Advantages and disadvantages of methods used to measure heart rate in birds.

Method	Method of measurement	Advantages	Disadvantages	Studies
Internal electro-cardiogram (ECG)	Sensors inserted under the skin detect electrical signals produced by the heart when it beats	Accurate Does not restrict movement of the bird	Invasive: requires an operation, recovery time and habituation to the apparatus. May cause harm to the individual Restricted to captive/easily caught birds Expensive and requires expertise to implant	Greylag geese *Anser anser* (Wascher et al. 2008) Adelie penguins *Pygoscelis adeliae* (Culik et al. 1989; Culik 1992) Starlings *Sturnus vulgaris* (Kostelanetz et al. 2009; Fischer et al. 2016) King penguins *Aptenodytes patagonicus* (Viblanc, Valette, et al. 2012; Viblanc, Smith, et al. 2012; Viblanc et al. 2015)
External electro-cardiogram (ECG)	Sensors attached to the brood patch (or bare patch of skin) detect electrical signals produced by the heart when it beats	Accurate Does not restrict movement of the bird Non-invasive Does not require expertise to use	Requires habituation to the apparatus Restricted to captive/easily caught birds Expensive	Adelie penguin *Pygoscelis adeliae* (Giese et al. 1999) Great cormorants *Phalacrocorax Carbo Carbo* (Storch et al. 1999) 19 species e.g. Whooper swan *Cygnus cygnus*; Black-legged kittiwake *Larus tridactylus* (Machida and Aohagi 2001)
Cardio-vibrometer	Piezoelectric crystals pick up vibrations in the body produced each time the heart beats, which are amplified and recorded on moving paper	Birds do not need to be restrained (but must be perched) Non-invasive Also records breathing, muscle tremors and movement by the bird	Unknown accuracy Measurements must be taken in a controlled environment (cannot be used *in situ*)	13 species e.g. mourning dove *Zenaida macroura*; song sparrow *Melospiza melodia*; house wren *Troglodytes aedon*; black-capped chickadee *Poecile atricapillus* (Odum and Kendeigh 1940; Odum 1941)

Table 5.1. Contd.

Method	Method of measurement	Advantages	Disadvantages	Studies
Microphone in artificial egg	Audio of the heart beating is recorded using a microphone in an artificial egg, which is placed under an incubating bird	Accurate Non-invasive Can be used *in situ* Inexpensive	Microphone requires contact with the brood patch, so use is restricted to incubation Subject to local electrical interference and radio frequencies Restricted to species with eggs large enough to fit FM bugs and batteries May cause nest displacement or egg rejection External noise (e.g. conspecific communication) masks the heart rate	Adelie penguin *Pygoscelis adeliae*; Antarctic fulmer *Fulmarus glacialoides*; Cape petrel *Daption capense* (Giese et al. 1999) Royal penguins *Eudyptes schlegeli* (Holmes et al. 2005) Northern giant petrels *Macronectes halli* (De Villiers et al. 2006) Ring billed gulls *Larus delawarensis*; Common terns *Sterna hirundo*; Caspian terns *Hydroprogne caspia* (Arnold et al. 2011) Yellow-eyed penguin *Megadyptes antipodes* (Ellenberg et al. 2013) American oystercatchers *Haematopus palliatus* (Borneman et al. 2014)
Reflectance pulse oximetry	Light is emitted onto vascularised tissue, and the amount of light reflected is measured: when the heart beats, capillaries increase slightly in volume, and the change in volume affects the amount of light reflected	Accurate Non-invasive Depending on the area of body tissue used, can be used *in situ* (when used on the brood patch in an artificial egg only)	When used on the brood patch in an artificial egg: Required radio equipment etc; unknown accuracy; Requires contact with the brood patch; restricted to the incubation stage and sitting behaviours; May cause nest displacement or egg rejection.When used on the tongue, wing or leg: the individual has been anesthetised so would not be employable *in situ*	Brood patch: Gentoo penguin *Pygoscelis papua* (Nimon et al. 1994; 1996); Adelie penguin *Pygoscelis adeliae* (Nimon et al. 1995) Tongue: Mute swan *Cygnus olor* (Schmitt et al. 1998) Wing: Chicken *Gallus gallus domesticus* (Lorenzoni and Wideman Jr. 2008) Leg: Pigeon *Columba livia*; Macaw *Aro* sp.; African grey parrot *Psittacus erithacus*, Senegal parrot *Poicephalus meyeri senegalus*, buzzard *Buteo buteo* (Müller et al. 2011)

Measuring stress

I aimed to develop a non-invasive method of monitoring stress in wild birds, which could: (1) be implemented *in situ* with minimal disturbance to the individual; (2) be used to monitor the stress-reduction abilities of specific behaviours (e.g. solitary living, allopreening), and; (3) have the potential to be used in a variety of avian species in the wild to monitor stress levels of populations and stress responses to environmental stimuli. To do this, we modernised a system used by Nimon et al. (1994, 1995, 1996) by using a pulse sensor in an artificial egg. Once we had designed and created a potential method, I aimed to test the accuracy of heart rate measurements recorded by the artificial egg against established methods of measuring heart rates, and to test the practicalities of using such a method in a wild, remote population of seabirds. If successful, I aimed to test the hypotheses that (1) group living is more stressful than solitary living, and (2) allopreening is associated with reduced stress in birds.

Methods

Ethical note

This project was carried out following ethical approval by the University of Sheffield (Reference Number: 014825), the University of Bristol under Dr Joanne Edgar (University Investigation Number: UB/14/054) and Natural Resources Wales (licence number: 61898:OTH:SB:2015).

Creating the artificial egg

Artificial eggs were modelled from a common guillemot's egg. This species' egg was chosen for the high potential for testing hypotheses on the stress of colonial living and the tension-reduction effects of allopreening, the relatively large egg size, and the ecological importance of this Species of European Conservation Concern. Using length and width measurements, and a photograph silhouette of a representative egg shape from a guillemot population on Skomer Island, Wales, a CAD file was created in SolidWorks. The file was adjusted to create the egg shape from two halves which would screw together to form a tight seal, and to include a hole and indentation for the pulse sensor to fit into without moving out of place (figure 5.1). Eggs were printed in nylon from this file using Laser Sintering technology. Extra holes were drilled next to the pulse sensor location for a proximity sensor, and at the pointed tip of the egg for a wire attachment. The pulse sensor we used emitted green light from an LED and produced a signal proportional to the amount of light reflected. When the heart beats, capillaries increase slightly in volume, and the change in volume affects the amount of light reflected; it is this small fluctuation in capillaries in the brood patch which we aimed to measure. Since the green light emitted from the artificial egg could have scared or disturbed the bird, a proximity sensor was used to ensure the pulse sensor switched on only when the proximity sensor was covered i.e. when the bird was incubating the egg. Recording data when the brood patch was in close proximity also preserves battery life and memory storage space. The proximity and pulse sensors were mounted on the inside of the printed egg using epoxy resin (Araldite Rapid), and a 7 cm length of swaged wire was attached at the tip of the egg to enable attachment to substrate (figure 5.2). To ensure that the artificial egg was water-tight, gaps around the pulse sensor, proximity sensor and swaged wire were filled with silicone moulding rubber (Reprorubber, Flexbar).

The signal (proportional to the amount of light reflected) was recorded to a micro SD card within the egg to maintain a simple, robust system that would perform reliably in remote conditions. This internal data storage avoids using radio equipment to transmit the data to an external storage device, which is expensive, complex, and requires considerable battery life, and also avoids the use of cables, which may have disturbed the birds and may be difficult to set up in remote conditions. A reading was recorded every 20 ms, which was calculated to be frequently enough to measure heart rates of up to a Nyquist limited frequency of 1500 bpm, while maintaining a battery life of ~50 h. The reading was recorded against time to allow the heart rate to be calculated from the waveform. File names were a time stamp to enable the time of the heart rate to be matched to specific behaviours.

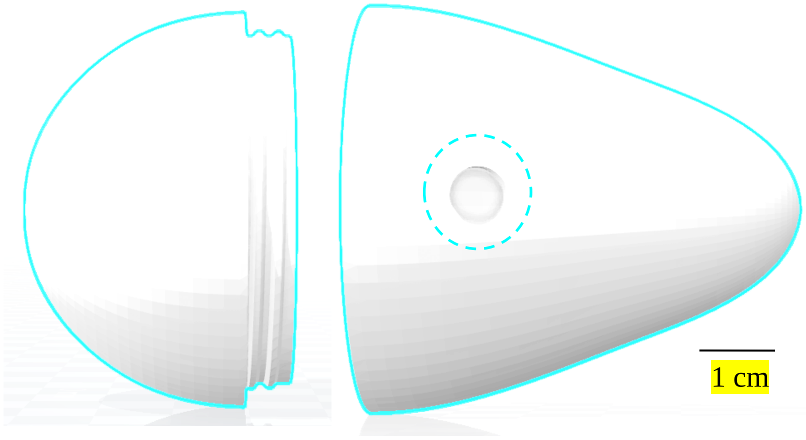


Figure 5.1. CAD file of the artificial guillemot egg: two halves which screw together with a hole and indentation (inside the egg, indicated here by dashed circle) for the pulse sensor. File created by Patrick Fairclough, file modified by Chris Rose and Chris J Smith, and artificial eggs were printed by Wendy Birtwistle, at the Department of Engineering at the University of Sheffield.

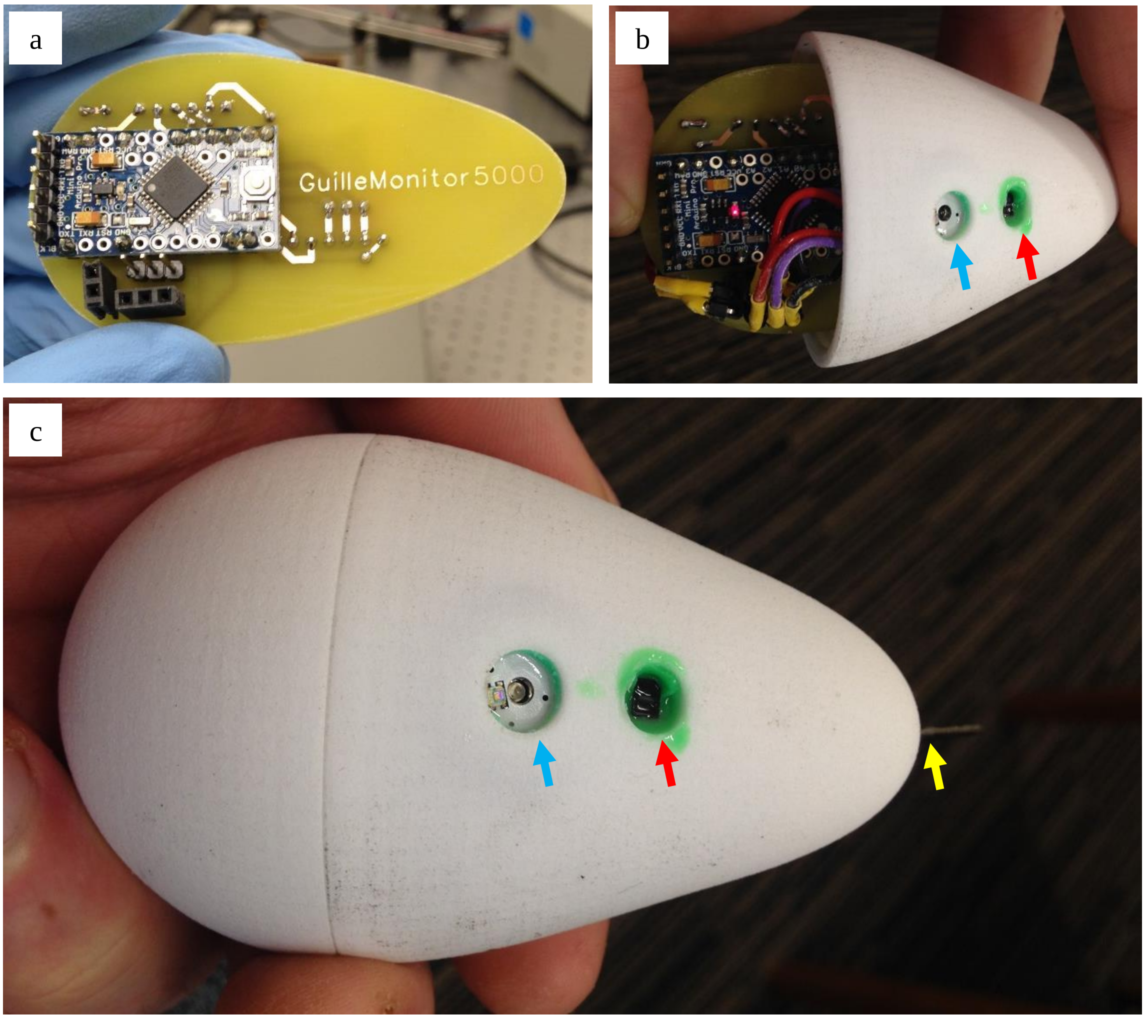


Figure 5.2. (a) Top of the completed circuit board (yellow) with Arduino (blue) and connectors for the battery and sensors; (b) circuit board fitted into the top of the 3D printed artificial egg, with pulse sensor (blue arrow) and reflectance sensor (red arrow) glued and sealed in place; (c) fully assembled GuilleMonitor with swaged wire (yellow arrow) for attachment to substrate. Designed by Ashley Cadby and developed and created by Nic Mullin at the Department of Physics and Astronomy at the University of Sheffield.

An Arduino Pro Mini with ATmega328 (3.3V, 8MHz) processor, a real time clock (DS3234 Real Time Clock IC) and microSD card writer were mounted on a homemade, double sided printed circuit board, which interconnected the 3.7V lithium ion polymer battery, proximity sensor, pulse sensor, clock and card reader. The circuit board was laid out using FreePCB software, then photomasks were printed onto tracing paper. Double sided, pre-sensitised copper-clad board (FotoBoard, Mega Electronics) was exposed to UV light through these masks to transfer the pattern into a pre-coated positive photoresist, which was developed using sodium hydroxide in water (10 g/l). The copper was then etched using a pre-mixed sodium peroxidisulfate etchant to transfer the pattern from the photomask into the copper. After etching, the boards were washed thoroughly in water before being drilled and cut to shape. The assembled electronics were placed inside the “sharp end” of the egg with the lighter side of the circuit board facing towards the pulse sensor to ensure the egg maintained an orientation with the proximity sensor facing up to the brood patch (figure 5.2). The circuit board was held in place by small tabs made from Milliput epoxy putty. Water tightness was tested by placing a fully assembled egg under a running tap for 10 minutes. The completed egg weighed approximately 76 g (mean weight of guillemot eggs on Skomer Island in 2017 = 101 g, range = 90 – 115 g, J. Thompson pers. comm.). Hereafter, this artificial egg will be referred to as the ‘GuilleMonitor’.

Investigating the viability: tests in humans

To test whether the GuilleMonitor measured heart rate accurately and reliably, heart rates of humans measured by the GuilleMonitor were compared with two other established methods. Subjects were six healthy human adults between the ages of 21 and 40. I measured their pulse rates using the following three methods simultaneously: (1) I placed two fingers on the subject’s neck, counted the number of pulses for 15 s, and multiplied this by 4 to calculate the beats per minute (BPM); (2) the subject placed a ring fingertip on an iPhone camera and flash light for 20 s while the iPhone app called “Instant Heart Rate: Heart Rate and Pulse Monitor” measured their heart rate using pulse oximetry; (3) the subject placed the other ring fingertip on the pulse sensor in the GuilleMonitor for 1 min. To test whether these methods measured a range of heart rates accurately, the subjects increased their heart rate by performing star jumps (jumping jacks) for 1 min, before having their heart rates measured again by the same three methods described above.

Investigating the viability: tests in hens

Next, I tested whether the GuilleMonitor measured heart rates accurately and reliably in chickens through their brood patch, by comparing heart rates of hens measured by the GuilleMonitor with those measured by an established non-invasive method which uses electrocardiogram ECG (Lowe et al. 2007; Edgar et al. 2011). Eight female chickens of a traditional breed (Australorp x Indian game) chosen for their increased likelihood of becoming broody, were group-housed in a floor pen (4 x 4 m), bedded with 5 cm of wood shavings, containing nest-boxes and perches. Broody hens were required because both methods of heart rate measurement use the brood patch, which non-broody hens do not have. To encourage broodiness, four infertile eggs were kept in each nest-box. Ad libitum layers mash was provided from two suspended feeders and water from two suspended drinkers. The temperature of the room was maintained at 23°C and the lighting schedule was 16L:8D.

Hens were ringed with unique identification rings and prepared for non-invasive heart rate monitoring. On day 1, each hen was fitted with a harness made from elastane, fitted around the back and tail and between the legs, and secured behind the neck with hook and loop fastenings, allowing free limb movement. The hens were returned into the group pen and left undisturbed for a period of 20 mins to habituate to the harness, after which the harness was removed. On day 5, hens were fitted with the heart rate monitors in the following way: the hen was placed gently on her back, two small sections of skin overlying the pectoralis muscle either side of the sternum (i.e. the brood patch) were cleaned using surgical spirit and cotton wool, and two self-adhesive electrode sensors (Ambu Blue sensor M-00-S) were applied to the cleaned skin, before fitting the harness. A non-invasive telemetric logging system (Lowe et al. 2007) was placed in the pocket of the harness positioned over the hen's back and connected to the sensors on the hens' skin using two attached wires. While the hen was on her back, the GuilleMonitor was held to the opposite side of the brood patch to the electrode sensors (approximately 10 cm away) for 1 min. Immediately after each test the harness and logging system were removed, and the hen was returned to the group pen. At the end of the study all hens were rehomed to responsible smallholders.

Investigating the viability: tests in common guillemots Uria aalge *and razorbills* Alca torda

I aimed to test how a functioning GuilleMonitor would work in remote and difficult conditions, and to test the following two hypotheses: that allopreening in birds reduces stress, and that colonial living is more stressful than solitary living. I chose to test these hypotheses in common guillemots *Uria aalge* (hereafter 'guillemots') and razorbills *Alca torda* for several reasons: (1) guillemots allopreen their neighbours as well as their partners, so the potential for observing allopreening was high; (2) guillemots and razorbills are phylogenetically closely related (Smith and Clarke 2015) and similar in size (Thaxter et al. 2010) yet guillemots breed in dense colonies, whereas razorbills usually breed in sheltered crevices, so provide a natural comparison of stress levels in colonial and solitary breeders; and (3) I had access to, and an understanding of, breeding sites of these species on Skomer Island, Wales, so was able to minimise disturbances to colonies when placing GuilleMonitors. I aimed to swap temporarily 10 guillemot eggs and 10 razorbill eggs with GuilleMonitors to measure adult heart rates while simultaneously recording their allopreening interactions to compare heart rates during (1) sleeping and allopreening, and (2) exposed colonial living razorbills and sheltered solitary living.

Study sites for measuring the heart rates of guillemots were selected based on two requirements: breeding sites should be accessible, to enable GuilleMonitor placement with minimal disturbance to the colony, and the behavioural interactions of birds at the breeding sites should be observable from <60 m (for observing allopreening interactions). Based on these requirements, two colonies on Skomer Island were chosen: the Amos Basin (AB) and South Stream Cliff (SSC). Before eggs were taken from the breeding sites, I took several precautions to ensure the eggs were replaced to the correct breeding site after the experiment: the eggs were given identification numbers which were written on the egg with permanent marker, the exact locations of the eggs were marked onto the cliff using waterproof paint-pens, and photographs were taken of these marked breeding sites with the marked identified eggs in place. Exposed razorbill study sites were chosen by their close proximity to suitable guillemot sites at AB and SSC to minimise disturbance to the colonies. Sheltered razorbill study sites were chosen by their ease of accessibility: many razorbills breed under large boulders in an area called Wick Basin (WB), some of which can be reached within an arm’s length, so this area was chosen for razorbill GuilleMonitor placement.

Guillemots have uniquely coloured and patterned eggs which allows them to distinguish their eggs from those of adjacent conspecifics (Tschanz 1959; Birkhead 1978a; Gaston et al. 1993), so GuilleMonitors needed to resemble the real egg as closely as possible to maximise the likelihood that guillemots would accept and incubate the GuilleMonitor. GuilleMonitors were painted to match the real eggs using acrylic paint (figure 5.3). Razorbill eggs do not vary in colour or pattern, so GuilleMonitors were painted white for placement at razorbill breeding sites. When the paint was dry, GuilleMonitors, were attached to the breeding site using the swaged wire emerging from the tip of the GuilleMonitor. SSC is a rocky cliff, so Milliput was moulded around the wire attachment, pushed into crevices and left to dry. AB is a muddy ledge covered with rotting wood, so nails were pushed through the wire attachment into the wood. At WB GuilleMonitors were attached to the ground only if there was a risk of the GuilleMonitor rolling into a crevice under the boulders. Care was taken to ensure the methods of attachment would not cause injury to the returning birds, and the short wire attachment did not restrict normal egg turning behaviour. GuilleMonitors were left in place for up to 48 h. The eggs were placed in an incubator as soon as possible after removal from the cliff (all within 1 h) and kept at 36ºC and 60% humidity. Behaviours of observable birds with GuilleMonitors were recorded using a Panasonic SDR-H80 camcorder from a distance of <60 m during hours of daylight.

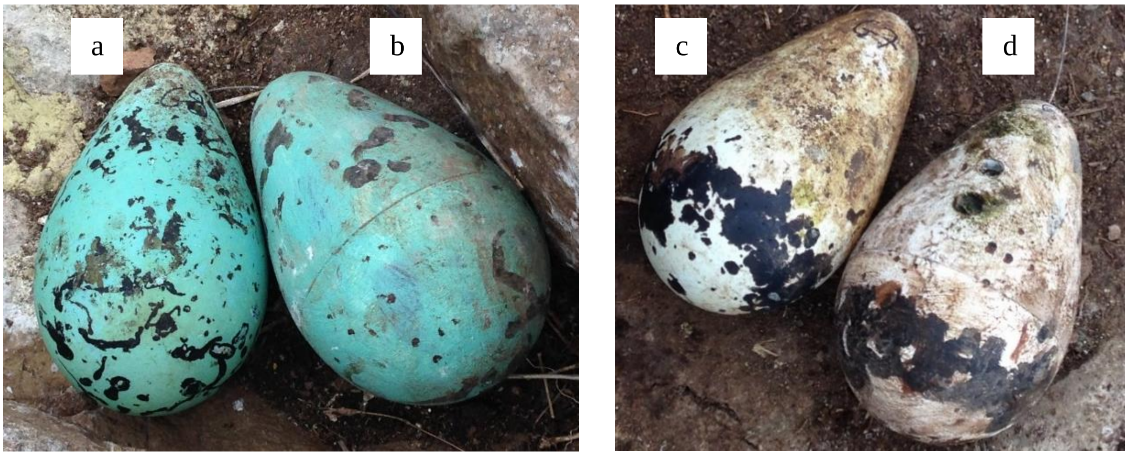


Figure 5.3. Real guillemot eggs (a and c) and artificial eggs (b and d) *in situ*.

Determining heart rate

Heart rate was measured in beats per minute (BPM). To determine the most likely BPM from the light signal measured from the GuilleMonitor I used autocorrelation analyses in ‘Python’ (www.python.org). The autocorrelation function (ACF) is found by sliding a copy of the signal along the x axis (time) and measuring the extent to which the original and the shifted copy line up. The amount of time between the two copies lining up – the period – is used to determine the most likely BPM. Measurement of the period requires (1) identifying peaks in the ACF, (2) selecting the peak associated with the heartbeat, and (3) evaluating the uncertainty on the period. Due to noise in the light signal, I smoothed the ACF (using Guassian kernel smoothing) to provide the best compromise between reducing noise and maintaining ACF signal. If the light signal contains a clear pattern, the above process yields a series of clear, regularly space peaks of gradually decreasing height. The first peak corresponds to the interval between patterns in the light curve which are clearly repeated, and is thus identified as the period (i.e. the time taken for one heartbeat). Later peaks repeat on an interval approximately equal to the period, and the scatter in the peak locations is used to estimate the period uncertainty. The frequency (BPM) is calculated as:

$$BPM = \frac{60}{period}$$

For example, if it takes 0.8 s for a pattern (e.g. heartbeat) to repeat, the frequency in BPM is 60/0.8 = 75 heartbeats per minute. ACF is a robust method for period detection in time series data such as heart beats (McQuillan et al. 2013; Tsalach et al. 2014).

For human data, BPM was estimated from values recorded by the GuilleMonitor using the method described above (ACF) with a smoothing function with a width of 12 data points, on 15 s of data.

For chicken data, BPM was estimated from data recorded by the GuilleMonitor using the method described above (ACF) with a smoothing function of 12 data points, on 60 s of data. BPM was estimated from ECG data using a method established by Lowe et al. (2007) and Edgar et al. (2011), using Spike 2 (Cambridge Electronic Design, UK) on 10 s of data. Since ECG data are recorded each millisecond, and GuilleMonitor data are recorded every ~20 ms, I tested whether this difference in sampling frequency affected the robustness of the ACF method for estimating BPM. I therefore estimated BPM from ECG data (sampled each millisecond) using ACF on 10 s data with smoothing function of 30 data points, and from a subset of ECG data containing data points at 20 ms intervals using ACF on 10 s data with a smoothing function of two data points. For guillemot and razorbill data, BPM was estimated from data recorded by the GuilleMonitor using ACF with a smoothing function of 12 data points on 15 s of data.

Statistical analysis

Correlations of BPM estimated from each method within species were calculated using Spearmann’s *rho* (‘cor’ function in R, R Core Team 2013).

Results

BPM was measured and estimated in humans, chickens, guillemots and razorbills by several methods, in order to verify the accuracy of heart rates measured by the GuilleMonitor and estimated using ACF (table 5.2). The high variation in BPM in humans is primarily due to variation between measurements before and after exercise, as well as between individuals, whereas the variation in BPM measured in chickens, razorbills and guillemots is due to variation between individuals (table 5.2).

Human heart rates measured by the GuilleMonitor and estimated using ACF (figure 5.4) were highly correlated with heart rates measured both by counting pulse rates and using an iPhone app (table 5.3). In chickens, heart rates measured by the GuilleMonitor and estimated using ACF (figure 5.5) were not closely correlated with other methods: the highest correlation was between BPM estimates from the ACF method and the established method of estimating BPM (table 5.4).

Measuring stress

Four GuilleMonitors were lost over the cliff at SSC because the birds returned to the breeding ledge sooner than anticipated, before the Milliput had set. All GuilleMonitors were incubated for at least part of the ~48 h placements: signals resembling heart rates were retrieved from all GuilleMonitors (figure 5.6), and three out of seven (43%) guillemot GuilleMonitors, and five out of nine (56%) razorbill GuilleMonitors were warm on retrieval. The standard deviation around the mean of the estimated BPM for each individual guillemot and razorbill varied considerably (table 5.5).

Table 5.2. Mean ± SD BPM of humans, chickens, guillemots and razorbills measured and estimated using a range of methods. * 60 s before exercise, 10 s after exercise.

Species	Method of measuring heart beats	Method of estimating heart rate	Time used for determining heart rate (s)	Mean estimated BPM ± SD
Human (n = 6)	Pulse rate	Count pulses 15 seconds	15	87.0 ± 20.5
	iPhone app	Phone app output	20	86.8 ± 24.3
	GuilleMonitor	ACF	60/10*	83.6 ± 19.2
Chicken (n = 8)	ECG	Spike software	10	347.4 ± 39.6
	ECG	ACF – sample every 1 ms, smoother function = 30	10	365.9 ± 38.1
	ECG	ACF – sample every 20 ms, smoother function = 2	10	348.6 ± 31.4
	GuilleMonitor	ACF – sample every 20 ms, smoother function = 12	60	30.3 ± 3.0
Guillemot (n = 7)	GuilleMonitor	ACF – sample every 20 ms, smoother function = 12	15	66.2 ± 5.6
Razorbill (n = 9)	GuilleMonitor	ACF – sample every 20 ms, smoother function = 12	15	72.0 ± 23.3

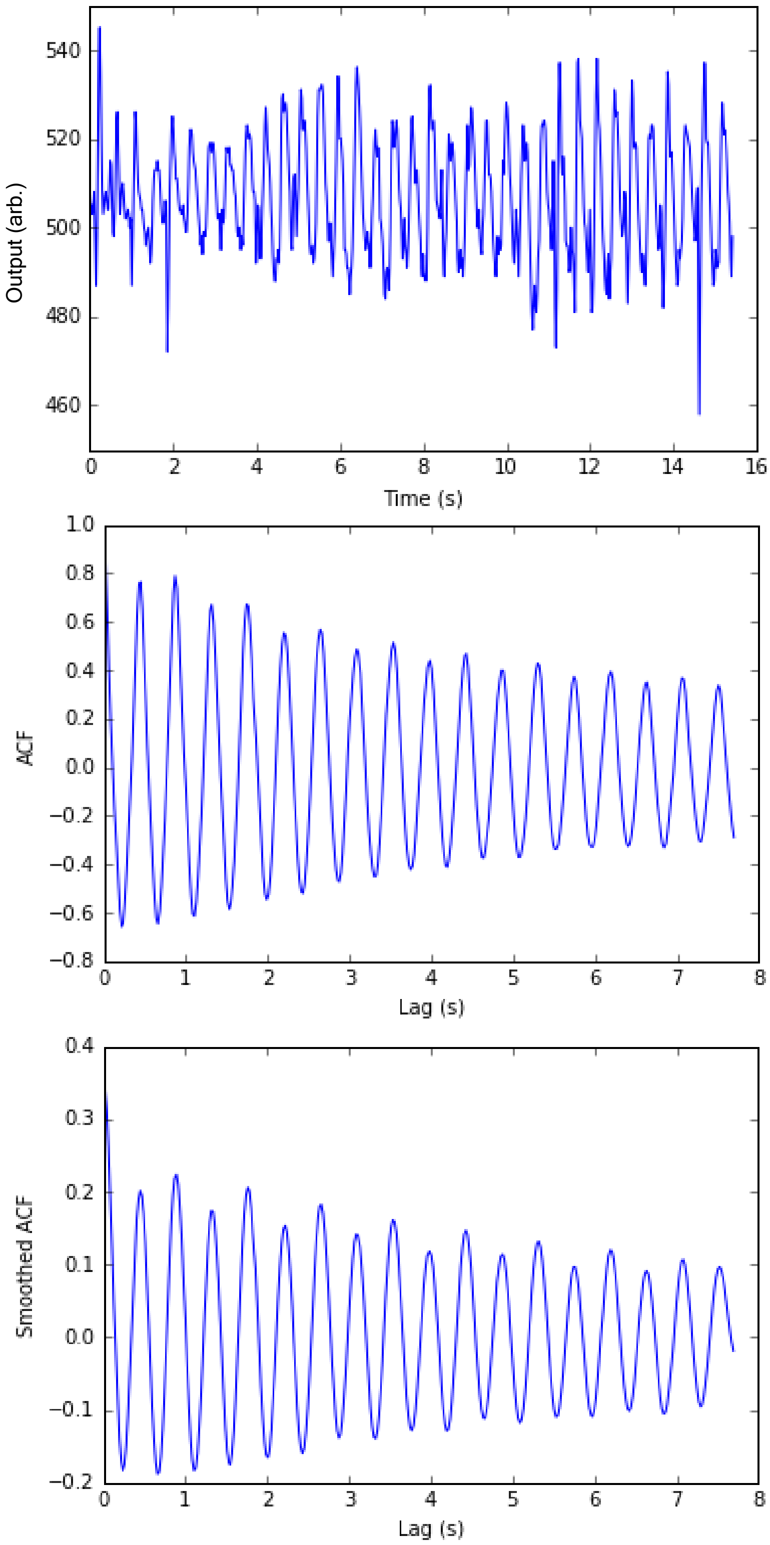


Figure 5.4. (a) Example trace produced by the GuilleMonitor held to the ring finger of a human over 15 s with (b) the corresponding ACF and (c) smoothed ACF, where 1 = perfect correlation. This signal was estimated as 67.3 ± 0.5 BPM (uncertainty is the width of the peak).

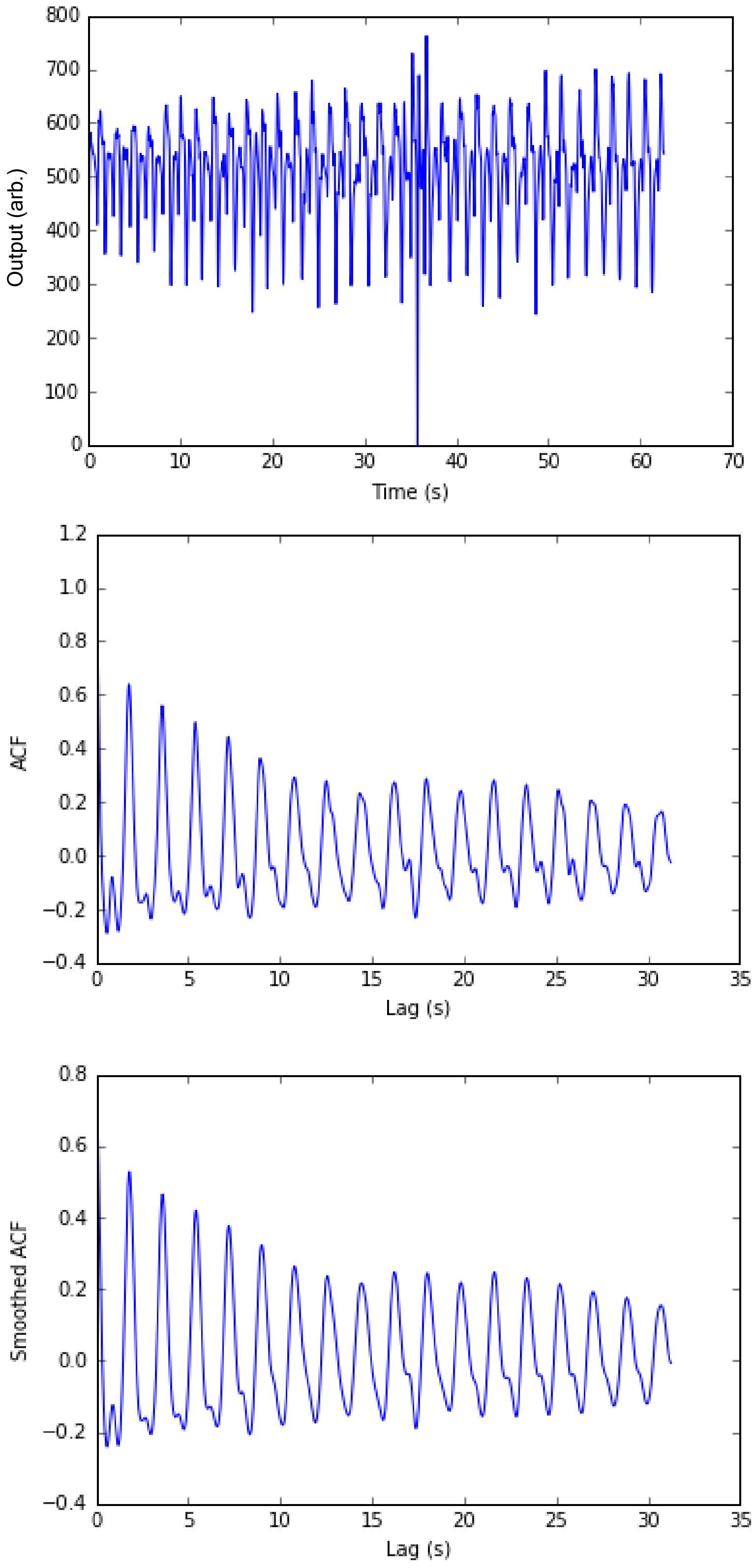


Figure 5.5. (a) Example trace produced by the GuilleMonitor held to the brood patch of a chicken over 60 s with (b) the corresponding ACF and (c) smoothed ACF, where 1 = perfect correlation. This signal was estimated as 33.3 ± 0.1 BPM (uncertainty is the width of the peak).

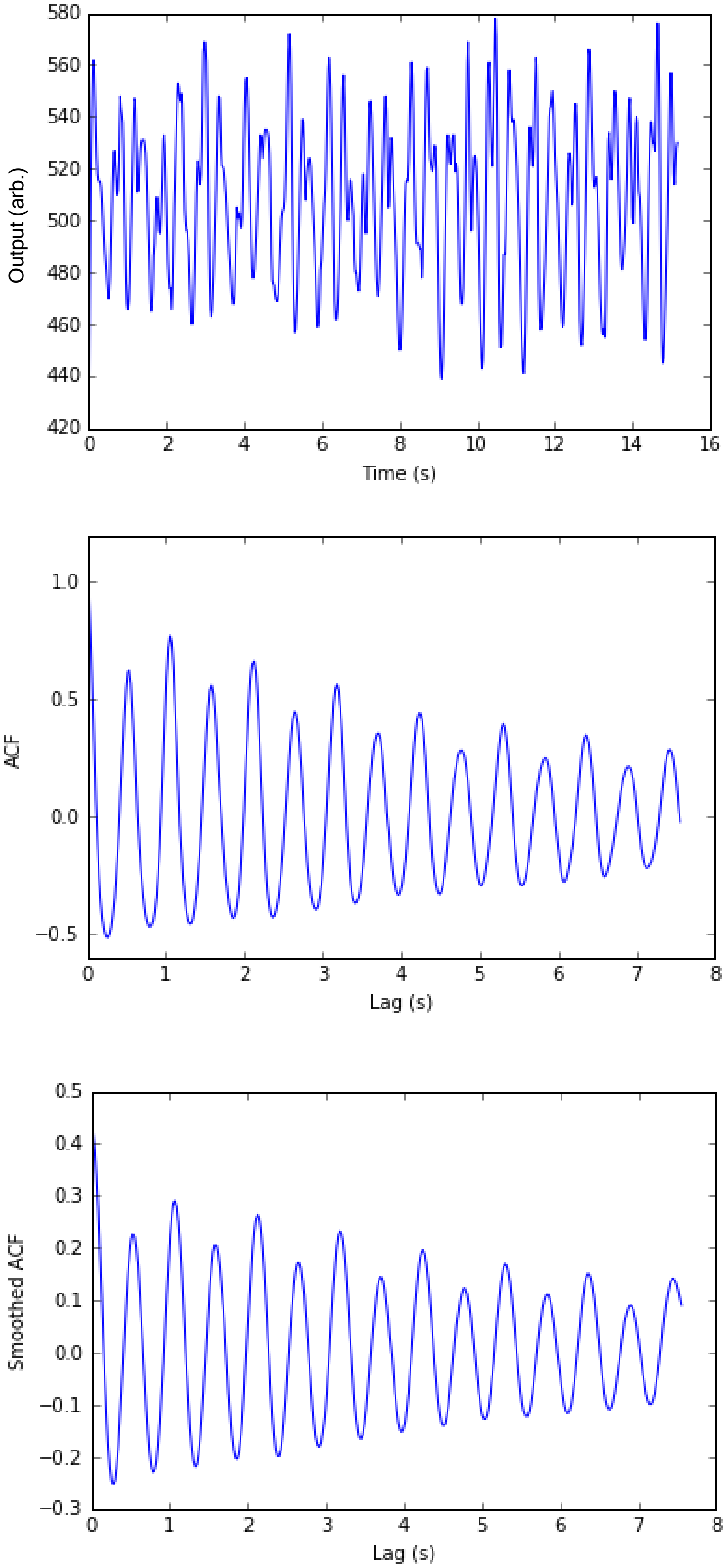


Figure 5.6. (a) Example trace produced by the GuilleMonitor under a common guillemot with (b) the corresponding ACF and (c) smoothed ACF, where 1 = perfect correlation. This signal was estimated as 56.4 ± 0.4 BPM (uncertainty is the width of the peak).

Table 5.3. Correlations (Spearmann's *rho*) of human heart rates (BPM) measured by three methods (a) before exercise, (b) after exercise, and (c) overall (n = 6 human subjects).

(a)	iPhone app	GuilleMonitor
Pulse rate	0.99	0.99
iPhone app	-	0.98

(b)	iPhone app	GuilleMonitor
Pulse rate	0.94	0.84
iPhone app	-	0.96

(c)	iPhone app	GuilleMonitor
Pulse rate	0.96	0.92
iPhone app	-	0.98

Table 5.4. Correlations (Spearmann's *rho*) of chicken heart rates (BPM) measured and estimated by four methods (n = 8 chickens). Bold typeface shows the correlation between the GuilleMonitor and the established method of measuring heart rate in chickens.

	ECG (estimated by ACF: 1 ms sampling frequency)	ECG (estimated by ACF: 20 ms sampling frequency)	GuilleMonitor (estimated by ACF: 20 ms sampling frequency)
ECG (estimated by Spike software)	0.65	0.89	**0.62**
ECG (estimated by ACF: 1 ms sampling frequency)	-	0.97	0.19
ECG (estimated by ACF: 20 ms sampling frequency)	-	-	0.61

Table 5.5. Mean estimated heart rate ± SD (BPM) calculated from three 15 s samples extracted at random from signals recorded from seven individual guillemots and nine razorbills at three locations on Skomer Island, Wales. Uncertainty in estimated BPM dominated by variation between the three samples for each individual. Amos Basin (AB) and South Stream Cliff (SSC) are guillemot colonies; Wick Basin (WB) is an area of large boulders where razorbills breed.

Species	ID	Location	Date set	Date retrieved	Mean estimated BPM ± SD
Guillemot	1	AB	19 May	20 May	69.6 ± 0.1
	2	AB	19 May	20 May	58.2 ± 18.9
	3	AB	19 May	20 May	70.2 ± 0.2
	4	SSC	16 May	17 May	66.1 ± 7.3
	5	SSC	16 May	17 May	70.4 ± 0.1
	6	SSC	16 May	17 May	58.3 ± 20.5
	7	SSC	16 May	17 May	70.4 ± 0.2
Razorbill	1	WB	13 May	15 May	70.4 ± 0.0
	2	WB	13 May	15 May	59.0 ± 19.7
	3	WB	13 May	15 May	62.8 ± 11.9
	4	WB	13 May	15 May	131.8 ± 73.8
	5	WB	13 May	15 May	62.2 ± 13.9
	6	WB	22 May	24 May	51.9 ± 17.2
	7	WB	22 May	24 May	69.1 ± 1.1
	8	AB	19 May	20 May	70.3 ± 1.7
	9	SSC	16 May	17 May	70.3 ± 0.1

Discussion

We designed and tested a new method of measuring heart rate in incubating birds: we produced a pulse sensor in an artificial egg to measure blood flow in the brood patch of incubating birds, and from this attempted to determine the heart rate of the bird. Tests showed that the artificial egg containing the pulse sensor, the 'GuilleMonitor', accurately measured heart rate in humans, but did not accurately measure heart rates in chickens. Thus, heart rates returned are unlikely to be accurate and therefore, in its current form, the GuilleMonitor cannot be used to measure stress in birds. However, GuilleMonitors were accepted by both guillemots and razorbills, so a functioning heart rate monitor in an artificial egg could be used to test the tension-reduction mechanism of allopreening. Possible explanations for the discrepancy between measurements from the GuilleMonitor and the expected heart rates from other studies (e.g. Machida and Aohagi 2001) are discussed below.

Our tests in humans show that the heart rate monitor we designed for an artificial egg accurately measured heart rate in humans. Furthermore, the close correlations between three different methods of measuring heart rate in humans (pulse rate, iPhone app and GuilleMonitor) also demonstrated that our process of determining heart rate from light signals recorded by the GuilleMonitor, autocorrelation function analysis (ACF), is an appropriate method. This accuracy is as expected since pulse oximetry is widely used in human healthcare initiatives (Thoms et al. 2007; Funk et al. 2010; Tamura et al. 2014), the pulse sensor was specifically designed and optimised for humans, and ACF is a reliable method of estimating blood flow (Tsalach et al. 2014).

Despite the success in human tests, the signals from chickens measured by the GuilleMonitor did not correlate closely with heart rates measured by the established method using ECG. This lack of correlation suggests that the GuilleMonitor did not measure chicken heart rates accurately. This in turn indicated that signals measured in guillemots and razorbills were also inaccurate. Since the GuilleMonitor accurately measured heart rate in humans, this indicates that there is some difference between the human, and chicken and seabird methodology which caused the discrepancy. This discrepancy could be due to differences between: (1) contents of mammalian and avian blood, (2) the locations of measurement (skin vs brood patch), (3) detection of blood flow, or (4) presence of blood flow. I now discuss each of these possibilities in turn.

Blood contents

Mammalian haemoglobin differs from avian haemoglobin such that the photometric behaviour is affected, which creates an issue for measuring oxygen saturation of avian blood using light. Traditional pulse oximetry measures oxygen saturation of haemoglobin by emitting both visible and infrared light and recording the relative wavelengths of light reflected from capillaries: oxyhaemoglobin reflects less infrared light (850-1000 nm), whereas deoxyhaemoglobin reflects less visible red light (600-750 nm), so as the proportion of oxy- and deoxyhaemoglobin changes with each heartbeat, the wavelength of light reflected changes. This type of pulse oximetry has previously been shown to be unsuitable for estimating oxygen saturation in avian blood (Schmitt et al. 1998). However, in the present study we avoided this issue by using a type of pulse oximeter which does not attempt to measure oxygenation of the blood. Instead, the pulse sensor we used was a simpler version which used visible light only to measure the fluctuations in light reflected by arterial pulses as the heart beats; the oxygenation of the blood is not measured, rather the change in light intensity reflected by the capillaries expanding and decreasing in size as blood is pushed through them by the heart. Therefore, the difference in photometric behaviour of human and avian haemoglobin is unlikely to account fully for the discrepancy between the accuracy of human heart rates and avian heart rates measured by our pulse sensor.

Contact with brood patch

The brood patch is typically a defeathered, swollen and highly vascularised area of ventral abdominal skin (Bailey 1952; Lea and Klandorf 2002). The high number and large size of blood vessels in the brood patch led us to believe that light signals reflected from the pulse oximeter would not be disturbed by other tissue, so would be a reliable method of measuring blood flow in birds with brood patches. Conversely, the pressure of the bird sitting on the artificial egg may have distorted the signal recorded, or could reduce the ability of the capillaries to expand as blood is pumped through them. The heightened pressure is unlikely to explain the lack of correlation between different methods of measuring chicken heart rates because the artificial egg was simply held to the brood patch, so would have been under similar pressure to the pulse sensor when tested on humans, and because a clear signal *was* produced, but at a slower BPM than expected. The signal from guillemots and razorbills, where the artificial eggs were incubated and under pressure from the body, may simply be noise. This potential lack of signal suggests that the body pressure may be reducing the ability of the capillaries to enlarge, although this would require further tests to clarify if this was the problem.

To read a signal the pulse sensor must be in direct contact with the brood patch. I attempted to ensure the pulse sensor was facing upwards towards the brood patch by weighting the egg appropriately, while also enabling normal egg-turning behaviour. It is possible, therefore, that at times the pulse sensor faced away from the brood patch, yet when the pulse sensor is in contact with a solid surface, such as the ground, a steady signal is recorded. The regular pulsing signal therefore suggests that the pulse sensor was in contact with an animate surface i.e. the brood patch or surrounding skin.

Detection of blood flow

Blood flow through the brood patch may be difficult to detect using the pulse oximeter for four reasons. First, the hyper-vascularisation (i.e. the increase in the number and size and of local blood vessels) during development of the brood patch is associated with an increase in the thickness of the muscular walls that line the arterioles (Lea and Klandorf 2002), so the brood patch blood vessel walls may be too thick to allow sufficient light through to detect a change. Galliformes exhibit a relatively lower degree of vascularity and oedema compared to a typical passerine (Jones 1971), which may be an additional factor reducing the suitability of chicken brood patches for pulse oximetry. However, it is clear that the pulse sensor recorded a strong signal in chickens in our study, which suggests that detection of blood flow was not an issue. Second, since the pulse sensor was designed and optimised for human use, it is possible that it is not sufficiently sensitive for use in birds. However, the strong signal recorded by the pulse sensor suggests that the sensitivity of the pulse sensor was not an issue. Third, it could be supposed that blood flow may be difficult to detect from the sampling frequency, but a sampling frequency of ~20 ms enables detection of signals up to 1500 BPM, so the sampling frequency did not restrict the detection of blood flow. Fourth, blood flow may be difficult to detect using our chosen statistical method of estimating heart rate. I was limited to using ACF because sampling was slightly irregular: samples were taken approximately every 20 ms (19-22 ms). If samples were taken regularly every 20 ms then I could have used Lomb-Scargle periodograms to estimate the signal repetition i.e. the heartbeat, which may be more appropriate. However, this is unlikely to be an issue in the detection of blood flow because this type of statistical calculation of the heart beat worked accurately in estimating human heart rates in the current study. In summary, detecting blood flow in the brood patch is unlikely to be restricted by either the thickness of the blood vessel walls, sampling frequency or statistical estimation of repeating patterns.

Presence of blood flow

The function of the brood patch is to transfer heat to the eggs by flowing warm blood close to the egg surface. This method of heat transfer suggests that a change in the rate of blood flow in the brood patch could quickly alter the temperature of the egg. For example, if the incubating bird becomes stressed and the heart rate quickens, the flow of blood through the brood patch would increase, and could cause the temperature of the egg to increase. Since it is imperative to maintain the developing embryo(s) close to a specific temperature (Webb 1987; DuRant et al. 2013), heat transfer from the incubating parent to the developing embryo is regulated by several means. First, by parental behaviour i.e. adjusting the duration and tightness of contact with the eggs (White and Kinney 1974) or parental regulation of heat production (Vleck 1981; Hill et al. 2014). Second, through embryonic behavioural and physiological plasticity (Du and Shine 2015), and third, using specialised morphology in the brood patch. Such morphological adaptations include the development of arteriolar musculature which permits more efficient reduction in blood flow to the brood patch when parent birds off the nest (Brummermann and Reinertsen 1992), arteriovenous anastomoses (AVAs) which are low-resistance medium-sized blood vessels through which blood can be shunted through without going to capillaries (i.e. play a chiefly thermoregulatory role) (Midtgard 1988), and temperature sensors in the skin of the brood patch to create a network of feedback loops (Brummermann and Reinertsen 1991). These sophisticated adaptive regulatory mechanisms by the brood patch may contribute to the mismatch between signals measured by the GuilleMonitor and the heart rate: the expansion and contraction of brood patch blood vessels can be regulated independently of the heart in response to temperature changes, yet the GuilleMonitor measures changes in blood vessel shape, presumed to be produced by the heart pumping blood through the blood vessels. This central nervous thermoregulatory system may be the cause of the misleading signals measured by the GuilleMonitor.

Another potential explanation for the inaccurate signals recorded by the GuilleMonitor may be due to the wavelength of light used by the pulse sensor. Our pulse sensor used visible light and recorded the visible light reflected, which changes as blood vessels slightly change shape. An early version of a pulse oximeter, a ‘photoelectric pulse transducer’, used infrared light in an artificial egg with the intention of measuring the heart rates of incubating penguins by contact with the skin of the brood pouch (Nimon et al. 1994; Nimon et al. 1996). Although heart rate measurements by this method were not verified by a second method, the heart rates of Adelie penguins *Pygoscelis adeliae* (83.8 ± 7.3 BPM: Nimon et al. 1995) were similar to those measured by implanted ECG electrodes (86 ± 5 BPM: Culik et al. 1989). This similarity suggests that infrared light can be used to measure heart rates (via change in oxygenation of blood as the heart pumps) via the brood patch in birds, whereas our results suggest that visible light may not be appropriate for measuring heart rate. Other studies using infrared pulse oximetry accurately measured heart rates from the tongue, wing and leg of anesthetised birds (Schmitt et al. 1998; Lorenzoni and Wideman Jr. 2008; Müller et al. 2011) providing further indication that infrared light may be more appropriate for measuring heart rates compared to the visible light used in the current study. Further work should investigate the use of terahertz (THz) light (between the microwave and infrared regions of the electromagnetic spectrum) because THz pulsed imaging shows promise for measuring and characterising blood flow *in vivo* in real time (Sun 2011; Jeong et al. 2013; Cherkasova et al. 2016).

Although the GuilleMonitor did not measure the heart rates of birds tested, regular signals were recorded. If the GuilleMonitor is not measuring heart rate, then what is it measuring? One possibility is breathing rate, which would be useful because respiration rate can also be used as a proxy for stress (Carere and Van Oers 2004). However, the regular signal pattern is unlikely to be breathing rate because signals recorded were sharp spikes, rather than the shallow waveform I would expect from breathing (Helfenbein et al. 2014). In guillemots and razorbills, however, the signals produced are more likely to be noise rather than a meaningful signal.

Despite the inability to measure heart rate in birds, this innovative prototype heart rate monitor has considerable potential for use in incubating birds. I have demonstrated that heart rate monitors inside artificial eggs can be accepted by species which use egg colour and pattern to recognise their egg, and shown that recent technological advances facilitate opportunities for detailed monitoring. I have characterised the limitations of pulse sensors, and encourage future work to focus on developing the use of alternative wavelengths of light for pulse oximetry in avian species. This project broadens possibilities for monitoring and understanding physiological responses to behavioural and environmental fluctuations in birds.

Chapter 6

General discussion

Discussion

In the preceding chapters I described the use of a long-term data set, field observations and comparative analysis to examine the role of allopreening in social relationships both within and between breeding pairs of birds, and the design of a method for investigating a proximal mechanism of allopreening. In this final chapter I summarise the findings of the previous chapters and discuss possible implications. I conclude by suggesting future work that would further expand our understanding of social grooming in group-living animals.

Summary of results

In Chapter 2 I examined the social structure of a common guillemot colony by quantifying site fidelity and natal philopatry of ringed individuals between 1997 and 2015. This study yielded four important findings. First, breeders returned to the same breeding site in consecutive years 90% of the time, creating a stable social structure in the colony. Second, breeders were more likely to return to the same site if they successfully fledged a chick in the previous year, so the stability of the colony structure was partially related to breeding success. Third, to a small degree, for young and inexperienced breeders, familiarity with neighbouring breeding conspecifics was positively associated with breeding success, but this is not the case for older and more experienced breeders. Fourth, measurements of natal philopatry suggest that related individuals are no more likely to breed at nearby sites than unrelated individuals, so the guillemot colony is not structured by kin. Together, these results indicate that cooperative behaviours between neighbouring breeding guillemots (e.g. anti-predator behaviours, alloparenting) are more likely to have evolved by reciprocal or mutualistic benefits, enabled by social stability, rather than kin-selected indirect fitness benefits.

In Chapter 3 I investigated whether rates of allopreening between neighbouring guillemot breeders was associated with the strength of their social relationships. I found that allopreening rates were higher between neighbouring conspecifics that were had been breeding at adjacent sites for more than four years, compared to those that had been breeding at adjacent sites for less than two years. I also found that allopreening rates between neighbouring breeders did not vary with age, sex, number of neighbours or stage of the breeding season. These findings demonstrate, for the first time, that breeding guillemots form social relationships outside the breeding pair bond.

To complement the findings of Chapter 3, in Chapter 4 I tested the hypothesis that allopreening is associated with strong pair bonds using a comparative phylogenetic analysis. I investigated whether rates of allopreening within breeding pairs are associated with several different aspects of the pair bond in 503 bird species. I found that species that allopreened were more likely to breed with the same partner in consecutive breeding seasons, and were more likely to share parental duties, compared to species that did not allopreen their breeding partner. However, allopreening was not associated with sexual fidelity, time spent together outside of the breeding season, colonial breeding or cooperative breeding. To understand the evolution of the role of allopreening in strengthening the pair bond, I analysed evolutionary transitions between the presence and absence of allopreening in relation to parental cooperation and divorce rates, which indicated that allopreening evolved from an ancestral state of either high parental cooperation or high partner retention.

In contrast to Chapters 2-4, which explored the ultimate causes of allopreening behaviour, Chapter 5 considered the proximate cause of allopreening within social relationships: I aimed to test the hypothesis that allopreening reduces stress. I designed and tested a novel method of measuring stress in group-living incubating birds, by using a heart rate monitor (pulse sensor) in an artificial egg. An artificial egg containing the pulse sensor (referred to as the 'GuilleMonitor') accurately measured the heart rate of humans, but did not accurately measure the heart rates of avian species tested. Consequently, the prototype GuilleMonitor is not yet useful in its current form for measuring stress in birds, but placement tests indicated that, with modifications, a functioning heart rate monitor in an artificial egg would plausibly work in remote and difficult environments.

Implications

In this thesis, my principal aim was to determine whether allopreening has a function in maintaining social relationships in groups and within breeding pairs of birds. Overall, my results support the hypothesis that allopreening is associated with strong social relationships: I provide the first evidence that guillemots form social relationships outside the breeding pair bond, and show, for the first time, that allopreening is associated with partner fidelity and contributions to offspring care across the avian phylogeny. These findings contribute to our knowledge and understanding of the proximate and ultimate functions of allopreening in birds, and have implications for the future study of social behaviour in birds.

Guillemot colonies fulfil criteria for reciprocity to occur: the population structure allows individuals to interact repeatedly with the same individual. However, a key finding of this thesis is that allopreening interactions were not reciprocated between all neighbouring breeders; rather, allopreening was selectively allocated to specific individuals. Since allopreening was selectively allocated to familiar individuals, this suggests that guillemots have sufficient cognitive ability to recognise, or at least distinguish between, familiar and less familiar conspecifics. It has been traditionally assumed that such social relationships are confined to species with higher cognitive capabilities, because a certain level of cognition is required to keep track of past interactions with specific individuals (Milinski and Wedekind 1998; Dugatkin 2002). However, the stable population structure of guillemot colonies enables individuals to form social relationships with specific neighbours. This suggests that the formation of social relationships does not require advanced cognition (Pfeiffer et al. 2005) and may therefore be widespread among long-lived and site-faithful species. My findings suggest that familiarity may influence social behaviour in other group-living avian species, and as such, should be investigated in other group-living birds.

The work presented in this thesis also has implications for our understanding of the evolution of allopreening behaviour. The phylogenetic comparative analysis of allopreening between breeding partners indicates that allopreening evolved where it was adaptive to breed with the same partner in consecutive breeding seasons and/or where it was adaptive for both parents to contribute equally to offspring care. One interpretation of this finding is that allopreening originally evolved for hygienic reasons in these species: in order to maximise the likelihood of a partner surviving to the next breeding season, or enable a partner to contribute effectively to offspring care, a partner should try to maintain the health of a partner by removing their ectoparasites. However, I think it is more likely that allopreening evolved to enable the partner to survive to the next breeding season and fulfil necessary parental duties, rather than to evolve specifically to maintain and encourage these behaviours. This interpretation aligns with the hypothesis that social grooming evolved primarily with a hygienic function, and later developed a social function (Alexander 1974; McKenna 1978; Dunbar 1991), but further work into the downstream physiological effects of allopreening would provide further insight.

Finally, the work of this thesis has furthered our understanding of the influences of group and population dynamics on each other. I showed that reproductive success influences, and is influenced by, individual site fidelity, and hence the social stability of the colony. Consequently, a highly productive colony is likely to be more socially stable than one with a lower reproductive success, and in turn, a socially stable colony is likely to be more productive than a less socially stable colony. This reinforcing feedback loop means that colonies with low social stability or low reproductive success may struggle to escape a cycle of low productivity i.e. an Allee effect (Courchamp et al. 2008). Low social stability is partially caused by low survival rates, which can be influenced by a range of environmental variables including as sea surface temperatures (SST) and the North Atlantic Oscillation (NAO), as well as human impacts such as oil spills (Sandvik et al. 2005; Votier et al. 2005; Sandvik et al. 2012). Consequently, the changing climate indirectly affects site fidelity, social stability and productivity, and may contribute to colonies being locked into an unfavourable cycle of diminishing reproductive output. Indeed, for locations where guillemot populations are declining (e.g. Scotland, JNCC 2016; Norway, Barrett et al. 2006) the results of this thesis have important implications for predicting population dynamics. Additionally, by showing the importance of social behaviour and familiarity with neighbouring breeders, this work contributes to our understanding of the different factors affecting population stability.

Common guillemots are an important indicator species; they are sensitive to environmental conditions in the oceanic ecosystem, and consequently can serve as a warning sign of environmental change to biologists and conservationists (Piatt et al. 2007). Long-term monitoring of such species is crucial for understanding the causes and consequences of changes in population dynamics (e.g. mortality and productivity), but this thesis suggests that incorporating observations of social behaviour may provide a deeper understanding of animal population dynamics in a changing climate.

Future directions

While this thesis has addressed the role that allopreening plays in social relationships, both within and between breeding pairs, several other issues have arisen that warrant consideration in future research.

First, I was unable to provide definitive evidence to support the hypothesis that allopreening is associated with reduced stress in participants. Unfortunately, the prototype heart rate monitor I developed did not accurately measure heart rates of incubating birds, although other studies suggest that a small modification to the pulse sensor used may resolve the issue. To employ this method of monitoring heart rate for investigating the proximate function of allopreening, the behaviour of the bird incubating the artificial egg would need to be recorded on video, and matched to the heart rate. The data file produced by the artificial egg contains the light signal measurement (recorded every 20 ms) and the time, to enable the measurements to be time-matched to the behaviours recorded. For example, if a bird received allopreening from 18:30:15 until 18:30:46, the researcher would look in the data file at the specific time and calculate the most likely heart rate during that allopreening interaction (using methods described in Chapter 5).

To test whether allopreening is associated with lower stress in birds, I would compare (a) the mean heart rate of birds at the beginning of receiving an allopreening bout with the end of receiving the allopreening bout, and (b) the mean heart rate of birds receiving allopreening with the mean heart rate of those same birds when they were resting or asleep; these comparisons have been employed to investigate whether allogrooming was associated with decreased heart rate in pigtail macaques *Macaca nemestrina* (Boccia et al. 1989), rhesus macaques *Macaca mulatta* (Aureli et al. 1999) and horses *Equus caballus* (Feh and de Mazieres 1993). Since there is a clear next step for developing the design of the heart rate monitor to enable accurate measurements in incubating birds, and the prototype was successfully introduced to incubating birds in large remote colonies, I strongly encourage that this prototype be developed. The potential of a functioning heart rate monitor in the form of an artificial egg is vast: as well as investigating the proximate function of allopreening, these artificial eggs could be used to monitor stress in a range of avian species in a variety of habitats during the critical reproductive stage of the life cycle. For example, as a wireless, inexpensive, robust and non-invasive method, this form of heart rate monitor could be employed by conservationists to monitor the effect of human disturbances on stress levels in birds, informing conservation practices. One context where such monitoring would be extremely useful is on Skomer Island: a Site of Special Scientific Interest and a Special Protection Area where tens of thousands of tourists visit each year. Currently, visitors are allowed to be extremely close to Atlantic puffin *Fratercula arctica* and Manx shearwater *Puffinus puffinus* burrows, which may impact the physiological wellbeing of these species. Monitoring and comparing the stress levels in these individuals with individuals elsewhere on the island would be useful in investigating whether such human disturbance impacts stress levels of these birds. Since microphones in artificial eggs would pick up sounds from the visitors, such monitoring methods cannot currently be used, yet a functioning heart rate monitor as described in Chapter 5 could elucidate any effect of human disturbances on stress levels in these seabird colonies of worldwide importance.

Second, future work on allopreening should include experimental studies. Research on the ultimate social function of allopreening has thus far been restricted to observational methods, yet experimental work is vital in order to provide the strongest evidence that allopreening is associated with social relationships. I designed and conducted an experiment to test whether allopreening rates were associated with social relationships, yet the outcome did not fulfil the experiment aims. I aimed to force familiar neighbouring guillemots to separate and breed next to unfamiliar birds, and compare those individuals' allopreening rates before, during and after this change in social environment. At the beginning of the breeding season guillemots spend 2 to 4 days on the Amos before returning to sea for 2 to 4 days, and repeat this cycle a number of times before laying their eggs (Birkhead 1978b). During one such cycle I recorded the allopreening interactions of specific birds for whom I knew the duration of their neighbour tenureship, and when the colony left the Amos I attached devices to the cliff at these locations to prevent guillemots from accessing their breeding site. However, the devices (a set of short wooden spikes arranged such that guillemots could not stand on them, but would not be harmed if pushed into them) did not sufficiently change the social environment: the guillemots simply squeezed in closer together so the individuals they interacted with remained the same as before the devices were attached, and I was constrained from repeating the experiment with larger devices by the onset of egg laying. One ideal experiment would require access to a captive population of birds, of a species that allopreen outside the pair bond, where the social environments can be manipulated. Allopreening interactions between familiar birds could be compared with allopreening interactions of the same individuals but with unfamiliar social partners, while controlling for changes in physical environment as well as individual differences in behaviours. If allopreening rates were higher between familiar individuals than unfamiliar individuals, and rates increased as familiarity increased, then this would be the first experimental evidence that allopreening was associated with social relationships.

Third, the development of allopreening behaviour from juveniles to adults has, to my knowledge, not been investigated. If allopreening is important for building social relationships, and the skill or effectiveness of allopreening develop with age and experience, then one contributing factor to the reduced productivity observed in young and inexperienced individuals (reviewed in Moreno 1998) may be a lack of the necessary social skills. Furthermore, the direction of causation of allopreening and social relationships remains a mystery: does allopreening create and maintain social relationships, or are social relationships formed by some other mechanism and subsequently maintained by allopreening? Tackling such questions would be an interesting direction for further research into allopreening.

Fourth, I would encourage those studying species that allopreen to quantify the amount of time individuals dedicate to allopreening, and record the identity of individuals to whom allopreening is allocated. Working with presence/absence data greatly limits the quality of information available, and therefore the questions we can ask and the conclusions we can draw. Quantifying rates of allopreening in a range of species would help to elucidate the impact of allopreening on fitness.

Concluding remarks

Allopreening is a relatively common behaviour in birds, yet its causes and consequences have received little attention. The association between social grooming and social relationships has been examined chiefly in primates (e.g. Seyfarth and Cheney 1984; Schino 2007, Silk 2009), although growing evidence suggests that social grooming also plays a social role in birds (e.g. Spoon et al. 2006; Gill 2012; Kenny et al. 2017; Chapters 3 and 4). Long-term studies enable investigations into social associations between individuals, and when combined with observational data, can provide further insight into the evolution of social behaviour in birds. I hope that the results of this thesis will contribute to future studies that examine the social role(s) of allopreening in birds and, in conjunction with similar studies, help us better understand the vital role of social behaviour in group-living.

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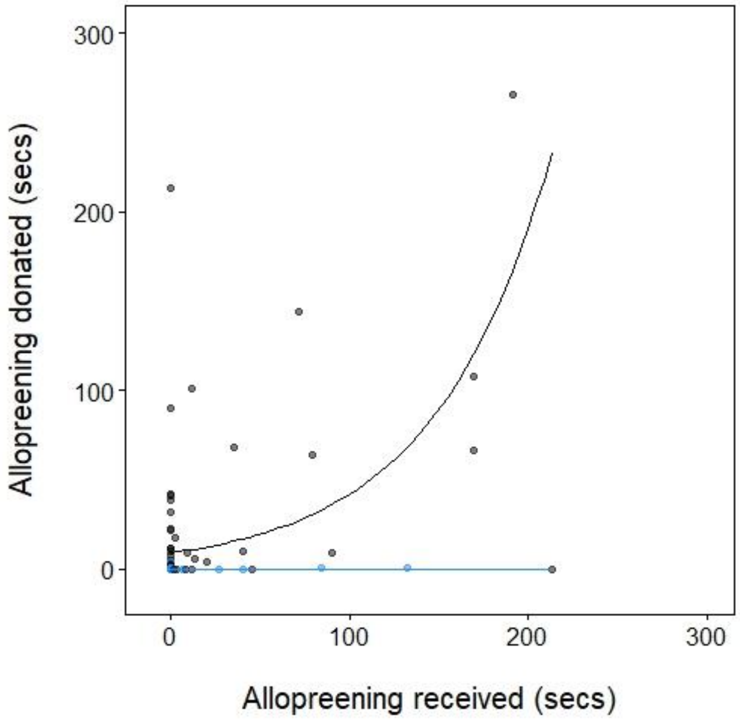
Appendix A

Supplementary material to Chapter 3



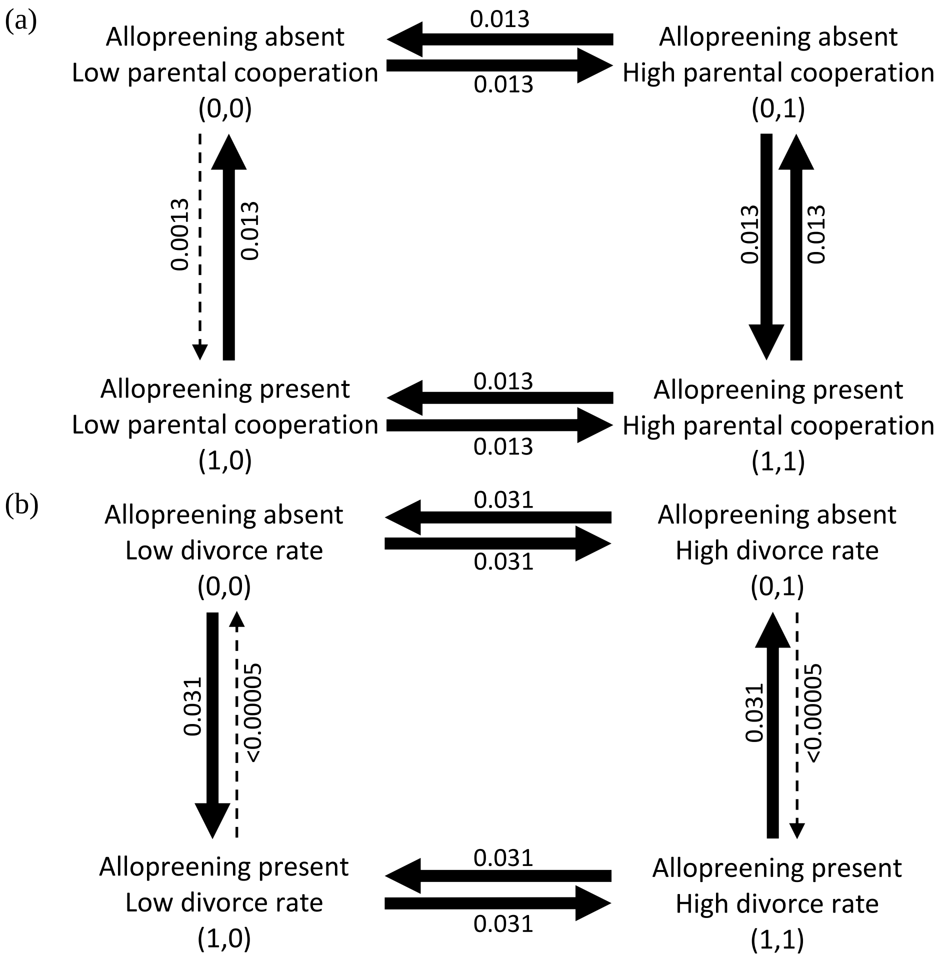
Appendix figure A1. Relationship between allopreening donated and received within dyads of common guillemots in short neighbour tenures (blue: n = 41 observations of 10 dyads) and long neighbour tenures (black: n = 70 observations of 12 dyads). The intensity of colour indicates point density. Lines show model predictions. One data point appeared to have particularly strong influence over the model predicted line for short neighbour tenures (p70), so has been removed. Consequently, the model predicted line for short neighbour tenures appears to fit the data much better.

Appendix B

Supplementary material to Chapter 4

Appendix table A1. Results from the full model testing the association between presence/absence of allopreening behaviour and measures of pair bond strength (n = 37 species). Estimates are modal estimates from 100 models. Lower CI = lower 95% confidence interval. Upper CI = upper 95% confidence interval. Parameter estimates were considered statistically significant when 95% confidence intervals did not include 0. Residual variance was set to 1.

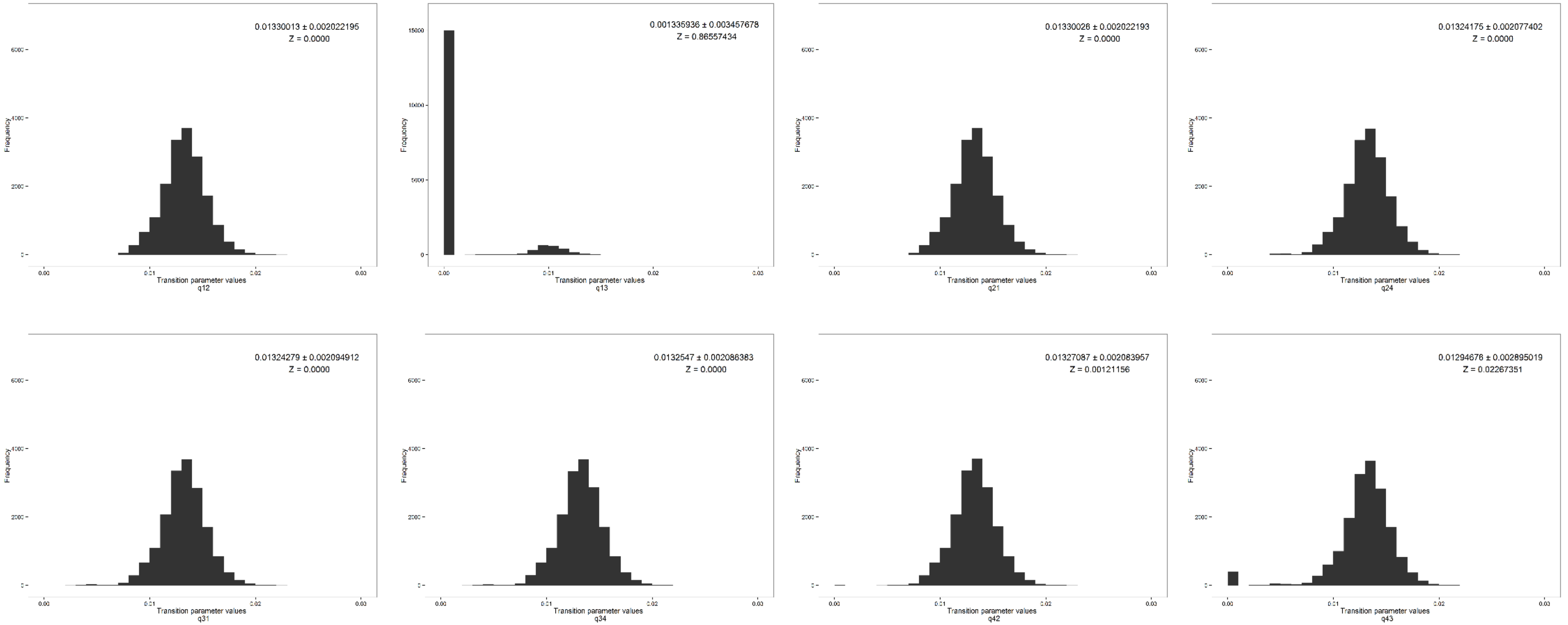
	Estimate (β)	Lower CI	Upper CI
Fixed terms			
Intercept	-0.29	-9.11	8.39
Parental cooperation	8.73	2.77	16.89
Total offspring care	-0.07	-0.19	-0.004
Divorce	-5.31	-15.25	3.25
Mortality	-9.93	-25.85	3.71
EPP	0.18	0.05	0.33
Partnership duration	2.30	-2.21	7.19
Random terms			
Phylogenetic variance	2.44	0.003	10.43
Residual variance	1.00	1.00	1.00



Appendix figure B1. Estimated transition rates for co-evolution of allopreening with (a) parental cooperation over offspring care and (b) divorce rates. ‘High’ and ‘low’ indicates whether species have divorce rates or parental cooperation scores equal to and above the median level (high) or below the median (low). Arrow thickness represents relative transition likelihood.

Appendix table B2. Estimated transition rates for coevolution of allopreening with parental cooperation over offspring care: 10% below median, median and 10% above median. For the ‘10% below median’ model, ‘high’ parental cooperation scores are equal to or greater than 10% below the median score, and ‘low’ parental cooperation scores are less than 10% below the median. For the ‘median’ model, high and low parental cooperation scores are divided at the median. For the ‘10% above median’ model, ‘high’ parental cooperation scores are equal to or greater than 10% above the median score, and ‘low’ parental cooperation scores are less than 10% above the median.

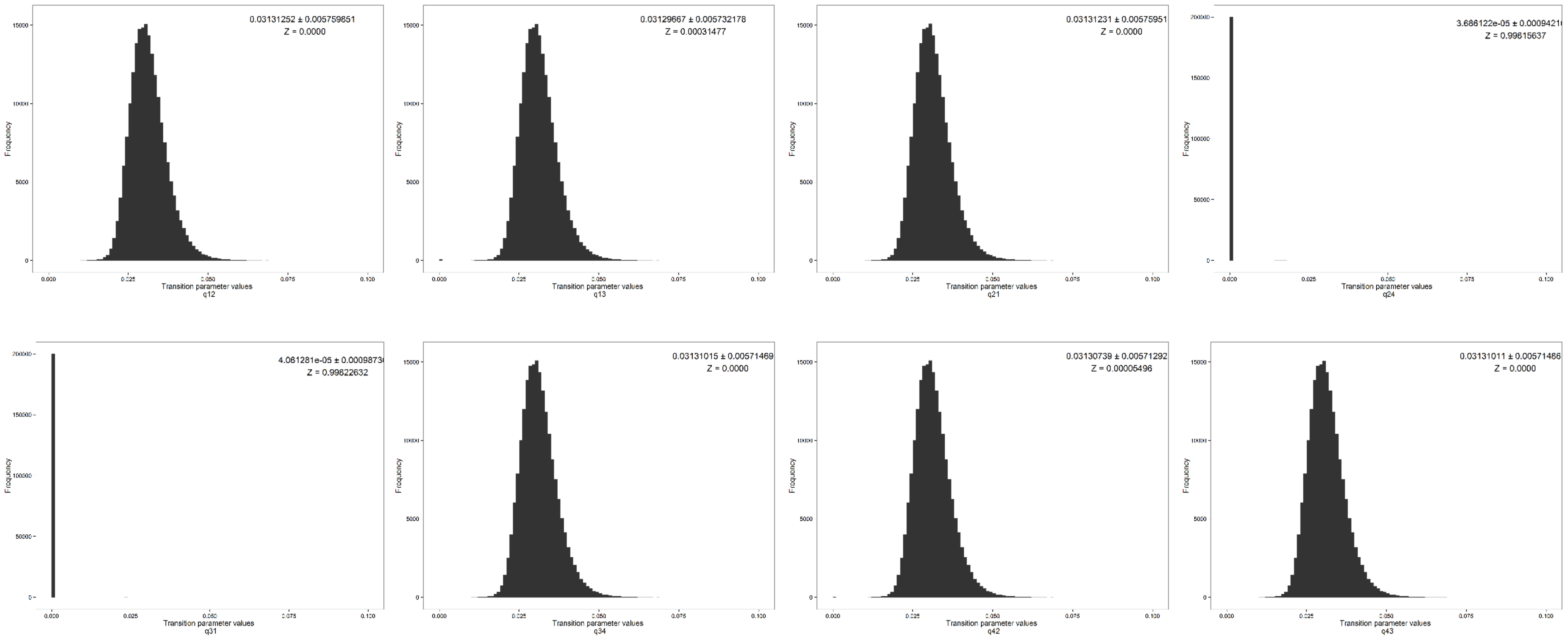
	Evolutionary transition		Evolutionary transition rates		
	From	To	10% below median	Median	10% above median
q12	Allopreening absent Low parental cooperation	Allopreening absent High parental cooperation	0.011	0.013	0.032
q13	Allopreening absent Low parental cooperation	Allopreening present Low parental cooperation	0.005	0.0013	0.032
q21	Allopreening absent High parental cooperation	Allopreening absent Low parental cooperation	0.011	0.013	0.080
q24	Allopreening absent High parental cooperation	Allopreening present High parental cooperation	0.011	0.013	0.008
q31	Allopreening present Low parental cooperation	Allopreening absent Low parental cooperation	0.011	0.013	0.090
q34	Allopreening present Low parental cooperation	Allopreening present High parental cooperation	0.011	0.013	0.008
q42	Allopreening present High parental cooperation	Allopreening absent High parental cooperation	0.011	0.013	0.008
q43	Allopreening present High parental cooperation	Allopreening present Low parental cooperation	0.010	0.013	0.002



Appendix figure B2. Posterior probability distributions of the values of the rate coefficients of the model of correlated evolution between parental cooperation and allopreening behaviour. Z values present the proportion of the sampled runs from the Markov chain in which the parameter was assigned a value of 0. Shown are the mean and standard deviation of the parameter.

Appendix table B3. Estimated transition rates for coevolution of allopreening with partner retention in three different models: 10% below median, median and 10% above median. For the ‘10% below median’ model, ‘high’ divorce rates are equal to or greater than 10% below the median rate, and ‘low’ divorce rates are less than 10% below the median. For the ‘median’ model, high and low divorce rates are divided at the median. For the ‘10% above median’ model, ‘high’ divorce rates equal to or greater than 10% above the median score, and ‘low’ divorce rates are less than 10% above the median.

	Evolutionary transition		Evolutionary transition rates		
	From	To	10% below median	Median	10% above median
q12	Allopreening absent Low divorce rate	Allopreening absent High divorce rate	0.033	0.031	0.031
q13	Allopreening absent Low divorce rate	Allopreening present Low divorce rate	0.031	0.031	0.031
q21	Allopreening absent High divorce rate	Allopreening absent Low divorce rate	0.033	0.031	0.031
q24	Allopreening absent High divorce rate	Allopreening present High divorce rate	<0.0001	<0.0001	<0.0001
q31	Allopreening present Low divorce rate	Allopreening absent Low divorce rate	<0.0001	<0.0001	<0.0001
q34	Allopreening present Low divorce rate	Allopreening present High divorce rate	0.033	0.031	0.031
q42	Allopreening present High divorce rate	Allopreening absent High divorce rate	0.031	0.031	0.031
q43	Allopreening present High divorce rate	Allopreening present Low divorce rate	0.033	0.031	0.031



Appendix figure B3. Posterior probability distributions of the values of the rate coefficients of the model of correlated evolution between divorce and allopreening behaviour. Z values present the proportion of the sampled runs from the Markov chain in which the parameter was assigned a value of 0. Shown are the mean and standard deviation of the parameter.