The mechanisms and consequences of parental coordination in Procellariiform seabirds

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Abstract

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Biparental care is a longstanding evolutionary conundrum. Why should parents continue to invest in their offspring cooperatively, when by abandoning their partner they can reap all the benefits with none of the work? Since the 1970s, several models have attempted to explain the evolution and maintenance of biparental care in animals, eventually converging on the solution of conditional cooperation: a parent's behaviour should depend on the investment decisions of its partner. This responsive strategy can lead to apparent coordination between parents, and many empirical examples have since been reported. However, it is difficult to determine whether there is active behavioural coordination between parents, or indeed the mechanisms underlying it. This thesis uses two long-lived, monogamous seabird species, the Manx shearwater *Puffinus puffinus* and the black-browed albatross *Thalassarche melanophris*, to investigate the occurrence and mechanisms of coordinated parental behaviour. Using both experimental field manipulations and quantitative observations I investigated the evidence for parental coordination in these species, and the mechanisms and information parents may use to achieve it. Firstly, I examined the incubation behaviour of parent Manx shearwaters, and found that their investment decisions were underlain largely by their available body mass reserves, matching life-history predictions that long-lived species should be selected to prioritise their own condition. Specifically, foraging birds determined how long they should spend at sea by the amount of mass gains they needed to make on their trip, with lighter birds spending proportionally more time foraging. However, I found that this decision was modulated by the partner's condition, with birds curtailing their trips when their partner was in poor condition, suggesting that cooperative processes, perhaps facilitated by a process of negotiation, may drive the coordination of care during incubation in this species. For chick-rearing shearwaters, I examined whether direct communication, or indirect information garnered from the behaviour of the chick, might facilitate the coordination of nest visitation. Neither putative sources of information appeared necessary for coordination in this species, and it was not possible to determine conclusively what information drives provisioning behaviour. Instead, I introduced the possibility that coordination at this breeding stage emerges passively through an entrainment process during incubation. Finally, I investigated the potential role of intra-pair display in facilitating coordination in the black-browed albatross, with a focus on allopreening. I report tentative evidence that display forms part of an assessment process whereby the outgoing parent determines its partner's willingness to invest in care, which may ultimately contribute to decision-making processes relating to foraging trip duration. Overall, I present evidence that biparental care in these species may be underlain by nuanced systems of intra-pair coordination, giving further insight into why and how animals are able to achieve cooperative behaviour.

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Declaration and Author Contributions

The work presented in this thesis is primarily my own. Fourteen other authors contributed to the work in this thesis, and their contributions are acknowledged below.

Tim Guilford contributed to the conception, fieldwork, analysis, and manuscript preparation for all chapters.

Oliver Padget helped to design and implement the experiments and analyses used in chapters 1 and 2, and helped with data collection in the field. He additionally provided statistical advice for all other chapters in the thesis.

Sarah Bond contributed ideas to the design of experiments and analyses for chapters 1 and 2, and participated in the fieldwork.

Annette Fayet participated in data collection in the field, contributed her ideas, and helped with manuscript preparation for chapter 1.

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Martyna Syposz helped to design and implement the experiments in chapter 3, contributed ideas and feedback to the conception of experiments for chapter 4, and participated in fieldwork for chapters 1, 2, 3, and 4.

Joe Wynn contributed to the analyses used in chapters 3 and 4 and aided in the manuscript preparation, helped with the design and conception of the experiments in chapter 4, and contributed to the fieldwork for chapter 1.

Cécile Vansteenberghe helped with the design and conception of chapters 3 and 4, and participated in the fieldwork for chapters 2, 3, and 4.

Chris Tyson helped to establish the automatic monitoring network described in chapter 4, and helped to conceive, design and implement the experiments in this chapter.

Paulo Catry helped to design and plan the experiments outlined in chapter 5, provided the demographic data used to support the analyses, and provided feedback on the manuscript.

"The spirit which haunted the coasts have originated in this noise, described as infernal. The disturbed spirit of a person shipwrecked on a rock adjacent to this coast wanders about it still, and sometimes makes so terrible a yelling that it is heard at an incredible distance. They tell you that houses even shake with it; and that, not only mankind, but all the brute creation within hearing, tremble at the sound. But what serves very much to increase the shock is that, whenever it makes this extraordinary noise, it is a sure prediction of an approaching storm. At other times the spirit cries out only, "Hoa, hoa, hoa !" with a voice little, if anything, louder than a human one."

–*Puffines of the Calf.* Account by Chaloner, 1656.

"This working of three to five days in shifts was an interesting discovery and something quite new in the practice of incubation. It was clear, too, that the sexes took a fairly equal share in the responsibility. And instead of the cock feeding the sitting hen, as is the case in so many species of birds, they arranged it more fairly: one was to fast while the other feasted, for so many days at a time. 'Adam', said Ada, 'I am off for a week-end at sea.' 'Very well', replied Adam, 'will it be a long or a short week-end, my dear?' 'Aha', said Ada mysteriously, 'that all depends on the little fishes.' And off she would go."

–Ronald Lockley, *Shearwaters*.

"Why would you waste your time with that? Didn't Lockley do it all in the 50s?"

–An eminent ornithologist.

Fortunately, there were some bits Lockley missed...

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Introduction

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1.1 Introduction

Though biparental care is one of the most conspicuous forms of cooperation between non-kin in the Animal Kingdom, it also poses a paradox. While the two parents have a shared stake in the rearing of their offspring, they must only pay the cost of their own investment (Chase, 1980). Consequently, any parent who can desert its offspring, and the associated costs of rearing them, serves to gain if its now-abandoned partner is capable of, and willing to, successfully rear the offspring alone. Because of this, biparental care should be evolutionarily unstable (Trivers, 1972), as the ensuing competition between parents to ensure their partner does the lion's share of the work should lead to abandonment by one parent, and thus uniparental care, or should result in the offspring of biparentally-caring parents having a lower fitness than if just one had provided care (Royle et al., 2002; McNamara et al., 2003). Despite this, biparental care has evolved multiple times and is widespread, particularly in birds, where 83% of species exhibit some degree of joint care (Cockburn, 2006).

For all animals, the decision whether and how much to provide care to the offspring reflects a careful evolutionary trade-off in which expenditure in a single breeding attempt must be balanced against the costs of this for future reproductive success and survival (Trivers, 1972; Drent & Daan, 1980). In plainer terms, animals are expected to invest in reproduction such that they produce the maximal number of surviving offspring over their entire lifespan (Lack, 1968). In species where both parents contribute to the care of offspring, striking this balance is complicated by the presence of a partner. Early models that sought to explain the existence and persistence of biparental care largely viewed parents as making their decisions in isolation of their partner: in these 'sealed bid' models (Chase, 1980; Houston & Davies, 1985), behaviour is fixed over evolutionary time and parents cannot adjust their responses dynamically. But parents are unlikely to make their investment decisions independently of each other's behaviour, and in many cases should be expected to observe and respond to one another's contributions so that they can care for the brood in such a way that maximises the efficiency and efficacy of their respective contributions. More complex models explored this idea in the form of conditional cooperation (Johnstone et al., 2014), whereby both parents determine their respective investment based on the contributions of the partner over a behavioural time-scale. Such a mechanism may give rise to synchronous patterns in the parental behaviour of partners, and this emergent behavioural interaction may be referred to as coordination (Ihle et al., 2019). Such behaviour has since been identified in a wide range of biparentally-caring species, but the mechanisms allowing parents to achieve coordination are largely not well understood.

This thesis aims to quantify and examine parental care behaviour and its coordination during the long breeding season of two long-lived, monogamous, Procellariiform seabird species: the Manx shearwater *Puffinus puffinus* and the black-browed albatross *Thalassarche melanophris*. Both species lie at the extreme slow end of the fast-slow life history continuum (Stearns, 1992), exhibiting delayed maturity, an extremely protracted period of parental care, and long-lasting socially monogamous pair bonds (Warham, 1980). Procellariiforms are notable for their long-duration foraging trips, which they undertake in order to exploit rich, unpredictable locations far from their breeding colonies. Such trips mean that during the breeding season, parents must provide care for their offspring cooperatively with the partner despite limited opportunity for direct communication. These species therefore represent a unique opportunity to examine the mechanisms by which coordination can be achieved in an unpredictable environment, and represent an extreme example of the importance and difficulties of information flow. As such, both are excellent models to elucidate the mechanisms and consequences of parental coordination in monogamous species. Such knowledge will help advance our understanding of how biparental care is maintained across the Animal Kingdom, which is fundamental to understanding the evolution of mating strategies.

1.2 A brief history of the study of biparental care

In 1972, Trivers first formalised the observation that biparental care necessarily leads to sexual conflict, as while each parent stands to benefit from parental investment, it only pays the cost of its own contribution. Given this, he predicted that the parent that has invested least in the breeding attempt so far should be selected to desert its partner, rendering biparental care evolutionarily unstable. Chase (1980) used these observations to describe how in any interaction between animals, individuals are expected to partition their investment between cooperative and non-cooperative behaviour such that they can maximise the net gains they will make from this. In any situation in which an animal can gain from the collective good of cooperative behaviour without themselves contributing, conflict will arise between the actors. Chase further formalised the biparental care conundrum, explaining that when animals care for their offspring in tandem with a partner, cooperative and non-cooperative behaviour can be viewed as investment in the breeding attempt versus investment in self-conservation respectively, and it is from individual parents' decisions on the optimal partitioning of this investment that conflict arises. While biparental care exhibits a reasonably limited phylogenetic distribution, occurring mostly in birds (Clutton-Brock, 1991), within this Clade it is extremely widespread, occurring in 83% of species (Cockburn, 2006). This demonstrates that biparental care can clearly exist as an evolutionarily stable strategy, and so this conflict must be resolved somehow. In the ensuing decades, a suite of authors sought to resolve this paradox using a series of modelling approaches.

In 1985, Houston and Davies developed the 'sealed bid' model of biparental care as a solution to this problem. In this model, each parent makes a single bout of investment (its 'sealed bid'), which is set independently of its partner's behaviour and does not thereafter change. By modelling the optimal strategies of males and females given a variety of conditions and situations, the authors modelled the best response curves for each parent over an evolutionary time scale. However, clearly a genetically-determined mechanism for setting investment levels would be vulnerable to cheating mutants that exploit the partner's contribution. In two seminal papers, McNamara et al. (1999, 2003) identified that to resolve this problem, parental investment needed to be considered on a behavioural, not evolutionary, time scale, as variation in mate quality means that individuals have varying costs of reproduction and therefore different optimal investments. While they used parental investment as an illustrative example, the models developed by McNamara et al. could apply to any interaction between animals in which there is a conflict in fitness interests between the actors. The authors were the first to explicitly introduce the concept of negotiation into models of biparental care, using an alternating model in which each parent takes it in turn to choose its level of investment in a cost- and benefit-free negotiation period. Each parent makes its 'bid' depending on the most recent choice of the partner, ignoring its own previous investment and any contributions made by the partner up to this time point. The negotiation ends when the parents reach a stable outcome, and their final decisions essentially become sealed bids. Through this, parents can identify their optimal level of investment according to the state of their partner, allowing individuals to tailor their decision-making to variation in partner quality.

These models are united by their prediction that individuals should only partially compensate for a decrease in their partner's effort as a means to avoid exploitation, which could ultimately lead to breeding failure or uniparental care. In other words, if one parent were to reduce its workload, the other would not make up for the shortfall in care completely, so that parents could not be selected to 'cheat' their partner by reducing their workload below their actual capacity. However, empirical evidence does not consistently align with these predictions (Harrison et al., 2009): the responses of parents to a reduction in care by the partner include no change in effort (Lifield & Slagsvold, 1990; Schwagmeyer et al., 2008; Beaulieu et al., 2009), partial compensation (Wright & Cuthill, 1990; Markman et al., 1995), or full compensation (Sanz et al., 2000; Osorno & Székely, 2004; Paredes et al., 2005). In an effort to explain this variation, Johnstone and Hinde (2006) extended the approach developed by McNamara et al. (1999, 2003) to allow uncertainty about brood need. If parents can learn about the state of their offspring based on the behaviour of their partner, this may select for different responses to a reduction in partner effort, including investment matching. As such, the responses of individuals to the effort of their partners will vary according to asymmetries in the information that is accessible to them.

Recent models have incorporated more complex mechanisms of negotiation that may more closely resemble the reality of parental behaviour, and have been adapted to allow behavioural negotiation to continue throughout the breeding attempt. Lessells and McNamara (2012) extended the negotiation concept by integrating the negotiation and investment phases and allowing these to continue throughout breeding. In brief, each parent continues to make a series of bouts of investment, but at each stage parents can assess how much care their offspring have received up to this point and decide their best response based on this. However, a crucial omission is that the state of the offspring cannot inform the parents on the relative contributions of its partner, and the resulting sexual conflict means that the amount of care provided to the offspring is still lower than would be expected from a single parent system. This led Johnstone et al. (2014) to introduce the concept of 'conditional cooperation', in which individuals alternate their provisioning in such a manner that allows them to a) directly assess the contribution of their partner and b) withhold care until the partner has contributed. Like the early McNamara models, in this model parents follow a negotiation paradigm in which they behaviourally respond to the investment of their mate over time. However, two key changes alter the predicted responses of parents: firstly, parents respond to both their own previous level of investment, and that of their partner, and secondly, parents can adjust their level of investment by changing their visitation rate to the nest. This reciprocal approach maintains efficient investment in the breeding attempt, results in a greater total parental investment, and leads to an optimal provisioning rate that maximises the fitness of both parents.

Such active turn-taking is an example of coordinated parental behaviour, in which individuals exhibit behavioural responsiveness to other family members relating to investment or tasks (Ihle et al., 2019). This approach to the problem of raising offspring with non-related individuals can reduce sexual conflict by allowing both members of a pair to maximise the efficiency of their parental investment in an evolutionarily stable manner. Observations of apparently coordinated parental behaviour have been reported in many species (Johnstone et al., 2014; Bebbington & Hatchwell, 2016; Koenig & Walters, 2016; Savage et al., 2017; Iserbyt et al., 2019; Khwaja et al., 2019; Mariette, 2019), but the mechanisms underlying these have been relatively less explored.

1.3 The coordination of parental care

Empirical examples of coordinated behaviour come in many forms. Some of the first evidence for coordinated parental care came from observations that many species exhibit more synchrony in the timing of nest visitation than would be expected if parents were visiting independently, suggesting that these visits are actively coordinated (Hinde, 2006). Apparently active synchronisation of nest visitation has now been observed in many species (Raihani et al., 2010; van Rooij & Griffith, 2013; Mariette & Griffith, 2015; Leniowski & Wegrzyn, 2018; Khwaja et al., 2019), and may provide direct benefits, for example by reducing predation risk (Raihani et al., 2010; Leniowski & Wegrzyn, 2018), but might also contribute to the coordination of care by facilitating alternation, whereby each parent takes it in turns to provide care to the offspring in a ‘tit-for-tat’ manner, reducing the opportunity for either parent to exploit the other (Johnstone et al., 2014; Bebbington & Hatchwell, 2016; Baldan et al., 2019; Griffioen et al., 2019). While much research has focused on the occurrence and maintenance of synchrony in nest visitation, coordinated parental behaviour may also take on more nuanced forms, such as task specialisation (Itzkowitz et al., 2002; Iserbyt et al., 2017; Lehtonen, 2017), maintaining equality in investment (Ahern et al., 2011; Massoni et al., 2012; Kavelaars et al., 2019), or deciding how much time to invest in foraging versus offspring care (Davis, 1988; Wojczulanis-Jakubas et al., 2018).

While apparently coordinated parental behaviour appears to be widespread, little attention has been paid to the specific mechanisms underlying it, despite the vital importance of this to understanding the evolution of stable biparental care. As the most common breeding pattern in birds, an understanding of the role that coordination mechanisms play in biparental care has wide-ranging implications for our understanding of other facets of avian life history. For example, many long-term monogamous species exhibit increased breeding success with increasing duration of the pair bond (Thomas, 1983; Black, 1996; Westneat and Hatch, 2008; Sanchez-Macouzet et al., 2014; Leach et al., 2020; though see Rebke et al., 2017), and recent evidence suggests that this may be determined at least partially by increased behavioural compatibility (Schuett et al., 2010; Gabriel & Black, 2012; Fox & Millam, 2014; Ihle et al., 2015). Consequently, elucidating the mechanisms by which parental behaviour may be coordinated has important implications for our understanding of mate choice. Furthermore, some forms of coordinated behaviour, for example, synchrony in provisioning visits to the nest, have important consequences for overall reproductive outcomes, having been found to be associated with measures of breeding performance such as nestling growth rate (Mariette & Griffith, 2015) and brood survival (Raihani et al., 2010).

Little research has been dedicated to investigating the putative role of classic avian signalling systems or displays in the coordination of care, despite the fact that most display between pairs of birds occurs after the pair has already formed (Huxley, 1914; Symes & Price, 2015), and therefore cannot be attributed solely to mate choice. Limited empirical evidence has been reported for the role of vocal duetting (Halkin, 1997; Elie et al., 2010; Boucaud et al., 2016) and even allopreening (Kenny et al., 2017) in the coordination of care. Such conspicuous and widespread behaviours have been well-studied in the context of intersexual display, but more cooperative social functions have received far less attention. Yet facets of display, such as allopreening (Spoon et al., 2006; Gill, 2012) and vocal signalling (Dahlin & Benedict, 2014) have been linked to partner retention and synchrony in breeding behaviour (Gill, 2012), supporting a potential cooperative function for such behaviours.

Whether or not parents are expected to coordinate their behaviour will to some degree depend on their breeding system, which explains in part the wide variety of care strategies exhibited across species. For those species in which the same individuals pair for multiple years, it may be prudent to share in the burden of care to ensure your partner is able to breed for the future years you expect to be together (Mariette & Griffith, 2015; Griffith, 2019). The extent to which partners exhibit conflict in their fitness interests varies enormously, and so, too, do the behavioural adaptations parents have evolved to deal with family conflicts when providing care. The amount of conflict existing between parents is set by their level of reproductive alignment, which is determined by the fecundity and mating strategy of a species (Griffith, 2019). Short-lived species that reproduce frequently with high mate replacement will have low reproductive alignment, and so are unlikely to factor their partner into their investment decisions (e.g. penduline tits *Remiz pendulinis*, Szentirmai et al., 2007). In contrast, for long-lived, sexually monogamous species that exhibit very low rates of divorce, there may be a high value to partner retention, leading to increased selection for compensation and coordination in care (e.g. kittiwakes *Rissa tridactyla*, Coulson, 1966). As such, when examining the mechanisms and functions of coordination, the behaviour of long-term monogamous species is of particular interest.

1.4 Seabirds as cooperative parents

In altricial birds, reproduction is characterised by periods of high energetic expenditure at every stage (Gabrielsen & Ellis, 2001; Elliott et al., 2014): while frequent visits to and from the nest during chick feeding are physically demanding (Warham, 1980), incubation also imposes high costs both through the reduced foraging opportunities associated with egg care, and the increased metabolic rate required to warm the embryo (Bech et al., 2002; Rønning et al., 2008; Welcker et al., 2013). This in part explains why biparental care is such a ubiquitous strategy within birds: the high costs of reproduction select for division of labour across the pair, and may even render uniparental care impossible in some species.

As largely central-place foragers, during the breeding season seabirds must travel long distances to fluctuating foraging sites from remote colonies (Schreiber & Burger, 2001). Foraging trips of short duration are generally uneconomical when birds are required to travel far from the nest, as the time and energy costs of transit and searching for prey is proportionally greater and could in fact exceed the gross gain from the foraging trip (Cuthill & Kacelnik, 1990; Hatch, 1990). As a result, foraging often necessitates long periods away from the nest. This makes particularly stark the conflict between investment in self-maintenance and reproductive effort, as both incubation and chick rearing reduce individual foraging opportunities and hence impose costs on the parents in the form of the depletion of body reserves (Chaurand & Weimerskirch, 1994). To achieve optimal reproductive output, the resulting conflict between preserving condition and offspring care must therefore be resolved. Both parents have a stake in this. Failure to coordinate decisions either to care for offspring or care for self may lead to egg or chick neglect and ultimately failure of the breeding attempt, a common consequence of poor coordination in seabirds (Davis, 1988). It is these constraints that have shaped the biparental care strategy that is obligate in seabirds.

Seabirds lie at the extreme of many facets of their life history. They are all extremely long-lived, exhibit low fecundity, and have very delayed maturity (Schreiber & Burger, 2001). These qualities place them at the slow end of the fast-slow life history continuum, and impose selection for preferential investment in future survival over the current breeding attempt, which comprises a very small fraction of their lifetime reproductive success (Stearns, 1992). This makes seabirds an interesting model system for asking questions about parental investment: with such strong selection to invest in somatic maintenance, it is easy to measure the costs of breeding and how changing these can alter the decisions made by individuals. Furthermore, most species form long-term monogamous pair bonds, meaning that the reproductive interests of pairs are especially highly aligned. As such, seabirds represent a unique opportunity to investigate how individuals factor the condition of their partner into their decision-making processes, as they include many examples of species in which the high cost of divorce and repairing may ultimately reduce the contribution of sexual conflict to the evolution of behavioural strategies (Culina et al., 2015).

1.5 General methodologies

This thesis makes use of two long-lived Procellariiform seabirds to investigate the mechanisms and consequences of parental coordination for species exhibiting a very slow life history pattern: the Manx shearwater and the black-browed albatross.

Manx shearwater

Manx shearwaters are medium sized (c.400g) Procellariid seabirds that form long-term, socially monogamous pair bonds and exhibit a low rate of divorce (10%, Brooke, 1990; Hamer, 2003). A combination of large, heavy eggs (15% of female body mass, Brooke, 1990) and the need to travel long distances to foraging locales gives rise to a typical biparental breeding strategy. During incubation, parents alternate shifts of around 5-7 days until the egg hatches (Brooke, 1978), at which point the parents engage in a ‘dual foraging’ strategy, whereby each parent will alternate between short, frequent visits to the nest to provision the offspring, and longer self-maintenance trips (Shoji et al., 2015). Long incubation and chick-rearing periods, totalling 120 days on average (Harris, 1966; Brooke, 1990), make breeding in this species energetically demanding and so presumably increase selection for coordinated parental behaviour. Manx shearwaters are easily accessible in their burrow nests, and exhibit low sensitivity to disturbance. As such, they are an excellent species for collecting data on behaviour at the colony as it occurs, and a prime candidate for experimental manipulations. Manx shearwaters breed on island colonies across the Atlantic, including Iceland, the Faroes, the Azores, Madeira, and the Canaries (Brooke, 1990). However, the vast majority of breeding pairs reside in British waters. The Manx shearwater data that appear in this thesis were sampled from Skomer Island, Wales, home to an estimated 300,000 pairs (representing more than 50% of the world population; Perrins et al., 2012), and from the much smaller Lighthouse Island population (Copelands group, Northern Ireland), home to just under 3000 pairs (Stewart & Leonard, 2007).

Black-browed albatross

The black-browed albatross is a large Procellariid of the Diomedeidae family that exhibits a circumpolar breeding range, encompassing the Falkland Islands, South Georgia, the South Sandwich Islands, and the Cape Horn Islands (Tickell, 2000). Like Manx shearwaters, they experience a long latency to sexual maturity (8-9 years), low fecundity (Burg & Croxall, 2006), and a protracted period of biparental care. The female lays a single egg in early October, which both parents incubate alternately for 68-71 days in shifts of approximately 5 days (Granadeiro et al., 2018). Parents then provision the hatched chick every 1-2 days for a total of 120-130 days (Figure 1.2A, Tickell, 2000). Unlike Manx shearwaters, they do not exhibit a dual foraging strategy during this time, which may reflect a lack of diversity in productivity in the foraging areas accessible from the breeding colony (Phillips et al., 2009). They have a low divorce rate (around 7.7% per year, Bried et al., 2003) and a reasonably low rate of extrapair paternity (0-9%, Burg and Croxall, 2006). The majority of the world's population of black-browed albatross breed in the Falkland Islands (85%, Croxall and Gales, 1998), with an estimated 30,000 pairs breeding annually on New Island, from where the data in this thesis were sampled and where a sub-sample of the total population has been monitored for the past 15 years (Catry et al., 2011). Each individual in the monitored colonies carries a large coloured

Figure 1.1: *(A)* Adult Manx shearwater carrying a geolocator (GLS) on the left tarsus. *(B)* Manx shearwaters at sea. *(C)* Anti-clockwise from top left: Adult Manx shearwater carrying a housed PIT tag on the tarsus, above the metal ring. Unhoused PIT tag with scale bar. RFID set-up, showing connections between the rechargeable battery pack, the two antennae, and the Arduino board. *(D)* A Manx shearwater chick being weighed.

ring printed with a field-readable individual ID (Figure 1.2B), and all nests carry a number unique to the sub-colony they are found on. This allows the direct observation of behaviour at the colony with minimal disturbance.

Measuring at-sea behaviour

Decisions made at the colony relating to parental care and coordination are not made in isolation of foraging. Success when foraging determines the resources available to be allocated to reproduction, growth, and survival, and so to fully understand the decisions

Figure 1.2: *(A)* Adult black-browed albatross preening its chick. *(B)* Adult black-browed albatross brooding its chick; blue colour ring visible on left tarsus (bottom right of image). *(C)* Allopreening between a pair of black-browed albatross.

made by individuals at the nest, we must gain a complete picture of the behaviour they exhibit outside of it. For seabirds, this requires gathering data during their foraging trips. However, these take place far from land, in typically inaccessible locations that render targeted direct observation essentially impossible (Figure 1.1B). While much of an individual's at-sea behaviour, such as trip duration and foraging gains, can be inferred from observations at the colony, garnering a complete picture of what an individual is doing on its trips requires the remote collection of data.

Advances in biologging technology have made it possible to collect data on the behaviour of many species remotely (Ropert-Coudert et al., 2010) and the use of miniaturised biologgers is now a cornerstone of seabird behavioural research. While modern biologgers can record almost any facet of an animal's behaviour, including fine-scale location, acceleration, and heart rate, they are often limited by size, battery life, and/or storage capacity. Some tracking devices may also impact normal behaviour, which when investigating questions about resource allocation, is an obvious problem. While there are many existing studies that investigate such potential impacts (reviewed by Barron et al., 2010; Bodey et al., 2018), these generally only consider breeding success as a measure, and do not consider more nuanced behavioural impacts that are of relevance to the sorts of questions considered in this thesis. Consequently, when designing experiments and observational studies it is important to consider the potential for biologging devices themselves to have impacts on the behaviour of focal animals, with larger, more cumbersome devices such as Global Positioning System (GPS) loggers being more likely to have a negative impact on natural activity levels. This may explain, then, why one of the first biologgers to become available to researchers, the salt-water immersion logger (Afanasyev & Prince, 1993), or geolocator (GLS), has remained such an important tool for seabird research. These very small (c.1.5g) loggers produce data comprising a time series alongside either the proportion of time the device was immersed in water for a pre-programmed epoch, or as a set of transitions between wet and dry states, as well as data on light levels. These variables give some indication of an individual's behaviour while at sea, with prolonged dry periods being likely to indicate flight, wet periods indicating resting on the water, and transitions between the two indicating take-off and landing from the water, which is mostly associated with foraging (Dean et al., 2013). For burrow-nesting seabirds, light data can furthermore be used to indicate incubation, in the form of periods of darkness during the daytime. These simple data have been used to broadly define at-sea behaviour in a number of species, including Murphy's petrels *Pterodroma ultima*, (Clay et al., 2019), wedge-tailed shearwaters *Puffinus pacificus* (Catry et al., 2009), black-browed albatross (Patrick et al., 2020), Antarctic prions *Pachyptila desolata*, thin-billed prions *P. belcheri*, and blue petrels *Halobaena caerulea* (Cherel et al., 2016), and Manx shearwaters (Guilford et al., 2009; Freeman et al., 2013; Dean et al., 2015; Fayet et al., 2016).

In this thesis, a key aim was to measure the behaviour and decision-making processes of individuals over the entirety of the breeding period. This extended time scale renders devices such as GPS or accelerometers of limited use, as the storage capacity and battery life would not be sufficient to capture behaviour over the period of interest. Furthermore, large (c.15g) devices such as these have the potential to disrupt the behaviour I sought to quantify. Instead, in 3 of my chapters, I use salt-water immersion loggers to capture the behaviour of parents at sea (Figure 1.1A). A variety of methods to characterise salt-water immersion data into bouts of activity have been explored: data can be classified using thresholds of, for example, proportional wet time (Lecomte et al., 2010); the number and duration of bouts may be directly informative (Yamamoto et al., 2008; Dias et al., 2012); or unsupervised machine learning algorithms such as Hidden Markov Models (HMMs) may be used to classify the data into putative behaviours (Dean et al., 2013; Fayet et al., 2016). Threshold methods have been previously used to elucidate behavioural categorisations that are clearly biologically meaningful (Shoji et al., 2015). As the threshold model is additionally well-equipped to deal with non-normal data, can be easily applied to data collected with different parameters e.g. recording frequency, and has been previously shown to produce behavioural classifications that are not meaningfully different from the outputs of HMMs (Fayet et al., 2016), this is the chosen method for quantifying behaviour in my thesis.

Measuring nest visitation

Even at the colony, manually tracking the behaviour of individuals can be logistically difficult. While during incubation, shifts on the nest are long and so can generally be recorded manually by checking the presence of parents daily, during chick-provisioning, parents make frequent, short visits to the nest at largely unpredictable times and simultaneously with other parents in the colony. As such, a manual observation approach is not adequate to accurately gauge the care decisions made by parents during this time, and could furthermore be highly disturbing if this required repeated checking of nests. To collect data on provisioning, we therefore required a minimally disturbing method of collecting real-time data on the visitation of individuals to their nests. To this end, for Chapter 5, I developed an automatic nest-detection system on a colony of Manx shearwaters, using radio-frequency identification (RFID) readers (see Bridge et al., 2019 for full details). RFID systems permit short-range wireless communication between a data-logging reader and a small, uniquely coded passive integrated transponder (PIT) tag.

When the tag passes within transmission range of an antenna attached to the RFID reader, it transmits a weak signal to the computer, which subsequently records the time of detection and the unique ID number.

RFID readers were deployed in the field next to nest entrances. Each comprised a rechargeable battery pack, an Arduino Uno board, and two external antennae (Figure 1.1C). Each target bird was equipped with a 2 x 12mm EM4102 glass PIT Tag (provided by Cyntag Cynthiana), which was attached to a 2mm cable tie using heat shrink plastic and wrapped around the tarsus (see Figure 1.1C insert). Two antennae were placed in the tunnel-shaped burrow entrance approximately 20cm apart from one another. This meant directionality of the nest visits could be inferred, with detection by the antenna at the entrance followed by the antenna further inside the tunnel indicating travel into the nest, and detection in the reverse pattern indicating departure from the nest. Using this system we could quantify visitation to the nest, as well as foraging trip duration, taken as the time between the last departure point and the first arrival point. Visitations were validated using daily mass chick data (Figure 1.1D), where an increase in chick mass indicated a visit by at least one of the parents.

1.6 Objectives and aims of the thesis

This thesis explores the patterns and mechanisms of the coordinated parental behaviour of pelagic seabirds during incubation and chick rearing. Each chapter has been written in a self-contained manuscript format, with its own introduction, methods, and conclusion, and can thus be read independently. At the time of writing, Chapter 2 is published in *Scientific Reports*, Chapter 4 is published in *Frontiers in Ecology and Evolution*, Chapter 6 is published in *Ibis*, and Chapter 5 is undergoing peer review in *Journal of Avian Biology*.

While biologging is a powerful tool to remotely study animal behaviour and ecology, the ways in which the attachment of devices to animals may alter their activity are not fully understood. When considering questions about the respective allocation of parental resources to the care of offspring and self-maintenance, it is vitally important to accurately collect data about behaviour. To this end, in **Chapter 2**, I make use of a 10-year dataset that includes parameters relating to foraging and parenting behaviour for Manx shearwaters carrying large GPS, small GLS, and no devices. I investigate whether these devices differentially impact the behaviour of shearwaters, and find that GPS-tagged shearwaters exhibit significantly altered foraging behaviour, but normal chick growth and ultimately breeding success, suggesting that the potential for long-lived species to buffer short-term increases in costs could preclude the identification of behavioural impacts when assessing the effect of carrying a device. I additionally find that there is no effect of the deployment of GLS devices on normal behaviour relative to untracked birds, supporting the use of these devices for quantifying behaviour in my later chapters.

In all egg-laying animals where both parents directly incubate the egg, the coordination of shifts is important to ensure continuous incubation, the temporary cessation of which can cause slowed embryonic development or even death (Webb, 1987). While incubation is a clear example of an opportunity to employ a turn-taking strategy when providing care, it is not well understood what underlies the decision of foraging parents to return to the nest, or for incubating parents to temporarily or permanently desert the nest. Understanding the decisions made during incubation is particularly important when investigating questions of allocation and parental coordination, as this is a clearly energetically costly part of breeding in which the relative investments of each parent can be directly and easily measured. In **Chapter 3**, I investigate, in detail, the patterns of incubation routine in Manx shearwaters. Over their 51-day incubation period, parent Manx shearwaters are known to exhibit well-coordinated and generally egalitarian delegation of behaviour as they take it in turns to incubate the egg in shifts (Harris, 1966; Brooke, 1978). I test the role of intrinsic factors such as sex, pair experience, and body mass as potential drivers of this behaviour, and in doing so reveal that body mass has a key role to play in the regulation of behaviour during incubation, underlying how long birds are able to sustain their shifts on their nest, how much time they spend at sea, and what behaviour they exhibit during this time. Through this largely descriptive, observational approach, I also reveal tentative evidence that shearwaters may engage in a process of negotiation to optimise their trip durations from the perspective of the pair as a whole. In Chapter 4, I explore this possibility experimentally.

In **Chapter 4**, I examine in more detail the observational results revealed by Chapter 3, by explicitly investigating the mechanisms by which Manx shearwaters coordinate their care during incubation. I aimed to forced shearwaters to the extremes of their decision-making processes during incubation, by physically handicapping one parent in a sample of nests to reduce their foraging efficiency, forcing them to choose between extending the foraging trip or to return to the nest before they have fully recovered their condition. I find that the duration of incubation shifts is largely driven by the need for foraging birds to recoup their condition: incubating shearwaters usually remain at the nest until their partners return to relieve them. However, I further find that the decision made by the foraging bird as to when to return to the nest is mediated by the condition of its partner. Those foraging birds whose partners were in poor condition returned to the nest earlier and at a lower mass than birds whose partners were in good condition. These findings suggest that information transfer between the partners may facilitate the coordination of incubation.

After focusing on parental coordination during incubation, in **Chapter 5** I shift focus to the chick provisioning period. Like many central-place foraging seabirds, Manx shearwaters exhibit a dual-foraging strategy when provisioning their offspring in which short, frequent visits to provision the chick at the nest are alternated with longer, self-maintenance trips (Shoji et al., 2015). It is now known that this strategy is coordinated between the two parents in the pair (Tyson et al., 2017), ensuring that chick feeds are distributed regularly in time and thus reducing the risk of starvation. However, the mechanisms underlying this change in trip strategy are unknown. Through a series of experimental and observational approaches, I examine what determines the provisioning frequency of Manx shearwaters. Specifically, I alter the information that parents have access to when provisioning their chicks, by preventing the reunion of parents at the nest when they both visit the colony on the same night, and by feeding chicks in advance of the parent's arrival so that it appears they have already been fed by the partner. While I do not find evidence for the importance of either sort of information in the coordination of provisioning, I speculate on whether apparent coordination in provisioning may emerge through an entrainment process during incubation.

Having considered potential sources of information for chick-provisioning Manx shearwaters, in my final chapter I explore the putative role of pair display in facilitating coordinated parental care. The functions of inter-sexual display have been historically viewed through the lens of sexual selection, and explained by fitness conflicts between the sexes. However, this paradigm may be less useful when considering the function of post-copulatory display that follows mate choice; indeed, tentative evidence suggests that such displays may in some species facilitate cooperation between pair members when they share a large proportion of their reproductive output (Kenny et al., 2017; Takahashi et al., 2017). In **Chapter 6**, I examine the patterns and putative functions of the conspicuous allopreening behaviour exhibited by black-browed albatross during the breeding season (Figure 1.2C). I conducted observations of display behaviour between paired black-browed albatross during the incubation and chick-provisioning periods, focusing specifically on allopreening behaviour. I aim to explore the patterns of allopreening within displays in this species, to investigate how facets of this behaviour relate to the subsequent foraging behaviour of parents, and to patterns of parent-offspring allopreening. I find that there is an inverse relationship between the amount of time parents spend engaged in display and the duration of the departing bird's foraging trip, and discuss the mechanisms by which these displays might facilitate the coordination of breeding behaviour between the partners.

Finally, in **Chapter 7**, I summarise and discuss the main findings of this thesis and what these might illuminate about parental coordination in the wider Animal Kingdom.

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2

Short-term behavioural impact contrasts with long-term fitness consequences of biologging in a long-lived seabird

Adapted from: Natasha Gillies, Annette L. Fayet, Oliver Padget, Martyna Syposz, Joe Wynn, Sarah Bond, James Evry, Holly Kirk, Akiko Shoji, Ben Dean, Robin Freeman, Tim Guilford. ‘Short-term behavioural impact contrasts with long-term fitness consequences of biologging in a long-lived seabird.’ *Scientific Reports*, **10**, (2020).

Contents

2.1 Abstract

Biologging has emerged as one of the most powerful and widely used technologies in ethology and ecology, providing unprecedented insight into animal behaviour. However, attaching loggers to animals may alter their behaviour, leading to the collection of data that fails to represent natural activity accurately. This is of particular concern in free-ranging animals, where tagged individuals can rarely be monitored directly. One of the most commonly reported measures of tagging impact is breeding success, but this ignores potential short-term alterations to individual behaviour, which when collecting ecological or behavioural data can have important consequences for the inference of results. Here, we took a multifaceted approach to investigate whether tagging leads to short-term behavioural changes, and whether these are later reflected in breeding performance, in a pelagic seabird. We analysed a long-term dataset of tracking data from Manx shearwaters *Puffinus puffinus*, comparing the effects of carrying no device, small geolocator (GLS) devices (0.6% body mass), large Global Positioning System (GPS) devices (4.2% body mass), and a combination of the two (4.8% body mass). Despite exhibiting normal breeding success in both the year of tagging and the following year, incubating birds carrying GPS devices altered their foraging behaviour compared to untagged birds. During their foraging trips, GPS-tagged birds doubled their time away from the nest, experienced a 64% reduction in daily foraging gains, and reduced flight time by 14%. These findings demonstrate that the perceived impacts of device deployment depends on the scale over which they are sought: long-term measures, such as breeding success, can obscure finer-scale behavioural change, potentially limiting the validity of using GPS to infer at-sea behaviour when answering behavioural or ecological questions.

2.2 Introduction

Biologging is a powerful tool for understanding the behaviour and ecology of animals. Individuals are now routinely fitted with miniaturised data loggers capable of recording a wealth of information, including location, acceleration, heart rate, dive depth, and temperature. As the power to size ratio of devices continues to increase, it is now routine for multiple devices to be deployed simultaneously (e.g. Dean et al., 2013) and on ever-smaller animals (including insects; Kissling et al., 2014) in a variety of environments (Williams et al., 2019). However, while the wide-scale usage of these devices has provided considerable insights into behaviour, movement, and physiology (e.g. Bowlin et al., 2005; Guilford et al., 2009; Handcock et al., 2009; Votier et al., 2013; Shoji et al., 2015a; Padget et al., 2018) it also has the potential to affect the tagged animal's behaviour and hereby distort or bias the results of studies. As such, understanding the behavioural impacts of tagging is critical.

This, however, is challenging. While the great advantage of remote biologging is that we can record data about the biology of animals without direct observation, this also makes it difficult to test whether the devices themselves change animal behaviour, and therefore to assess whether the behavioural and ecological data collected are unbiased and representative. Meta-analyses of device effects have repeatedly found that tag deployment can lead to significant negative impacts on animals relating to survivorship, reproduction, and activity (Barron et al., 2010; Bodey et al., 2018). In particular, behavioural impacts are widespread and phylogenetically diverse, and include impairments in locomotory ability (Yuma myotis bats *Myotis yumanensis*, Aldridge and Brigham, 1988; sharks, Hammerschlag et al., 2011; bottlenose dolphins *Tursiops truncatus*, Irvine et al., 1982; van der Hoop et al., 2014; grey partridges *Perdix perdix*, Putaala et al., 1997), increases in energetic expenditure (fish, Jepsen et al., 2015; great cormorants *Phalacorax carbo*, Vandenabeele et al., 2015), alterations to social behaviour (bald ibis *Geronticus eremita*, Puehringer-Sturmayr et al., 2020), increased autopreening (gyrfalcons *Falco rusticolus*, Booms et al., 2011; African penguins *Spheniscus dermsus*, Wilson and Wilson, 1989) at the expense of other behaviours such as feeding (Barrow's goldeneye *Bucephala islandica*, Robert et al., 2006), and reductions in general activity levels (house mice *Mus musculus*, Pouliquen et al., 1990; freshwater mussels *Margaritifera margaritifera*, Wilson et al., 2011), foraging effort (emperor penguins *Aptenodytes forsteri*, Kooyman et al., 1992), and nest attendance (Atlantic puffins *Fratercula arctica*, Harris et al., 2012; alcids, Wanless et al., 1989). The impacts of tagging procedures vary across and within taxa, meaning that rather than employing a general measure of impact across all types of study, researchers must consider, in detail, the impacts of carrying a device on the specific species of interest and in the context of the experimental design. When studying the behaviour of animals, effects such as these can have important consequences for the validity of the data collected. These may have important implications for behavioural studies or the interpretation of results, yet remain poorly understood.

Despite this, many authors neglect to consider fully the impacts that their devices may have. Though 80% of authors do make some reference to the impacts of their tagging procedures, only 42% of these directly compare untagged and tagged individuals (Barron et al., 2010). Increasingly, authors use breeding success to determine the effects of their tagging protocols (Wanless et al., 1989; Rodríguez et al., 2009; Arlt et al., 2013; Scandolara et al., 2014). However, this may be blunt. Devices may have more subtle and complex effects on behaviour that don't manifest in changes in breeding success. For example, individual plasticity may allow individuals to buffer against the costs of tagging in a way that preserves their reproductive success. Handicapping studies demonstrate that alterations to behaviour may not necessarily manifest in costs to the offspring if these are absorbed by the handicapped individual (e.g. great tits *Parus major*, Griffioen et al., 2019; burying beetles *Nicrophorus vespilloides*, Ratz et al., 2019), its partner (e.g. northern flickers *Colaptes auratus*, Wiebe, 2010), or some combination of the two (e.g. pied flycatchers *Ficedula hypleuca*, Cantarero et al., 2014). Furthermore, single fitness-based measures are often unable to capture complex, long-term impacts on individuals. Negative effects of tagging on breeding success may not manifest until the years following the procedure (e.g. king penguins *Aptenodytes patagonicus*, Saraux et al., 2011), may cause reductions in return rates (e.g. adelie penguins *Pygoscelis adeliae*, Beaulieu et al., 2009), or increases in divorce (e.g. thick-billed murres *Uria lomvia*, Paredes et al., 2005). Yet in spite of mounting evidence that breeding success may not always be an appropriate measure of impact, particularly for behavioural studies, only 26% of published tagging studies in which impact is reported consider behavioural effects (Bodey et al., 2018).

A recent meta-analysis of the impacts of device deployments on a range of species has revealed significant effects of deployment on reproductive success, foraging behaviour, and survival (Bodey et al., 2018). In the Manx shearwater *Puffinus puffinus*, a small diving seabird of the order Procellariiform, hatching success has been previously reported as unaffected by device deployment (Dean et al., 2015), but effects on behaviour have not been investigated. Here, we draw a multifaceted approach to determine the impact of device deployment on Manx shearwaters. Specifically, we investigate the effects of tracking on several behavioural measures in addition to breeding success. Our approach compares short- and long-term measures, across different combinations of devices, and between untagged and tagged animals, to determine precisely the effects of carrying a device for this species. We expected to find that device deployment does affect the behaviour of Manx shearwaters, with larger back-mounted devices having a greater effect than small leg-fitted ones (Barron et al., 2010), and that these effects differ between incubation and chick-rearing because of the differing energetic demands of these two periods on the breeding adults (Guilford et al., 2009; Shoji et al., 2015b). By comparing the impacts arising in measures of behaviour and fitness, we demonstrate that in this species, behavioural alterations associated with instrumentation do not necessarily translate into altered fitness, meaning changes to one do not necessarily inform on the other.

2.3 Methods

2.3.1 Study site and sampling Methods

The study was conducted from 2009 – 2017 on UK Manx shearwater breeding colonies and long-term study sites at Skomer Island, Wales (51°44' N, 5°17' W) and Lighthouse Island in the Copelands group, Northern Ireland (54°44' N, 5°31' W). Manx shearwaters breed on dense island colonies between April and September, during which time they come onto land only at night. In April, females lay a single egg in an underground burrow, which is incubated for about 51 days, with stints of 5-7 days taken by each parent (Harris, 1966; Brooke, 1990). Following hatching, both parents feed the chick most nights for approximately 60 days. Occupancy and breeding success were monitored at the Skomer colony each year, with birds on both islands being easily accessed at the nest through the burrow entrance or purpose-built inspection hatches. To allow individual identification, all birds in this study were ringed with a permanent stainless steel ring, provided by the British Trust for Ornithology. Females were identified at the point of laying through cloacal inspection (Boersma & Davies, 1987), and males by inference.

GPS tracking campaigns lasted for approximately two weeks during the incubation (May – June) and chick rearing periods (July – August). Deployments on the two islands were carried out simultaneously in each given year. We analysed the foraging trip metrics during incubation and provisioning behaviour of birds subject to four different device deployments: no device (ring only, 0.78g), a geolocator (GLS) only (2.5g), a single global positioning system (GPS) device (total attachment mass 17g), or a GPS device and geolocator (GLS, c. 19.5g). The sample sizes in each of these groups can be found in Table 2.1.

Table 2.1: Sample size (summed across years) for each deployment type

No device	**GLS**	**GPS**		**Combined**	
		Inc	***CR***	***Inc***	***CR***
85	106	59	56	181	54

Notes – *Inc* = incubation period; *CR* = chick-rearing period

For individuals carrying no logger, foraging trips durations were determined by directly identifying the incubating parent once a day from laying to hatching, by removing the adult from the nest and reading its ring number, which took no longer than 1 minute, adding to a total of c.20 minutes over the whole incubation period. Whichever bird was not present at the nest was deemed to be on a foraging trip.

GLS (Migrate Technology Intigeo-C250 or Intigeo-C65; BioTrack Mk4083; British Antartic Survey MK-14 or MK-19), were either deployed and retrieved simultaneously with GPS (combined group) or deployed at the beginning of the breeding season (GLS group), in April, and retrieved at the beginning of the breeding season the following year. GLS were attached by two small cable ties to a plastic leg ring to ensure immersion when sitting on the sea (Figure 2.1A; see Guilford et al., 2012). The deployment and retrieval of GLS was conducted in the field and handling time did not normally exceed 5 minutes. As part of a separate experiment, 27 individuals carrying GLS were handled daily, as per the 'no device' birds. We analysed whether these two subgroups differed in their mean foraging trip duration; as they did not, we pooled the subgroups for the remainder of the analysis (see 2.6 Appendix). GPS loggers (Mobile Action i-GotU GT-120) were waterproofed using lightweight heat-sealed plastic sleeves and attached to the dorsal feathers of birds using 5 strips of marine cloth Tesa tape (Figure 2.1B; see Guilford et al., 2008, for details). Birds were captured on the nest during changeover with the partner (egg incubation) or during a provisioning visit to the nest (chick rearing), after they had been allowed approximately 30 minutes to feed their chick. GPS deployment was carried out in a darkened lab and processing time was approximately 10 minutes. On both islands the lab is close to the colony and so transportation did not exceed 10 minutes, giving a total maximum handling time, from capture to release, of 20 minutes. Following deployment of the GPS, the bird was returned to the nest and allowed to depart on its foraging trip naturally. Incubating birds were recaptured as soon as they returned from foraging; efforts to recapture chick-provisioning birds began 3 days after departure until their subsequent return to the nest. The foraging trip duration of incubating birds could thus be identified as the period it was not found in the nest.

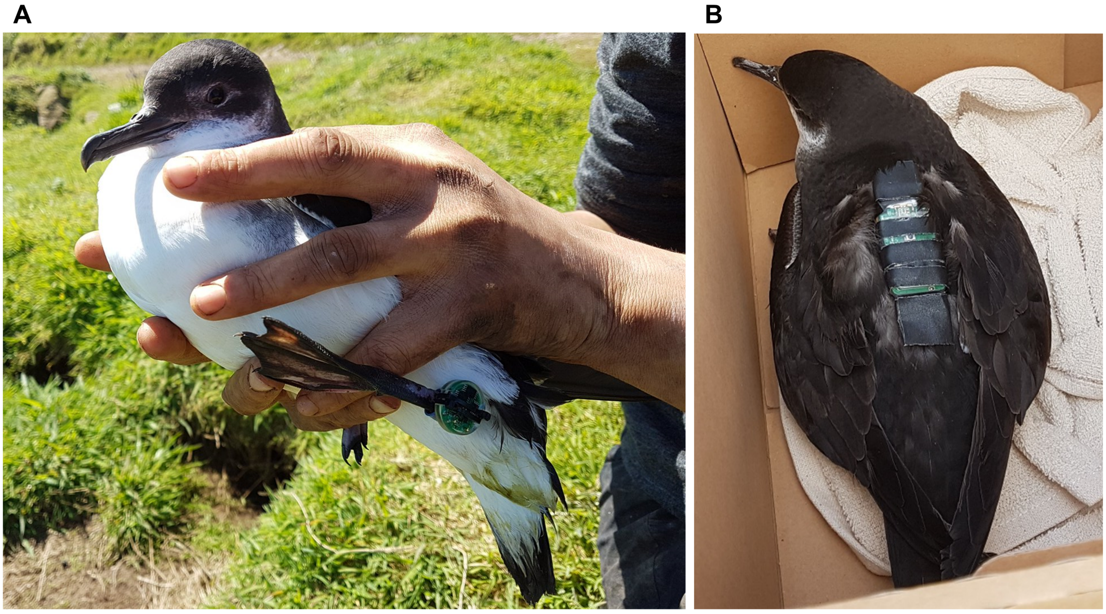

Figure 2.1: *(A)* Deployment of a geolocator (GLS) on the left tarsus of an adult Manx shearwater. *(B)* Deployment of an iGot-U global positioning device (GPS) on the dorsal feathers of an adult Manx shearwater.

2.3.2 Mass changes and breeding success

To measure foraging gains from each trip, mass measurements were taken for all GPS birds at deployment and retrieval, and were taken daily during the direct observations of non-instrumented and 23 GLS-tracked nests made during incubation in 2015 and 2016. Birds were inserted head first into a draw-string muslin bag attached to a 600g Pesola spring balance (precise to 5g). The resulting mass change (mass at return – mass at departure) was divided by the duration of the foraging trip (in days) to give a measure of daily mass gain.

To determine the approximate meal sizes provided by parents, chick masses were collected on Skomer from 96 nests where at least one parent carried a GPS, 48 where at least one carried a GLS, and 89 where neither parent carried a device, between 2013 and 2017. Chicks were placed into a plastic box and weighed on a digital balance precise to 1g. Chick masses on Skomer were collected daily from the day following hatching until the chick was not found in the nest for 3 consecutive days, at which point it was presumed to have fledged. For each nest, the duration of the provisioning period was identified as the time between hatching and the last known feed (taken to be an increase in the chick's body mass). For those chicks surviving to fledgling stage, the maximum mass attained, total number of nights fed, and average daily mass change was calculated. At the end of the season, breeding success was determined for each nest in the Skomer study colony. Data on breeding success were not available for Copeland birds.

2.3.3 Extracting foraging trip metrics

As foraging trip durations were not available for unmanipulated or GLS-carrying birds during chick-rearing, differences in foraging trip metrics were only investigated during the incubation period. For each year and tracking campaign, only foraging trips from GLS-only and no device birds that occurred simultaneously with the GPS-tracking period were used in the analysis. GLS devices tested for saltwater immersion every 3 or 6 seconds and recorded the proportion of samples immersed in water in each 10- or 5-minute epoch respectively. The frequency distributions of total daily immersion (sum of each 10- or 5-minute immersion score) recorded by the GLS were used to separate incubation stints from foraging trips, using the expectation that the days birds spent incubating in the burrow would be characterized by a distribution of very low total immersion values. The `R` package `mixtools` (Benaglia et al., 2009) was used to fit a Gaussian mixture model to the frequency data, and the clusters output from this used to assign days with lower total immersion as incubation days. These assignments were subsequently validated using individuals for which we knew through direct observation whether the bird was incubating or not. This yielded a 92% accuracy for the assignment of foraging dates.

At-sea behaviour was classified using immersion data, using the threshold methods outlined by Dean et al. (2013) and Fayet et al. (2016), where classifications were outlined as: <2% maximum immersion for directed flight, >98% maximum immersion for resting on the water, and intermediate values for foraging. Intermediate values are caused by the bird taking off and landing on the water, and have been shown to be indicative of foraging behaviours in this species through validation with dive loggers (Dean et al., 2013).

2.3.4 Statistical analysis

All statistical analyses were completed using `R` version 3.2.2 (core Team, 2018). The `R` package `lme4` (Bates et al., 2015) was used to construct linear mixed effects models (LMMs), and p-values were obtained by comparing models to null models without the effect of interest, using a likelihood ratio test. Least squares means for each level of the deployment type were calculated using the `R` package `emmeans` (Lenth et al., 2018), and Tukey's range test used to calculate significant differences between them. Visual inspection of diagnostic residual plots was used to assess model fit to the data. Over the entire data collection period, 78 individuals were tracked for multiple years. To ensure that these repeated measurements from the same individuals did not impact our parameter estimates, all models included the random intercept of individual nested within year. For the same reason, in our models where the response variable was generated for the pair as a whole (i.e. breeding success, chick growth variables), we included a random intercept of burrow identity nested within year to account for repeated measurements from the same burrows.

To investigate differences in breeding success according to deployment type, a generalized linear mixed effects model with a binomial distribution was fitted to breeding success in the current (t) and subsequent ($t + 1$) year. Breeding success in $t + 1$ additionally included the fixed effect of breeding success in t.

To ensure that differences in trip length could not be explained by differences in the starting masses of birds, an LMM was fitted to determine the effect of deployment type (no device, GLS, GPS, or combined) on 1) starting mass (g). Further LMMs were fitted to examine the effect of deployment type on 2) foraging trip duration, 3) daily foraging gain, and 4) total foraging gains. Models 2-4 included the fixed effect of starting mass (g) and sex; model 2 additionally included the interaction of deployment type and body condition as a fixed predictor, as it was plausible that the effect of condition on trip duration may depend on device the bird carried. To allow for an increased sample size and greater variation in foraging trip duration across the treatments, foraging trips from both Copeland and Skomer birds were included in the analysis. As mean foraging trip duration differs between the two islands, island was included as a fixed effect in all models. For data collected during the chick rearing period, LMMs were fitted to 5) provisioning trip duration, 6) maximum chick mass obtained, 7) daily feed size, and 8) number of nights fed.

To investigate differences in at-sea behaviour during foraging trips for birds in the GLS and combined deployment groups, LMMs were fitted to determine the effect of deployment type on the proportion of time spent in each of foraging, resting, and flight states per day of the trip. Trip duration and island were additionally included as fixed effects.

2.3.5 Ethical note

All methods and procedures adhere to ASAB/ABS Guidelines for the Use of Animals in Research, and were approved by the British Trust for Ornithology (BTO) Unconventional Methods Technical Panel (permit number C\5311) and by the Wildlife Trust for South and West Wales under the name of Prof. Tim Guilford. Ethical approval was received from the Local Ethical Review Process of the University of Oxford. This project is covered by Northern Ireland Environment Agency (NIEA) permits, and holds Islands Conservation Advisory Committee (ICAC) approval. To reduce the potential for stress, handling time was kept to a minimum.

2.4 Results

In total, 591 foraging trips were extracted for subsequent analyses, representing 405 individuals from 174 nests. To ensure that all our measures were fully comparable, we subset these trips to include only those individuals for which overall breeding success and, if applicable, measures of chick provisioning, were known. From this, 171 foraging trips, representing 130 individuals from 72 nests, remained. All ensuing analyses were performed on both the complete and comparative datasets; effect sizes and significance values did not differ depending on which dataset was used. For brevity, only results from the subset comparative dataset are presented here. Results from analyses conducted on the complete dataset are reported in the appendix (section 2.6). Figures include data from the entire dataset.

The starting masses for birds in each deployment group did not significantly differ (no device: 388.82 ± 9.20g, GLS: 405.28 ± 7.30g, GPS: 397.37 ± 6.23g, combined: 402.73 ± 3.92g; n = 110 trips for 97 individuals, χ^2 = 3.98, df = 3, p = 0.26). Given these mean starting masses, the percentage body mass of each device equated to 4.85 ± 0.041% for the combined deployment, 4.30 ± 0.063% for the GPS-only deployment and 0.68 ± 0.075% for the GLS deployment. The metal ring carried by all birds equated to 0.19 ± 0.013% of body mass.

2.4.1 Effects of tagging on breeding success

Deployment type did not significantly predict breeding success in the year of deployment (n = 117 records for 97 nests, χ^2 = 0.42, df = 3, p = 0.94) or the subsequent year (n = 112 records for 69 nests, χ^2 = 3.09, df = 3, p = 0.38). A breakdown of the percentage of eggs surviving until at least late-stage chicks is shown in Table 2.2.

Table 2.2: Percentage eggs resulting in late stage chicks for each deployment group in the year of deployment (t) and the year following deployment ($t + 1$).

	No device	**GLS**	**GPS**	**Combined**
t	73.8 %, n = 42	75.6%, n = 42	80.0%, n = 30	66.7%, n = 63
t + 1	72.3%, n = 26	63.6%, n = 33	84.2%, n = 19	76.5%, n = 34

Notes – *n* = number of eggs recorded in each group.

2.4.2 Effects of tagging on foraging behaviour

Birds tracked on Skomer embarked on foraging trips during incubation that were significantly longer than those of birds on Copeland, in keeping with findings by Dean et al. (2015; Figure 2.2; Copeland: 3.13 ± 1.23 days, Skomer: 9.12 ± 0.75 days; n = 110 trips for 97 individuals, χ^2 = 25.89, df = 1, p < 0.0001).

Birds carrying either a GPS or GPS in combination with a GLS embarked on foraging trips during incubation that lasted significantly longer than birds carrying only a GLS or no device (Figure 2.2; no device: 2.65 ± 1.38 days, GLS: 3.87 ± 1.27 days, GPS: 8.95 ± 1.075 days, combined: 9.03 ± 0.84 days; n = 110 trips for 97 individuals; overall effect of device: χ^2 = 39.16, df = 3, p < 0.0001; see Table 2.3 for pairwise comparisons of each level of device). There was no significant effect of the interaction of deployment type and starting mass (n = 110 trips for 97 individuals, χ^2 = 2.9, df = 3, p = 0.4). Compared to birds tracked with only a GLS, on their foraging trips combined deployment birds spent a lower proportion of their day in flight (GLS: 0.18 ± 0.015, combined: 0.15 ± 0.020; n = 880 trips for 76 individuals, χ^2 = 5.99, df = 1, p = 0.014; Figure 2.3). GLS and combined deployment birds did not differ in the proportion of their day dedicated to rest (GLS: 0.35 ± 0.023, combined: 0.38 ± 0.026; n = 880 trips for 76 individuals, χ^2 = 3.12, df = 1, p = 0.077) or foraging (GLS: 0.47 ± 0.021, combined: 0.47 ± 0.0; n = 880 trips for 76 individuals, χ^2 = 0.15, df = 1, p = 0.69).

Table 2.3: Pairwise comparison of foraging trip duration during incubation for each deployment type. Significant values (p <0.05) are in bold.

Device A	Device B	Mean diff (A - B)	t-value	p
No device	GLS	-0.8 ± 0.9	-0.9	0.791
	GPS	**-5.1 ± 0.9**	**-5.1**	**<0.0001**
	Combined	**-5.0 ± 0.8**	**-6.0**	**<0.0001**
GLS	**GPS**	**-4.3 ± 0.9**	**-4.6**	**<0.0001**
	Combined	**-4.2 ± 0.6**	**-6.5**	**<0.0001**
GPS	Combined	0.1 ± 0.9	-0.1	0.999

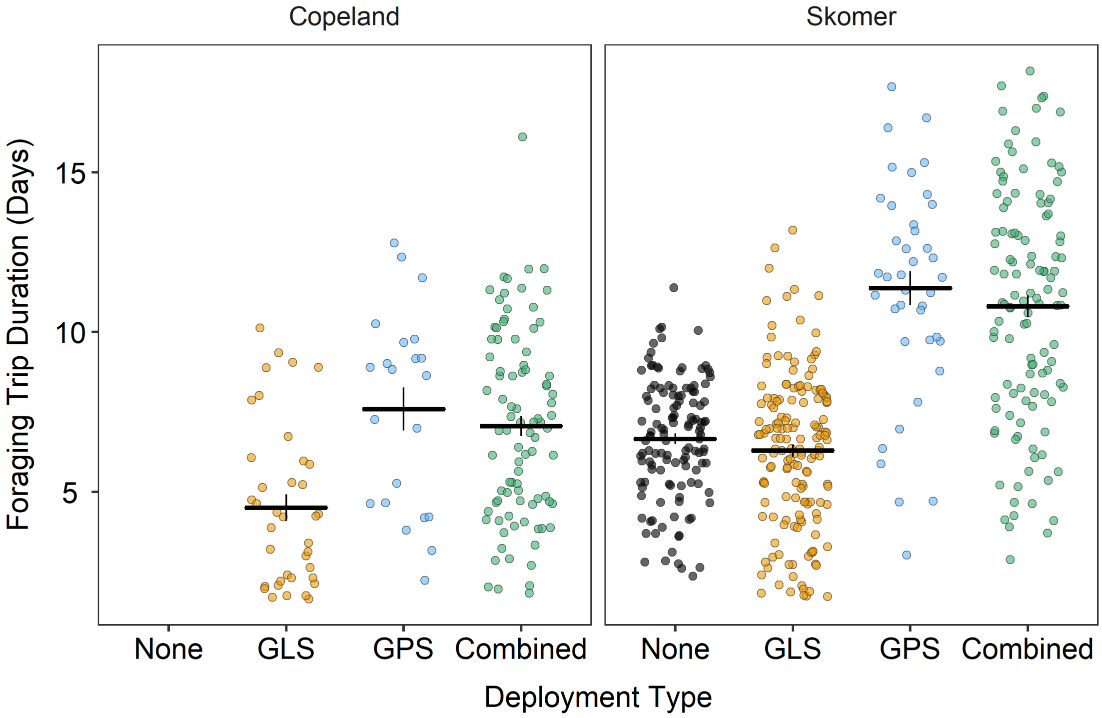

Figure 2.2: Foraging trip duration in days grouped by deployment type for each island. Black horizontal lines indicate mean, vertical black lines indicate standard error. Data are plotted with horizontal 'jitter' for clarity.

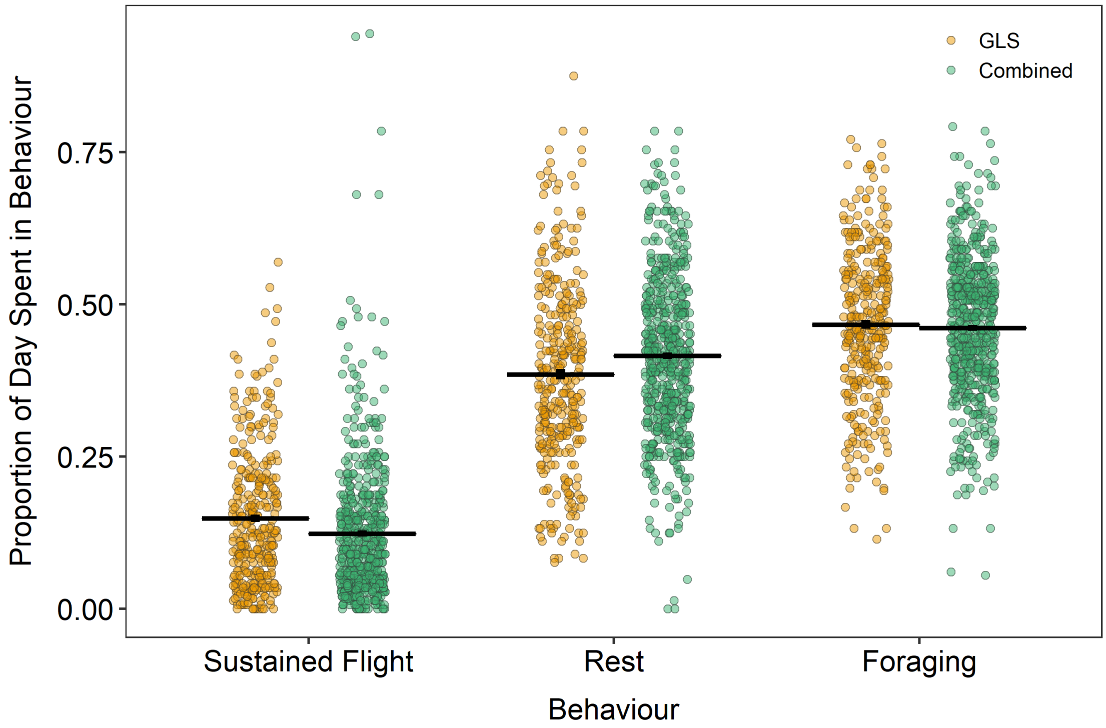

Figure 2.3: Proportion of each 24 hour period spent in rest, flight, or foraging behaviour according to deployment type, where yellow = GLS only and green = combined GPS deployment. Black horizontal lines indicate mean, vertical black lines indicate standard error. Data are plotted with horizontal 'jitter' for clarity.

2.4.3 Effects on Foraging Efficiency

Deployment type had a significant effect on the mass gained per day of the foraging trip during incubation (n = 99 trips for 87 individuals; overall effect of device: χ^2 = 38.91, *df* = 3, p < 0.0001; see Table 2.4 for pairwise comparison of each level of device). Birds carrying GPS, whether or not in combination with a GLS, gained less mass per day of their foraging trip than GLS-tracked or untracked birds (Figure 2.4; no device: 8.96 ± 1.12g, GLS: 9.08 ± 1.052g, GPS: 2.49 ± 0.88g, combined: 3.80 ± 0.67g). Considering the entire foraging trip, birds carrying GPS were found to gain less mass overall than GLS-tracked birds on their trips, despite their longer durations (no device: 55.51 ± 9.72g, GLS: 64.76 ± 9.039g, GPS: 28.86 ± 7.22g, combined: 40.11 ± 5.76g; n = 105 trips for 92 individuals; overall effect of device: χ^2 = 12.28, *df* = 3, p = 0.0065; see Table 2.5 for pairwise comparison of each level of device). We found no difference between untagged birds and GPS-tagged birds when considering the subset comparative dataset, but did find that GPS-tagged birds gained less mass when considering the entire dataset (see Appendix, section 2.6), which, taken together with the large effect sizes and relatively small p-values, may suggest this is a Type 2 error resulting from our reduced sample size.

Table 2.4: Pairwise comparison of daily mass gain during incubation foraging trips for each deployment type. Significant values (p <0.05) are in bold.

Device A	Device B	Mean diff (A - B)	t-value	p
No device	GLS	0.51 ± 1.39	0.037	0.98
	GPS	**5.99 ± 1.34**	**4.45**	**0.0020**
	Combined	**5.61 ± 1.29**	**4.35**	**0.0080**
GLS	**GPS**	**5.47 ± 1.30**	**4.21**	**0.00064**
	Combined	**5.10 ± 1.048**	**4.86**	**0.00039**
GPS	Combined	0.38 ± 1.026	0.37	0.98

Table 2.5: Pairwise comparison of total mass gain during incubation foraging trips for each deployment type. Significant values (p <0.05) are in bold.

Device A	**Device B**	**Mean diff (A - B)**	t-value	p
No device	GLS	-1.83 ± 10.12	-0.18	0.99
	GPS	25.47 ± 10.95	2.33	0.11
	Combined	24.53 ± 10.34	2.37	0.10
GLS	GPS	27.30 ± 10.60	2.58	0.060
	Combined	**26.36 ± 8.66**	**-3.044**	**0.020**
GPS	Combined	0.93 ± 7.92	0.12	0.99

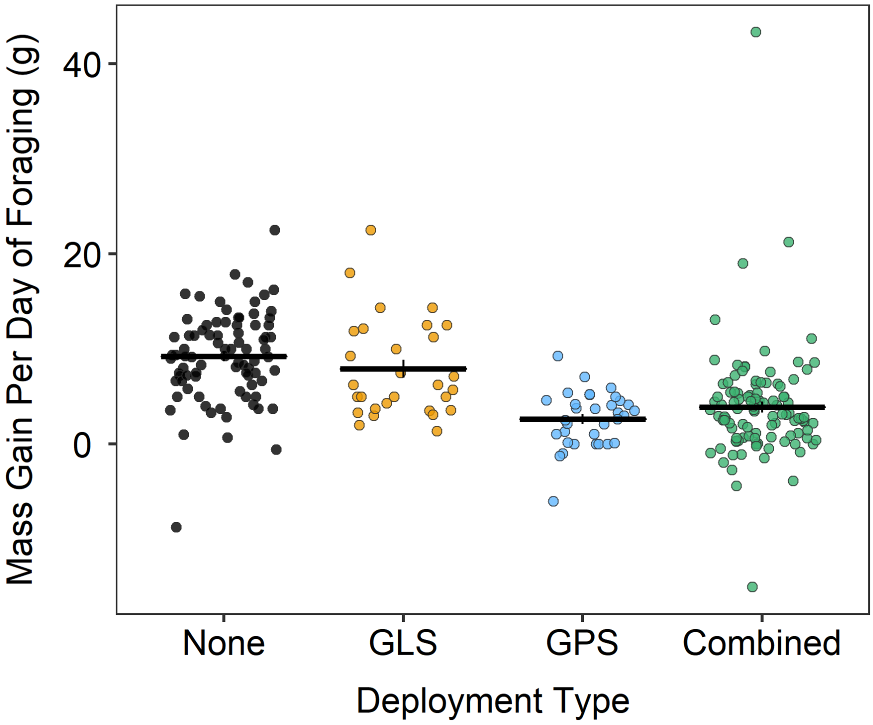

Figure 2.4: Mass gain per day of the foraging trip during incubation (g) according to deployment type. Black horizontal lines indicate mean, black vertical lines indicate standard error. Data are plotted with horizontal 'jitter' for clarity.

2.4.4 Effects on Chick Provisioning

In total, the mass changes of 48 chicks were recorded over the years 2013-2017. Neither deployment of GLS or GPS during the provisioning period, nor deployment of GPS during incubation, had an effect on the duration of the provisioning period for chicks, the number of nights they were fed, the maximum mass they attained, or their average feed per night, relative to chicks of non-tracked parents (Table 2.6). During the tracking period itself, the average food delivery per nest visit did not differ between parents subject to different deployment combinations (no device: 29.35 ± 0.79g, GLS: 29.06 ± 0.95g, GPS: 30.37 ± 0.96g, combined = 30.75 ± 1.015g; n = 218 years' data for 148 nests, χ^2 = 3.087, df = 2, p = 0.38).

Table 2.6: Pairwise comparison of metrics of provisioning effort for each deployment type. p-values calculated relative to the 'no device' group.

Deployment	**Nights fed**		**Peak mass (g)**		**Average feed (g)**		**Provisioning days**	
	Mean	***p-value***	***Mean***	***p-value***	***Mean***	***p-value***	***Mean***	***p-value***
No device	29.27 ± 1.70	-	543.06 ± 13.85	-	29.35 ± 1.21	-	50.95 ± 3.32	-
GLS	28.77 ± 1.72	0.98	542.29 ± 14.54	1.00	29.41 ± 1.31	1.00	49.92 ± 3.34	0.862
GPS	29.35 ± 1.69	1.00	552.92 ± 13.64	0.93	30.54 ± 1.15	0.91	50.87 ± 3.31	1.00
GPS (incub)	29.19 ± 1.85	1.000	557.94 ± 18.19	0.90	30.47 ± 1.82	0.98	51.18 ± 3.44	0.99
Combined	29.30 ± 1.70	1.00	545.37 ± 13.91	0.99	30.75 ± 1.21	0.91	51.95 ± 3.32	0.90

Notes – *nights fed* = total number of nights in which a provisioning visit was detected; *peak mass* = maximum mass attained by the chick; *average feed* = mean feed per night when a provisioning visit was detected; *provisioning days* = total number of days from hatching until last visit detected.

2.5 Discussion

By comparing behavioural and fitness measures of tagging impact in a free-ranging breeding seabird, we reveal that the short-term deployment of GPS tags on Manx shearwaters was associated with significant foraging behavioural changes during incubation, but that these did not translate into reduced breeding success in either the year of tagging or the subsequent year. More specifically, during incubation, shearwaters that carried a GPS doubled their foraging trip durations, reduced their flight time, and gained less mass per day of their trips. However, during chick rearing, no effects on parental provisioning could be observed: pairs in which one adult was tagged provisioned as much and as often as unmanipulated pairs. Thus, the perceived impact of tag deployment depends on the measure used to assess it, and breeding success may be insufficient to capture short-term alterations in behaviour.

There are several mechanisms by which the attachment of the GPS tag could have led to our observed changes in behaviour, including increased mass, increased drag forces, modifications to the centre of mass, or via the attachment procedure itself, which may induce stress and, in turn, lead to alterations in behaviour (Paredes et al., 2005; Guilford et al., 2008; Dean et al., 2015; Shoji et al., 2015b). While the masses of our devices exceeded the 3% threshold (Phillips et al., 2003) upheld by some authors, the negative impacts associated with tagging have not been found to increase linearly with tag mass (Bodey et al., 2018), suggesting that a reduced mass threshold would not necessarily have been sufficient to eliminate the effects we observed here. Indeed, the attachment of tags <3% of body mass has been found to cause negative impacts in a wide variety of species (e.g. great cormorants, Vandenabeele et al., 2015; common starlings *Sturnus vulgaris*, Pennycuick et al., 2012; grey seals *Halichoerus grypus*, Hazekamp et al., 2010; Magellanic penguins *Spheniscus magellanicus*, Wilson et al., 2004; green turtles *Chelonia mydas*, Watson and Granger, 1998; bottlenose dolphins, van der Hoop et al., 2014). In particular, the disruption of air or water flow associated with attaching an external tag to an animal means that the cost of movement can be increased substantially (Pennycuick et al., 2012; Elliott et al., 2014), especially for aquatic or volant species. In addition to differences in the mass or impediment imposed by the different deployments discussed here, there were small differences in the duration and type of handling experienced by each group of birds, and it is possible that these also contributed to the observed effects. However, any such differences were unlikely to be the primary driver of our observed results. All birds, even those that were untagged, experienced handling, which was always short, and during deployments we did not observe visible signs of stress such as vocalisation or escape behaviour. The fact that we found no differences in foraging trip duration between GLS birds that had experienced occasional versus frequent handling also supports this. Responses to handling have been shown to be less disturbing than device deployment in other seabirds (Kelly et al., 2015), and several studies in other Procellariiformes have shown that heart rate increases associated with handling return to base levels within a few hours (Weimerskirch & Guionnet, 2002; Müller et al., 2018). It is therefore probable that in our study the effects of handling dissipated quickly, and that the longer-term behavioural changes in flight and foraging behaviour we observed were driven by the persistent effects of carrying the device.

This may be the case for Manx shearwaters, which exhibited reduced flight time when carrying a GPS. It is unlikely that the birds in this study were physically prevented from ranging to long distance, profitable sites: while it was not possible to compare with untracked controls, GPS-tracked Manx shearwaters forage at considerable distances from the colony, covering the length of the Irish sea (approximately 280km, Guilford et al., 2008), with trips averaging a total length of 1517km (maximum 2117km, Dean et al., 2013). However, if increased flight costs compromise competitive ability, tracked birds may be competitively displaced from profitable patches, as appears to be the case for immature shearwaters (Fayet et al., 2015). Alternatively, the reduction in flight time observed may reflect a decrease in foraging efficiency associated with tagging. While tagged shearwaters in our study did not alter the amount of time they dedicated to foraging, it is possible that they increased foraging effort within this time. If shearwaters operate under an intrinsic energy ceiling (Elliott et al., 2014), and GPS-tagged birds invest more time in high-energy foraging, it may be the case that this increased energetic expenditure must be traded-off against reduced flight behaviour (energetically expensive) and increased rest (energetically inexpensive). Finally, while the change in rest time for GPS-tracked birds was not found to be significant, it is possible that the marginal increase in resting behaviour could reflect time 'wasted' pecking or preening at the tag (Wilson & Wilson, 1989), with flight reducing as a consequence. If this is the case, individuals may be expected to habituate to tags over longer or multiple deployments, and so eventually return closer to baseline behaviour, though we did not have sufficient repeated measures for individuals to examine this in our dataset. Regardless of the specific mechanisms, we found that foraging gains per day were reduced. That overall foraging trip duration was substantially increased in GPS-tagged individuals may reflect birds attempting to compensate for their compromised foraging ability by extending the length of the trip itself. Consequently, the behaviour of GPS-tagged shearwaters is unlikely to be faithfully representative of unmanipulated individuals.

Despite this substantial disruption to behaviour, we did not observe changes in breeding success that could be related to device deployment type. This may in part reflect compensation by the partner. It is well established that in many species (e.g. Kentish plovers *Charadrius alexandrinus*, Müller et al., 2018; burying beetles, Suzuki and Nagano, 2009; starlings, Wright and Cuthill, 1990), including seabirds (e.g. Cape gannets *Morus capensis*, Bijleveld and Mullers, 2009; great frigatebirds *Fregata minor*, Dearborn, 2001; Cory's shearwater *Calonectris borealis*, Navarro and González-Solís, 2007), a reduction in care by one parent can be compensated by the partner. It is possible in this case that tagging disrupts the normally equally shared (Brooke, 1990) parental care burden. If the costs of tagging during chick rearing are absorbed by the un-tagged parent, then overall breeding success may not give an accurate assessment of tagging impacts in this species. This has been observed in thick-billed murres (Paredes et al., 2005) and black-legged kittiwakes *Rissa tridactyla* (Heggøy et al., 2015), where a reduction in provisioning rate by tagged adults appears to be compensated by the partner, leading to normal fledging success. The stark differences in impact we observed between the two halves of the breeding season may therefore reflect the fact that during incubation we can measure precisely individual investment, while during chick-rearing we only measure the response of the pair as a whole, meaning compensation could occlude finer scale impacts on individual behaviour. It will therefore be important for future work to test whether nest visitation and food delivery differs between GPS-tracked and untracked parents. Individual costs may additionally be absorbed into future reproductive attempts, as has been observed in northern wheatears *Oenanthe oenanthe* (Arlt et al., 2013). In Manx shearwaters, an experimental increase in parental effort in one year has been found to lead to reduced breeding success in the following year (Fayet et al., 2016), while natural release from breeding costs in one year (through breeding failure or by skipping breeding altogether) leads to improved breeding success in the subsequent year (Shoji et al., 2015b). Consequently, long-term assessment of breeding success may be required to identify costs to reproduction. In long-lived species that produce few offspring, breeding success at a single point in time is unlikely to capture the full breadth of impact on an instrumented bird sufficiently. In our study, even major changes to individual behaviour, here identified as significant disruption to behaviour when foraging, were not reflected in breeding outcomes as we measured them. These results demonstrate that focusing on breeding success is inadequate to identify the full complement of impacts experienced by animals carrying tags.

It is now well understood that the instrumentation of wild animals can lead to undesirable effects on their fitness and behaviour. However, it is less clear how well fitness can provide a proxy for behavioural changes. Here, we identified major alterations to foraging behaviour that were not reflected in our measures of breeding success, highlighting the critical need for alternative measurements when considering the impacts of tagging. It is likely that the disjunction between the effects on fitness and behaviour observed here are commonplace in instrumented species. Consequently, careful consideration of which impacts are of interest from the perspective of the study design are necessary to determine whether data collected are representative of the wider population. By considering tagging impacts beyond coarse measures such as breeding success in a single season, authors can better identify from where their impacts arise and hence attempt to mitigate them. Even simple measures, such as comparisons of individual condition (easily measured as mass) or assessments of behavioural measures (such as trip length), in comparison to controls, will give a more complete picture of the often complex impacts of tag deployment on individuals, ultimately giving us a better toolkit with which we can answer fundamental questions about animal behaviour.

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2.6 Appendix

Here, we report the effect sizes and statistical values for the analyses performed using the complete dataset (see Methods, section 2.3 for details).

Starting masses by deployment group

No device: 387.80 ± 5.57g, GLS: 399.67 ± 6.82g, GPS: 400.20 ± 4.92g, combined: 401.70 ± 3.44g

Overall effect of device on starting mass: n = 333 trips from 281 individuals, χ^2 = 6.9, df = 3, p = 0.074

Foraging trip duration by island

Copeland: 4.069 ± 0.69 days, Skomer: 8.48 ± 0.55 days

n = 333 trips from 281 individuals, χ^2 = 72.98, df = 1, $p < 0.0001$

Foraging trip duration by deployment group

No device: 3.61 ± 0.75 days, GLS: 3.74 ± 0.86 days, GPS: 9.078 ± 0.65 days, combined: 8.67 ± 0.54 days

Overall effect of device on foraging trip duration: n = 333 trips from 281 individuals, χ^2 = 93.91, df = 3, $p < 0.0001$. See Table 2.7 for a pairwise comparison of trip durations.

There was no significant effect of the interaction of deployment type and starting mass (χ^2 = 0.8, df = 3, p = 0.8).

At-sea activity by deployment group

n = 288 trips from 195 individuals

Proportion of time in flight

GLS: 0.13 ± 0.0083, combined: 0.11 ± 0.011

$\chi^2 = 6.15$, $df = 1$ $p = 0.013$

Proportion of time in resting state

GLS: 0.37 ± 0.013, combined: 0.40 ± 0.014

$\chi^2 = 6.00$, $df = 1$, $p = 0.014$

Proportion of time spent foraging

GLS: 0.50 ± 0.010, combined: 0.49 ± 0.012

$\chi^2 = 2.44$, $df = 1$, $p = 0.12$

Mean daily foraging gain by deployment group

No device: 8.77 ± 0.82g, GLS: 9.36 ± 0.99g, GPS: 2.75 ± 0.80g, combined: 4.71 ± 0.53g

$n = 316$ trips from 265 individuals; overall effect of device: $\chi^2 = 45.94$, $df = 3$, $p < 0.0001$. See Table 2.8 for pairwise comparison of each level of device.

Total foraging trip mass gain by deployment group

No device: 58.66 ± 4.98g, GLS: 65.95 ± 5.94g, GPS: 30.74 ± 4.87g, combined: 39.88 ± 3.26g

$n = 316$ trips from 265 individuals; overall effect of device: $\chi^2 = 26.88$, $df = 3$, $p < 0.0001$. See Table 2.9 for pairwise comparison of each level of device.

Discerning the impacts of handling

To investigate whether differences in handling time could have precipitated the observed behavioural changes between deployment groups, we compared the foraging trip durations of GLS tracked birds that were handled daily (high intensity handling) with those handled only once prior to data collection, to deploy the GLS device (low intensity handling). We constructed an LMM that fitted foraging trip duration as a function of handling intensity, island, and sex, and included a random intercept of ring number nested within year. For GLS-tracked birds, differences in handling intensity (daily vs once for deployment) were not associated with differences in foraging trip duration (low intensity handling: 5.86 ± 1.22 days, high intensity handling: 6.37 ± 1.34 days; n = 196 trips for 106 individuals, χ^2 = 1.07, df = 1, p = 0.30). As there were no differences in trip duration between these two subgroups, they were combined for all other analyses.

Table 2.7: Pairwise comparison of foraging trip duration during incubation for each deployment type. Significant values (p <0.05) are in bold.

Device A	Device B	Mean diff (A-B)	t-value	p
No device	GLS	-0.13 ± 0.67	-0.19	0.78
	GPS	**-5.47 ± 0.62**	**-8.81**	**<0.0001**
	Combined	**-5.063 ± 0.64**	**-7.87**	**<0.0001**
GLS	**GPS**	**-5.34 ± 0.77**	**-6.97**	**<0.0001**
	Combined	**-4.93 ± 0.73**	**-6.72**	**<0.0001**
GPS	Combined	0.41 ± 0.56	0.73	0.77

Table 2.8: Pairwise comparison of daily mass gain during incubation foraging trips for each deployment type. Significant values (p <0.05) are in bold.

Device A	Device B	Mean diff (A - B)	t-value	p
No device	GLS	-0.40 ± 1.12	-0.35	0.98
	GPS	**5.43 ± 0.96**	**5.65**	**<0.0001**
	Combined	**4.32 ± 0.88**	**4.91**	**0.011**
GLS	**GPS**	**5.83 ± 1.14**	**1.43**	**<0.0001**
	Combined	**4.72 ± 1.009**	**4.68**	**0.00011**
GPS	Combined	1.11 ± 0.77	1.43	0.48

Table 2.9: Pairwise comparison of total mass gain during incubation foraging trips for each deployment type. Significant values (p <0.05) are in bold.

Device A	Device B	Mean diff (A - B)	t-value	p
No device	GLS	-4.43 ± 6.45	-0.69	0.90
	GPS	**28.34 ± 5.83**	**4.86**	**<0.0001**
	Combined	**25.56 ± 5.60**	**4.57**	**0.00042**
GLS	**GPS**	**32.77 ± 7.06**	**4.64**	**<0.0001**
	Combined	**30.00 ± 6.44**	**4.66**	**0.0004**
GPS	Combined	-2.77 ± 4.82	0.58	0.94

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3

The role of body mass in the coordination of incubation behaviour in the Manx shearwater *Puffinus puffinus*

With contributions from Oliver Padget, Martyna Syposz, Sarah Bond, and Tim Guilford.

Contents

3.1 Abstract

Animals are expected to balance the allocation of their resources to either reproduction or survival in such a way that maximises the number of surviving offspring produced over their reproductive lifespan. For long-lived, monogamous species, these investment decisions should to some extent be balanced between the two partners. In birds, the trade-offs involved in making these decisions become particularly stark during incubation, as maintaining constancy in egg warming usually requires a period of fasting by at least one of the parents. Parent Manx shearwaters share incubation duties in a largely egalitarian manner, with both members of the pair taking it in turns to incubate the egg for around 6 days at a time. While the patterns in incubation routine in this species are well-described, it is not clear what mechanisms underlie its scheduling. Using a 5-year dataset, we explored how body mass changes relate to decision-making during incubation in Manx shearwaters. Specifically, we explored whether and to what degree shearwaters exhibit sex differences in their incubation behaviour, what role body mass plays in its scheduling, and how decisions made by nesting birds relate to their subsequent foraging behaviour. We found that body mass is a fundamental driver of the behaviour of Manx shearwaters, dictating the amount of time they spend on foraging trips, the proportion of that time they invest in rest, flight, and foraging behaviours, and the decision of incubating birds to neglect the egg. We furthermore find evidence that foraging birds might account for the mass of their partners when determining trip duration, supporting the possibility that a process of negotiation may help parent shearwaters come to cooperative decisions about their behaviour during incubation.

3.2 Introduction

To maximise lifetime reproductive output, parents should strike a balance between their investment in the current breeding attempt and future attempts (Trivers, 1972). How these costs and benefits are traded-off is predicted by life history theory, with those species lying at the ‘slow’ end of the continuum, characterised as being long-lived with a low reproductive output, being selected to invest conservatively in their offspring in favour of survival, and those short-lived, high output species lying at the ‘fast’ end being selected to invest more heavily in reproduction, at the expense of future survival (Stearns, 1992). For long-term monogamous species, finding this balance is additionally complicated by the needs of the partner. Where there is a substantial benefit to pairing with the same individual for multiple years (or a substantial cost to divorce), then exploitation of the partner may be costly over the long-term, and so individuals may be selected to allocate resources cooperatively (Griffith, 2019). The allocation decisions an animal makes over its lifetime have significant consequences for its behaviour, most notably during breeding (Boggs, 1992).

Body mass is a good indicator of the reserves available to an individual that can be allocated to survival or reproduction. Variation in body mass has important consequences for various aspects of reproduction, including decisions as to whether to breed (e.g. *Vipara aspis*, Naulleau and Bonnet, 1996; lesser scaup *Aythya affinis*, Warren et al., 2014; common eider *Somateria mollissima*, Jean-Gagnon et al., 2018) or provide care to offspring (e.g. common eider, Bustnes et al., 2002), and when (e.g. Florida scrub jay *Aphelocoma coerulescens*, Schoech, 1996; sociable weaver *Philetairus socius*, Covas et al., 2004; mallard *Anas platyrhynchos*, Devries et al., 2008) and the overall success of a breeding attempt (e.g. black-browed albatross *Thalassarche melanophris*, Pinaud and Weimerskirch, 2002; burrowing parrot *Cyanoliseus patagonus*, Masello and Quillfeldt, 2003; smooth snake *Coronella austriaca*, Reading, 2004). As such, measuring the mass of individuals in different behavioural contexts might give insight about the strategic allocation of available resources.

In birds, the incubation period might provide insight into the optimisation of life-history trade-offs since it inevitably entails at least some degree of fasting for the caring parent, which must be carefully managed to ensure that sufficient reserves are retained for the rest of the breeding season or for future reproductive attempts. This is especially the case in species constrained to breed far from foraging grounds, such as seabirds, where long bouts of fasting are necessary to allow parents to spend substantial periods of time foraging at sea. In these species, it is in the interests of both parents to manage incubation cooperatively (Jones et al., 2002): failure to align incubation stints with the partner may leave the egg exposed and at risk of predation, damage, or chilling. Consequently, it is at this point in breeding that cooperation between the parents might be most conspicuous. The management of incubation shifts is associated with large fluctuations in body mass as parents alternate between fasting and foraging. Failure to time these shifts cooperatively could lead to starvation if the sitting bird is forced to sit for excessively long incubation shifts, or could alternatively lead to breeding failure if it chooses to abandon the nest in search of food. As long-lived, mostly monogamous birds, seabirds should be selected to manage their incubation shifts in a cooperative manner with their partner (Griffith, 2019), both to minimise the costs to future reproductive success incurred during the breeding attempt and to ensure that the investment can be sustained for the entirety of breeding.

Procellariiform seabirds exhibit unusually long incubation shifts (Brooke, 2004), which probably represent an adaptation allowing them to exploit long-distance, rich foraging sites and hence increase the probability of finding food. Consequently, these birds should be under strong selection to manage their body mass. Evidence suggests that the regulation of body condition, for which mass is a key factor, plays an important role in the scheduling and coordination of incubation shifts in many Procellariiform species (southern fulmar *Fulmarus glacialoides*, Weimerskirch, 1990; blue petrel *Halobaena caerulea*, Chaurand and Weimerskirch, 1994; Antarctic petrel *Thalassoica antarctica*, Tveraa et al., 1998; storm petrel *Hydrobates pelagicus*, Bolton, 1996; Gould's petrel *Pterodroma leucoptera*, Kim et al., 2018). While most incubation shifts will be ended by the arrival of the partner, many seabirds are known to temporarily desert the nest before the partner has returned (henceforth 'neglect'; Boersma and Wheelwright, 1979). It is not clear what drives neglecting. The evidence that this might reflect a mass threshold at which birds choose to neglect the egg is equivocal, with some studies reporting clear evidence for such a set point (herring gull *Larus argentatus*, Sibly and McCleery, 1985; blue petrel, Chaurand and Weimerskirch, 1994; Ancel et al., 1998) and others finding none (grey-faced petrel *Pterodroma macroptera gouldi*, Johnstone and Davis, 2008; cape petrel *Daption capense*, Weidinger, 2008; short-tailed shearwater *Puffinus tenuirostris*, Carey, 2011; Gould's petrel, Kim et al., 2018). As neglect is likely to increase the risk of egg failure (Boersma & Wheelwright, 1979; Brooke, 1990; Ronconi & Hipfner, 2009), its occurrence should reflect the point at which the cost to the current reproductive attempt is sufficiently overcome by improved survival, and therefore future breeding success. While many seabird embryos are known to be resistant to temporary chilling during incubation (Schreiber & Burger, 2001), egg neglect is likely to proportionally extend the incubation period (Ronconi & Hipfner, 2009), which will increase the investment required by the parents and could cause chicks to fledge at a time that is suboptimal for their survival (Perrins, 1970, 2008). By sharing the costs of incubation with their partner, parents can minimise this risk: if longer than normal foraging trips drive incubating birds to neglect by forcing their body condition to decline excessively, parents should ensure they reduce the time they spend at sea so that their partner does not need to neglect.

The Manx shearwater *Puffinus puffinus* is a medium-sized Procellariiform seabird that exhibits characteristically long incubation shifts, which are divided between the two parents. During incubation, Manx shearwaters experience a daily mass decline of around 10g (Thompson, 1987), which, with an average incubation shift duration of 6 days (Harris, 1966), equates to a total percentage body mass decline of around 15% for each shift. Over their 51-day incubation period, parent Manx shearwaters exhibit largely egalitarian and well-coordinated incubation shifts, the scheduling of which has already been well described (Harris, 1966; Thompson, 1987; Brooke, 1990). However, it is not understood how the regulation of these is controlled. The regulation of mass is likely to be important to the Manx shearwater, both to ensure that the parents are able to sustain the energetic chick provisioning period that follows hatching of the eggs, and because birds that end breeding in poor condition are more likely to skip or fail the following year (Shoji et al., 2015a).

We examined how the investment decisions made by Manx shearwaters during incubation related to their body mass changes and foraging behaviour over a 5-year observational study. To this end, we had 3 broad aims: first, to detail the general patterns in incubation routine observed in Manx shearwaters across the entire period; second, to explore how mass varies during this time and how this relates to decisions relating to incubation behaviour; and third, to examine the interplay between foraging behaviour and success and the decisions made by parents at the nest. In many species, higher breeding success is associated with increased pair experience (e.g. kittiwake *Rissa tridactyla*, Coulson, 1966; Thomas, 1983; Eurasian oystercatcher *Haematopus ostralegus*, van de Pol et al., 2006; bearded reeling *Panurus biarmicus*, Griggio and Hoi, 2011, blue-footed booby *Sula nebouxii*, Sanchez-Macouzet et al., 2014), including Manx shearwaters (Harris, 1966; Brooke, 1978b). As part of aim 1, we explored whether incubation behaviour varied systematically with pair experience and whether this subsequently led to differences in breeding success between new and established pairs. For aim 2, we examined the regulation of body mass during incubation shifts, whether this differed between the sexes, and whether this influenced how long incubating birds decided to remain at the nest for. Finally, one of the key determinants of the resources available to parents during their incubation shifts is their foraging success during the preceding excursion at sea. To this end, as part of aim 3, we explored the role of parental condition in determining foraging trip duration, how mass gains on the trip relate to foraging behaviour, and what variables determine the behavioural profile of foraging shearwaters.

3.3 Methods

3.3.1 Study system

We collected data on the daily mass changes and behaviour of Manx shearwaters breeding in a long-term study plot on Skomer Island, Wales (51°44’ N, 5°17’ W) during the incubation period between 2015 and 2019. Egg laying in this species begins at the end of April, and continues into early June. The incubation period lasts for approximately 51 days (Brooke, 1990) and is split into shifts of around 5-7 days, which are alternated between the parents, who exchange incubation duties during nocturnal colony visits. At the study plot, occupancy and breeding success of approximately 100 nests are monitored annually, which are easily accessed either through the natural nest entrance or via purpose-built inspection hatches. All individuals were identified with a permanent stainless steel ring, provided by the British Trust for Ornithology.

3.3.2 Sampling methods

Individual identity, mass measurements, and pair experience

As part of the annual long-term monitoring, nests were checked daily for the presence of an egg, from mid-April until early June. When an egg was found, the sitting parent could be identified using the metal ring, and its partner was identified when the pair later exchanged incubation duties. Females could be sexed by cloacal inspection (Boersma & Davies, 1987) and males by inference. To determine incubation shift durations and adult mass changes, all nests used in the study were checked daily to determine individual occupancy and to weigh the incubating bird, by inserting it head first into a draw-string muslin bag that was attached to a 600g Pesola spring balance, precise to 5g. This continued from the point of laying to the day that the egg hatched. Where the egg was found unguarded, the burrow continued to be inspected daily, either until the egg was depredated or it was no longer possible for the egg to be still viable (>10 days). If either parent later returned to the egg, it was deemed to have been ‘neglected’; eggs to which neither parent returned were deemed ‘abandoned’. Occupancy, but not mass data, were collected in 2017. In total, 74 nests were used in the study.

As historical breeding data were available for many of the pairs in this study, pair experience could be determined for each nest. As the year in which the pair bond was initially formed was not known for many birds, experience was determined as a binomial factor of ‘new’ or ‘experienced’. Pairs were defined as ‘new’ when either individual in the pair was known to have nested with a different partner in the previous year. Pairs that were known to have bred together in at least two previous years were considered ‘experienced’, and pairs that had only been observed in a single season were designated ‘unknown’.

Foraging behaviour

To measure at-sea behaviour, 54 individuals were fitted with light level geolocators (Migrate Technology Intigeo-C250 and Intigeo-C65) with integral salt-water immersion logging facility. These were attached by two small cable ties to a plastic ring on the tarsus to ensure immersion when sitting on water (see Guilford et al., 2009 for details). Geolocators were deployed at the beginning of the breeding season and were retrieved either at the end of the same breeding season or at the beginning of the season the following year.

3.3.3 Statistical methods

All statistical analyses were carried out in `R` version 3.5.1 (core Team, 2018). The `R` package `lme4` (Bates et al., 2015) was used to construct linear mixed effects models (LMMs) and generalized linear mixed effects models (GLMMs), and Beta GLMMs were constructed using the `glmmTMB` package (Magnusson et al., 2020). We assessed model fit using through manual visual inspection of residual plots. P-values were obtained by comparing models to null models without the effect of interest using a likelihood ratio test. For categorical variables, least squares means for each level of the factor were calculated using the `R` package `emmeans` (Lenth et al., 2018). To account for repeated measures and any systematic variation that might be attributed to year, all models were fitted with individual and/or burrow, nested within year as appropriate, as a random (intercept only) effect. Data are presented as means and 95% confidence intervals (given in square brackets) unless otherwise specified.

Patterns in incubation

To determine the drivers of variation in lay date, we fitted an LMM to Julian lay date with the fixed effects of pair experience and year (model 1). We further examined the effect of pair experience, year, and breeding success on the duration of incubation (model 2) using a Poisson GLMM to account for the discrete nature of the response variable. Nests for which any of these parameters were unknown were excluded from the models, leaving 73 records across 58 nests.

To explore, in detail, variation in the patterns of incubation scheduling and how this is shared between the two parents, we examined how well sex and pair experience explained variation in the proportional contribution of the female to incubation (model 3), the number of shifts taken on by each parent (model 4), and the duration of the very first (model 5) and subsequent (model 6) incubation shifts. In model 6, we controlled for potential temporal changes in incubation behaviour by including the fixed effect of 'egg age'. As model 3 included a proportional response variable, this was fitted as a Beta GLMM. Models 4, 5, and 6 included count response variables and so were fitted as Poisson GLMMs. To control for the number of days parents had available to them to take incubation shifts, model 4 included the additional fixed effect of incubation duration. Model structures can be found in Table 3.1. We additionally attempted to replicate previous observational findings (Harris, 1966; Brooke, 1978a) that males are more likely to take the first incubation shift, using a two-tailed binomial test that compared the observed proportion of first shifts taken by the female to a null expectation of 0.5. For these analyses, we removed nests where data on the first incubation shift had not been recorded, leaving 62 records for 52 nests.

We determined to what extent the duration of incubation shifts might be constrained by the duration of the shift preceding it by calculating the correlation coefficient between consecutive incubation shift durations using the package `rmcorr` (Bakdash & Marusich, 2017). We computed a repeated measures correlation between the duration of an incubation shift and the duration of the previous shift for each burrow in a given year.

In some seabird colonies, colony attendance is observed to be temporally aggregated across nests, which may reflect responses to endogenous rhythms and/or environmental conditions (e.g. Cruz et al., 2013; Huffeldt and Merkel, 2016). We aimed to test whether such aggregation might exist in Manx shearwaters by examining the distribution of changeover events (points at which the two parents exchange nesting duties) across the entirety of incubation. If shearwaters return to the colony in an aggregated way, we would expect to observe that nights with intermediate numbers of changeovers are less frequent than expected by chance, since this implies that most nights either have many changeovers or very few, and hence there is some colony level synchronicity in visitation. This is the equivalent of examining whether nights with very high or very low numbers of changeovers are more frequent than we expect by chance. To this end, for each year we measured the proportion of nights on which there were 0 changeovers, and compared this to the expected number of nights with 0 changeovers for the same number of birds, beginning incubation at the same time, but with randomly drawn incubation shift lengths, sampled with replacement from the appropriate year's incubation shift lengths. This allowed us to account for the differing number of nests actively incubating across the dates included in the study (owing to variation among nests in phenology) and to account for the aggregation that may be driven by similar lay dates and subsequent incubation shifts. If a larger number of nights with very few changeovers exists in the real data than the randomly drawn data, this suggests that shearwaters are aggregating their visits to the colony temporally, while fewer low numbers would suggest that shearwaters have roughly equal colony attendance across nights and thus are unlikely to be responding to similar cues. To assess whether putative aggregation in the real data was significant, we measured whether the real proportion of nights with 0 changeovers fell outside the 95% quantile range of 10000 randomly shuffled colony incubation periods, separately for each year. A two-tailed p-value was hence calculated as the proportion of randomly shuffled incubation periods in which the observed value fell within the 95% quantile range.

Table 3.1: Model structures for 2.3.1. Patterns in incubation

Type of model	**Model**	**Parameters** ***Response***	***Fixed***	***Random***
LMM	1	Julian lay date	Exp + year	Nest
Poisson GLMM	2	Total incubation duration (days)	Exp + outcome + year	Nest
Beta GLMM	3	Proportional share of incubation	Exp + sex	Year: Nest
Poisson GLMM	4	N shifts	Exp + sex + inc dur	Year: Nest
Poisson GLMM	5	Shift duration – shift 1 (days)	Exp + sex	Year: Nest: ID
Poisson GLMM	6	Shift duration – all others (days)	Exp + sex + egg age	Year: Nest: ID

Notes – *exp* = pair experience, experienced or new; *outcome* = of incubation, hatched or failed; *sex* = male or female; *inc dur* = total duration of the incubation period, days; *ID* = individual identity; *egg age* = number of days since the egg was laid

Mass changes during incubation

As one of the key determinants of the resources available to parents during incubation, we explored how mass varied both over single shifts of incubation and the incubation period in its entirety. We investigated what factors influenced the mass at which parents began their incubation shifts (model 7), and the rate of mass decay during these shifts (model 8). Where gaps were present in the daily mass data for individuals, they were linearly interpolated based on the current trajectory of mass loss for the incubating bird. We excluded individuals for which we had been unable to collect mass data, leaving 103 individuals across 52 nests. We predicted that mass at the start of incubation would be a key determinant of whether or not the incubating bird chose to neglect the egg. To this end, we modelled how well mass at the start of an incubation shift predicted the decision to neglect (model 9) using a binomial GLMM. For those shifts that did end in neglect (n = 43 across 21 individuals), we additionally explored whether the duration of time parents incubated for before they abandoned the nest was predicted by their mass (model 10) using a Poisson GLMM. As the sample size for this analysis was very small, we did not have the degrees of freedom to include the random effect of year, and instead use only bird ID. Finally, we used a binomial GLMM to determine whether the number of days of neglect predicted the likelihood of egg hatching, using all nests for which we had neglect and breeding success data (n = 73 records for 58 nests; model 11). Model structures can be found in Table 3.2.

Table 3.2: Model structures for 2.3.2 Mass changes in incubation

Type of model	**Model**	**Parameters**		
		Response	***Fixed***	***Random***
LMM	7	Start mass (g)	Sex + egg age + exp	Year: ID
LMM	8	Daily mass decline (% body mass)	Sex + egg age + shift day + exp	Year: ID
Binomial GLMM	9	Probability shift ends in neglect	Start mass + shift dur + sex + egg age + exp	Year: ID
Poisson GLMM	10	Shift duration following neglect	Start mass + egg age + sex + exp	ID
Binomial GLMM	11	Probability of hatching	Days neglect + exp	Year: ID

Notes – *sex* = male or female; *egg age* = days since egg laid; *exp* = pair experience, experienced or new; *ID* = individual identity; *shift day* = day of the incubation shift; *start mass* = mass of incubating bird at beginning of incubation shift, g; *shift dur* = duration of the incubation shift

Foraging behaviour

Since normally incubation shifts end when the foraging bird returns to the nest (egg neglect is relatively rare), the duration of the incubation shift is usually determined by the decision of the foraging bird to return to the colony. Consequently, we investigated whether the mass of the incoming bird, mass of the outgoing bird, and sex predicted foraging trip duration (model 12). This model included 130 individuals from 65 nests for which we had mass data for both parents. We further examined how well starting mass, sex, foraging trip duration, and time spent foraging predicted foraging gains as a percentage of body mass (model 13). All 54 GLS-carrying individuals were used in this analysis. The aim was to disentangle the factors that the pair might respond to in order to coordinate incubation stints, so as to reduce both egg neglect and the risk of excessive mass loss, which might have a long-term impact on their condition or survival. Model structures can be found in Table 3.3.

The immersion logging function of geolocators was used to determine at-sea behaviour. Geolocators tested for saltwater immersion every 3 or 6 seconds, and recorded the number of samples immersed in each 5 or 10 minute bin respectively. These immersion data were used to classify behaviour using previously verified threshold methods (Dean et al., 2013; Fayet et al., 2016a) whereby we considered 5 or 10 minute bins where <2% of recorded states were immersed as sustained flight, > 98% as resting on the water, and intermediate values as foraging. Time spent foraging as identified by this classifier has been shown to be indicative of foraging behaviour through validation with dive loggers (Dean et al., 2013), and so is considered a robust method for interrogating at-sea behaviour using immersion devices. The proportion of each 24 hour period (00:00 – 23:59) spent in each of the three behaviours was calculated.

To determine how facets of the incubation shift might subsequently affect at-sea behaviour, we modelled the proportion of time spent in each behaviour state as a function of starting mass and trip duration for the 54 individuals carrying GLS, using separate Beta GLMMs (model 14/15/16) for each behaviour. It might be expected that differences in the proportion of time dedicated to specific behaviours could arise due to differences in relative commuting time: shorter duration trips, for example, may exhibit more flight behaviour as a greater proportion of the trip was spent travelling to the foraging locale (Dean et al., 2013). To account for this possibility, we included a dummy variable of 'proportion commuting time', assuming that the first and last days of the trip would be mostly comprised of commuting.

Table 3.3: Model structures for 2.3.3 Foraging behaviour

Type of model	**Model**	**Parameters**		
		Response	***Fixed***	***Random***
LMM	12	Foraging trip duration (days)	Start mass + partner mass + sex	Year: Nest: ID
	13	Percentage daily mass gain	Start mass + sex + trip dur + prop forage	Year: ID
	14/15/16	Prop forage/rest/flight	Start mass + sex + trip dur + prop commute	Year: ID

Notes – *start mass* = bird mass at beginning of foraging trip, g; *partner mass* = partner mass at start of corresponding incubation shift, g; *sex* = male or female; *ID* = individual identity; *trip dur* = foraging trip duration, days; *prop forage* = proportion of each day spent foraging; *prop commute* = proportion of trip spent commuting

3.3.4 Ethical note

All methods and procedures adhere to ASAB/ABS Guidelines for the Use of Animals in Research, and were approved by the British Trust for Ornithology (BTO) Unconventional Methods Technical Panel (permit number C\5311) and by the Wildlife Trust for South and West Wales under the name of Prof. Tim Guilford. Ethical approval was received from the Local Ethical Review Process of the University of Oxford. This project holds Islands

Conservation Advisory Committee (ICAC) approval. Handling time during ringing, weighing, and geolocator deployments was kept to a minimum; deployment and retrieval of geolocators was conducted in the field and did not normally exceed 5 minutes.

3.4 Results

3.4.1 Patterns in incubation

Lay date varied significantly between years (Figure 3.1; χ^2 = 16.27, df = 1, p = 0.027). New pairs laid their eggs slightly later than experienced pairs but this was not significant (mean date new: 16th May, experienced: 13th May; χ^2 = 3.48, df = 1, p = 0.062).

The mean incubation duration for failed nests was considerably shorter than that of successful nests, probably because nest failure truncated the breeding attempt (failed = 35.2 [32.9, 37.7] days; successful = 50.9 [48.3, 53.6] days; χ^2 = 53.21, df = 1, $p <$ 0.0001). There was no difference in incubation duration for experienced vs new pairs (χ^2 = 0.81, df = 1, p = 0.37) nor according to year (χ^2 = 0.55, df = 4, p = 0.97).

Males took a greater proportional share of incubation than females (male = 0.53 [0.51, 0.55], female = 0.47 [0.45, 0.49]; χ^2 = 18.25, df = 1, $p <$ 0.0001). These shares were not related to pair experience (χ^2 = 0.00, df = 1, p = 1). Despite the greater overall contribution of males, males and females did not differ in the number of incubation shifts they took on (male: 4.27 [3.61, 4.93], female: 4.13 [3.48, 4.77] shifts; χ^2 = 0.15, df = 1, p = 0.70). There was no difference in shift number between experienced and new pairs (experienced: 4.03 [3.51, 4.55], new: 4.36 [3.52, 5.21]; χ^2 = 0.57, df = 1, p = 0.45).

Males were usually present when the egg was laid. Females took the first incubation shift in 39.74% of breeding attempts, versus 60.25% for males, but these proportions were not found to be statistically significant (two-sided binomial test: p = 0.088). However, when the first shift of incubation was taken by the female, this was significantly shorter (male: 3.95 [3.01, 5.20], female: 2.56 [1.84, 3.56]; χ^2 = 7.64, df = 1, p = 0.0057), though notably, in all subsequent shifts, males and females were not found to differ in duration (male: 5.56 [4.93, 6.26], female: 5.20 [4.62, 5.87]; χ^2 = 2.54, df = 1, p = 0.11). Incubation shift duration additionally did not change over the course of incubation (χ^2 = 0.082, df = 1, p = 0.78), nor was there an effect of pair experience (*first shift*: experienced: 3.30 [2.55, 4.29], new: 3.07 [2.14, 4.39]; χ^2 = 0.25, *df* = 1, p = 0.67; *all shifts*: experienced: 5.50 [4.93, 6.13], new: 5.26 [4.45, 6.22]; χ^2 = 0.25, *df* = 1, p = 0.62).

There was a significant correlation between the duration of an incubation shift and the duration of the previous shift by the partner (Pearson's correlation coefficient = 0.26 [0.12 – 0.40]; p = 0.00044). The temporal aggregation of changeover events across study nests during incubation was not greater than random, hence providing no support for a temporal clustering of changeover behaviour (p = 0.71, n iterations = 10,000 per year).

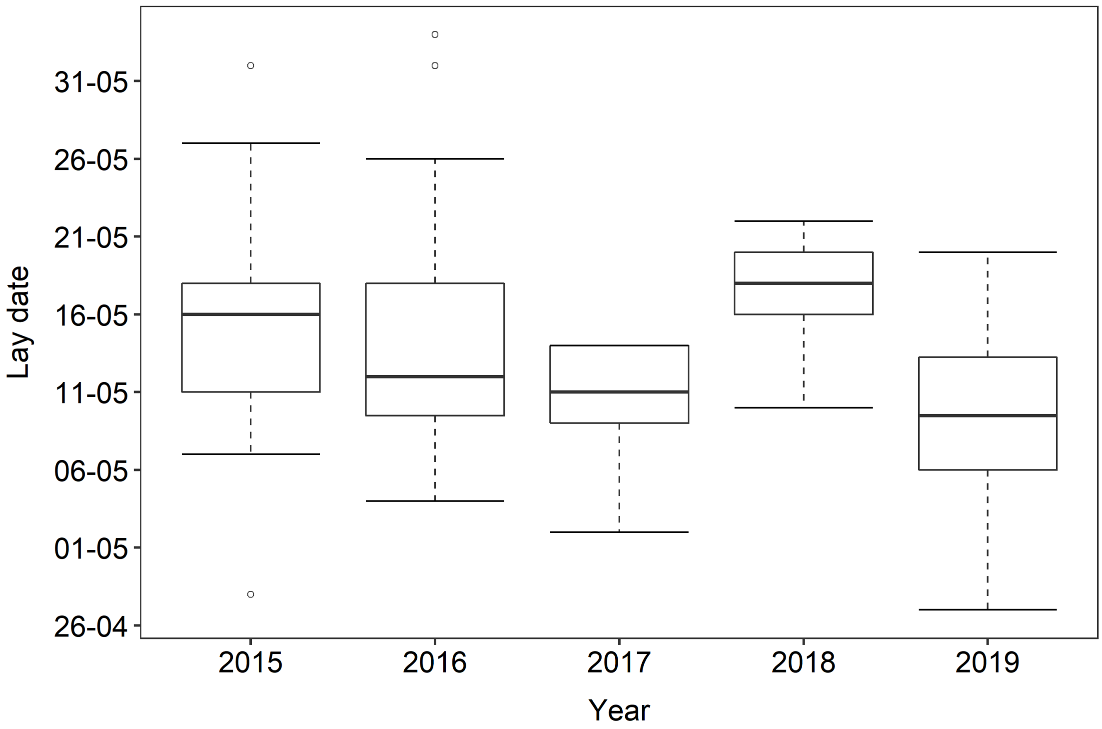

Figure 3.1: Variation in lay date according to year. Horizontal lines indicate median; upper and lower hinges represent third and first quantiles respectively; whiskers extend from hinges by 1.5 times the interquartile range.

3.4.2 Mass changes during incubation

Males began their incubation shifts at a higher mass than females (male: 458 [448, 467]g, female: 433 [423, 443]g; χ^2 = 35.16, *df* = 1, $p < 0.0001$). The starting masses of parents increased over the duration of the incubation period equally for both males and females, increasing by 0.21 [0.076, 0.34]g for each day since the egg was laid (χ^2 = 9.54, *df* = 1, $p = 0.002$; Figure 3.2). There was no effect of experience on starting mass (χ^2 = 2.96, *df* = 2, $p = 0.23$).

Incubating birds lost 2.31 ± 0.17% of their body mass each day, equating to a decline of 10.03 ± 7.42g daily. This daily mass decay did not differ between males and females (male: 2.73 [2.63, 2.84]% per day, female: 2.69 [2.58, 2.80]% per day; χ^2 = 0.42, *df* = 1, $p = 0.52$), and was consistent over both the scale of a single incubation shift (day of stint: χ^2 = 3.20, *df* = 1, $p = 0.74$) and the incubation period in its entirety (χ^2 = 2.93, *df* = 1, $p = 0.087$). There was no effect of experience on the body mass declines experienced by parents (χ^2 = 1.41, *df* = 1, $p = 0.23$).

Over the 5-year study period, 8.26% of incubation shifts ended in neglect. The probability that an incubation shift ended in neglect was significantly predicted by the mass at which the incubating parent began incubation (Figure 3.3). The estimated coefficient for this parameter was 0.98 [0.96, 0.99] for each gram increase in starting mass; this is a log odds ratio owing to the logit link in the GLMM and in real terms equates to an approximate reduction in the probability of neglect of 7.10% for a 50g increase in mass (χ^2 = 7.63, *df* = 1, $p = 0.0057$). The duration of the incubation shift (χ^2 = 2.086, *df* = 1, $p = 0.15$), sex (χ^2 = 2.72, *df* = 1, $p = 0.099$), and egg age (χ^2 = 0.28, *df* = 1, $p = 0.60$) had no effect on the probability of neglect. However, new pairs were more likely to neglect than experienced pairs (experienced probability: 0.025 [0.0095, 0.063], new: 0.068 [0.025, 0.17]; χ^2 = 4.13, *df* = 1, $p = 0.042$). For those shifts that did end in neglect, the mass at which a parent had begun its shift predicted how long it sustained incubation for before neglecting the egg, with heavier birds remaining at the nest for longer before departing for sea (Figure 3.4; χ^2 = 10.05, *df* = 1, $p = 0.0015$). The number of days parents remained at the nest before neglecting increased by 3.13 [3.10, 3.15]% for each gram increase in starting mass; this corresponds to an increase in shift duration of 1.29 days for a 50g increase in mass. Males remained at the nest for less time than females before leaving the egg unattended, exhibiting incubation shifts that were 68.64 [68.17, 69.12]% of the duration of females (Figure 3.4).

Each day of neglect decreased the odds of hatching ($\chi^2 = 19.82$, $df = 1$, $p < 0.0001$); the estimated log odds ratio coefficient for this parameter was 0.49 [0.28, 0.84). The effect of neglect on hatching success showed diminishing returns over time: while 3 days of neglect reduced the probability of hatching by 48.9% compared to no neglect, the difference in hatching probability between 15 and 13 days of neglect was only 0.024% (Figure 3.5). Experience alone had no effect on the probability of hatching ($\chi^2 = 0.88$, $df = 1$, $p = 0.35$).

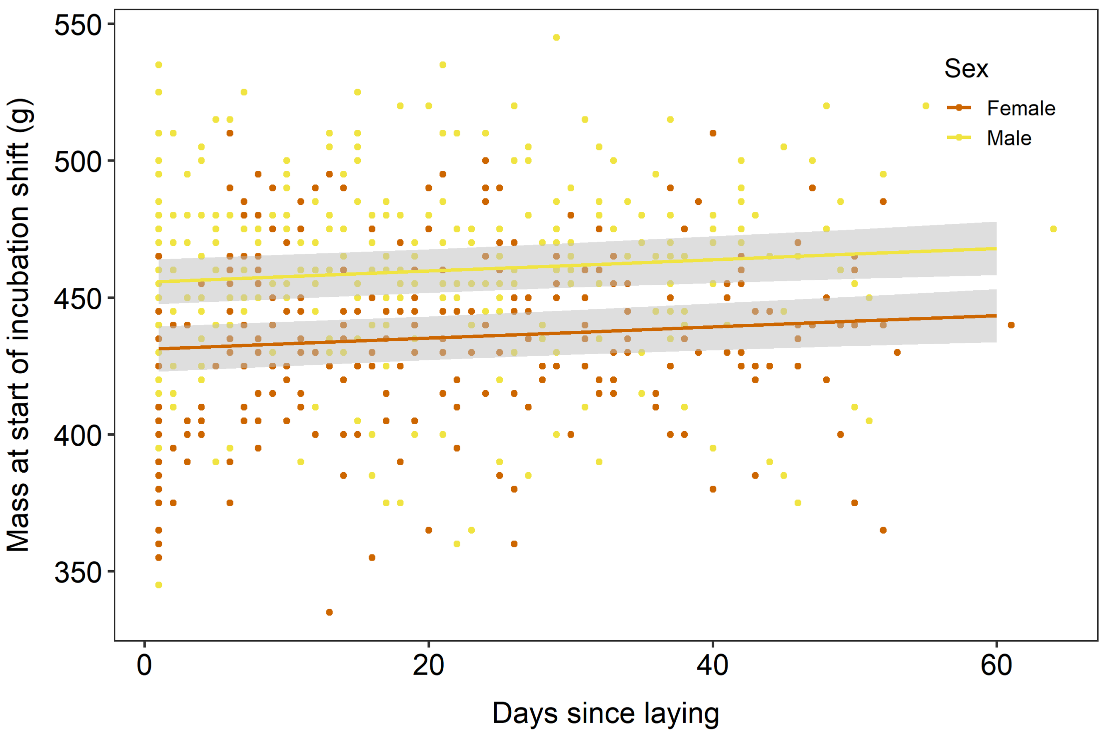

Figure 3.2: Mass (g) at start of individual incubation shifts according to time since the egg was laid (days). Females in dark red, males in yellow. Shaded areas indicate 95% confidence intervals.

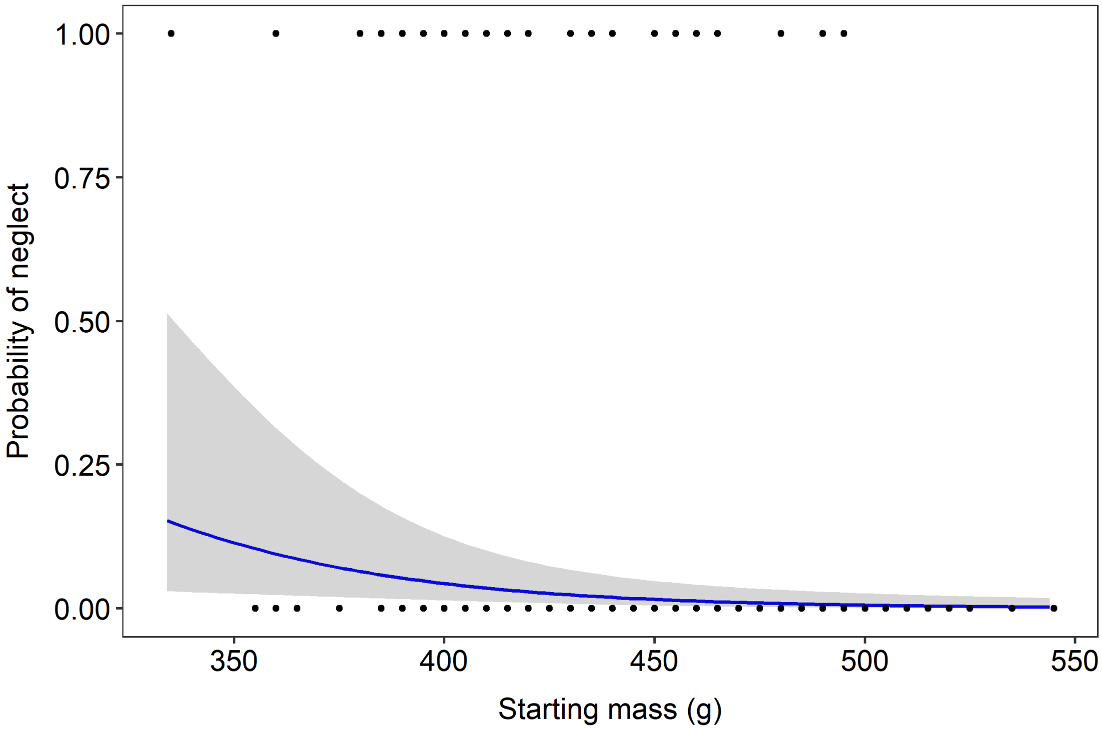

Figure 3.3: Predicted probability of neglect for a given starting mass (g). Grey shaded area indicates 95% confidence intervals. Black points indicate real shifts which ended in neglect (1) or did not (0) according to starting mass.

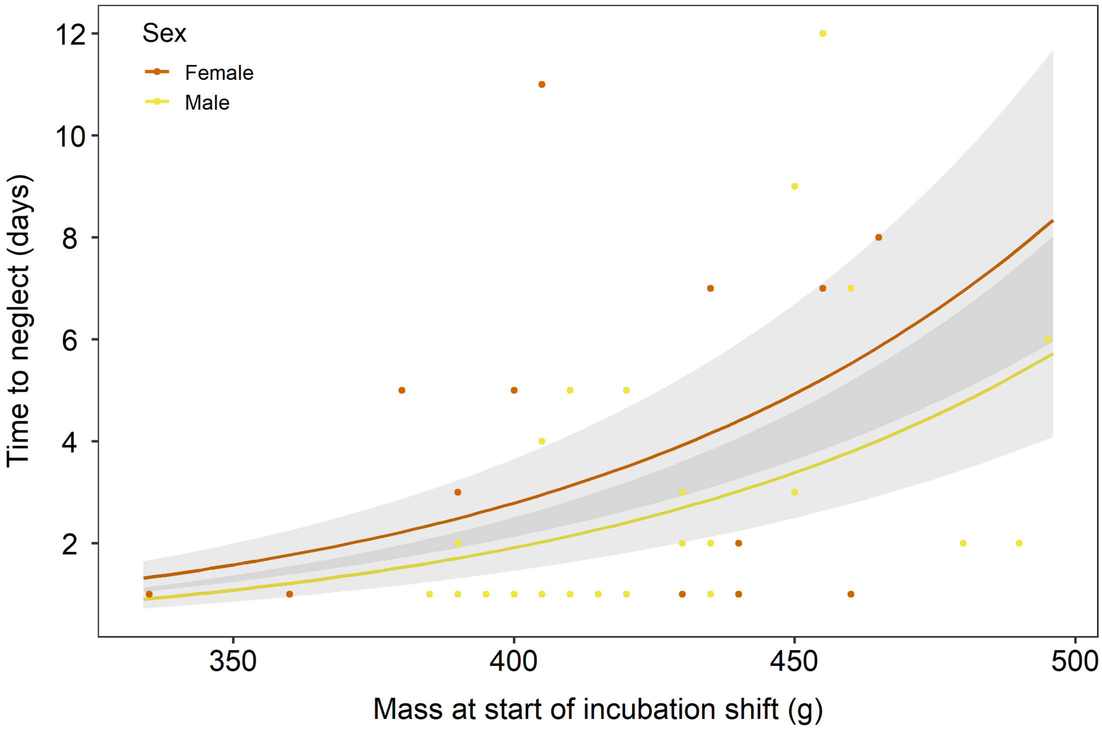

Figure 3.4: Number of days until neglect occurred as a function of mass at the start of the incubation shift (g) for females (yellow) and males (orange).

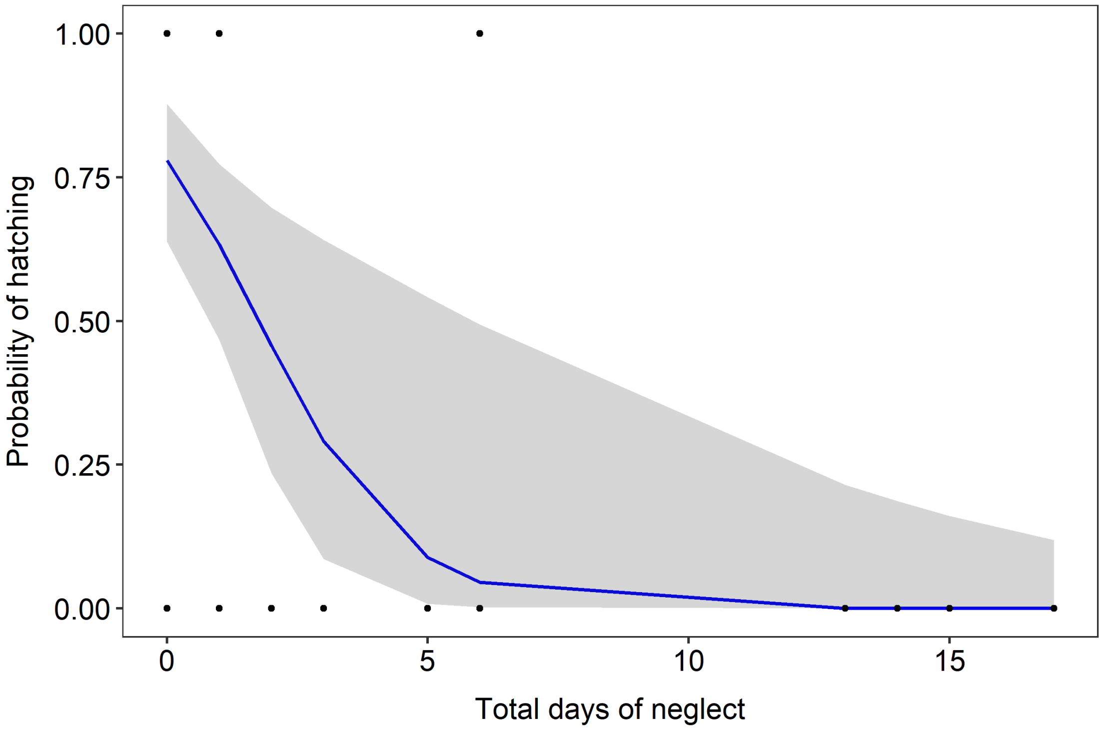

Figure 3.5: Predicted probability of hatching for a given number of days of neglect. Grey shaded area indicates 95% confidence intervals. Black points indicate actual nests where the breeding attempt was successful (1) or not (0) according to the number of days the parents neglected the egg for.

3.4.3 Foraging behaviour

Birds that left the nest at a higher mass went on shorter foraging trips (χ^2 = 19.03, *df* = 1, $p < 0.0001$). The log odds coefficient for this parameter was -0.0031 [-0.0045, -0.0017], which corresponds roughly to a decrease in trip duration of 1.08 days for a 50g increase in starting mass. Birds whose partners were in better condition went on longer trips: the estimated coefficient was 0.0024 [0.00011, 0.0037] (log odds ratio; χ^2 = 9.14, *df* = 1, p = 0.0025), corresponding to an increase in trip duration of approximately 0.84 days for a 50g increase in partner mass (Figure 3.6). There was no effect of sex on trip duration (male: 6.07 [5.65, 6.52] days, female: 5.96 [5.55, 6.41] days; χ^2 = 0.11, *df* = 1, p = 0.74).

Over their entire foraging trips, shearwaters gained a mean 12.63 ± 9.24% of their body mass, corresponding to approximately 50.00 ± 33.89g. The mass at which a bird began its foraging trip significantly predicted its total percentage mass gain, with birds gaining 0.29 [0.25, 0.32]% less mass per gram increase in their starting mass (Figure 3.7; χ^2 = 123.40, *df* = 1, $p < 0.0001$). Males were found to gain a greater percentage of mass on their trips (male: 16.05 [12.49, 19.60]%, female: 9.74 [6.45, 13.00] %; χ^2 = 11.89, *df* = 1, p = 0.00057). Total foraging gains were not related to foraging trip duration (χ^2 = 1.21, *df* = 1, p = 0.27) or the amount of time the bird spent foraging (χ^2 = 0.070, *df* = 1, p = 0.79). However, our failure to find a relationship between foraging gains and trip duration may reflect the fact that both total foraging gains and foraging trip duration were strongly predicted by starting mass.

During their foraging trips, birds spent 42.25 ± 10.87% of their time foraging, 39.90 ± 14.43% of their time resting, and 17.86 ± 13.02% of their time in flight (mean ± standard deviation). The mass at which a bird began foraging significantly predicted the time it spent foraging and resting: heavier birds spent less time foraging, and more time resting (Table 3.4, Figure 3.8), such that a bird weighing 400g would reduce foraging time by 6.00% and increase resting time by 7.05% compared to a bird weighing 350g. We did not find evidence for a relationship between mass and flight behaviour.

Table 3.4: Test statistics for models 13/14/15, examining parameters affecting the proportion of time spent in foraging, resting, and flight behaviour respectively. Significant parameters in bold. Estimates given as logits.

Parameter	**Foraging**			**Resting**			**Flight**		
	Estimate	χ^2	p	***Estimate***	χ^2	p	***Estimate***	χ^2	p
Start mass	**-0.0024 [-0.0035, -0.0013]**	**17.46**	**<0.0001**	**0.0030 [0.0013, 0.0047]**	**13.15**	**0.00029**	-0.00039 [-0.0024, 0.0016]	0.15	0.70
Sex (male)	0.083 [-0.040, 0.21]	1.76	0.18	-0.0014 [-0.18, 0.15]	0.026	0.87	-0.078 [-0.27, 0.12]	0.61	0.43
Trip dur	-0.012 [-0.039, 0.0015]	0.76	0.38	-0.0095 [-0.049, 0.030]	0.22	0.64	0.036 [-0.013, 0.085]	2.035	0.15
Prop commute	0.22 [0.15, 0.24]	0.97	0.32	0.037 [-0.59, 0.67]	0.014	0.91	0.39 [-0.39, 1.16]	0.92	0.34

Notes – *start mass* = bird mass at beginning of foraging trip, g; *sex* = male or female; *trip dur* = foraging trip duration; *prop commute* = proportion of trip spent commuting

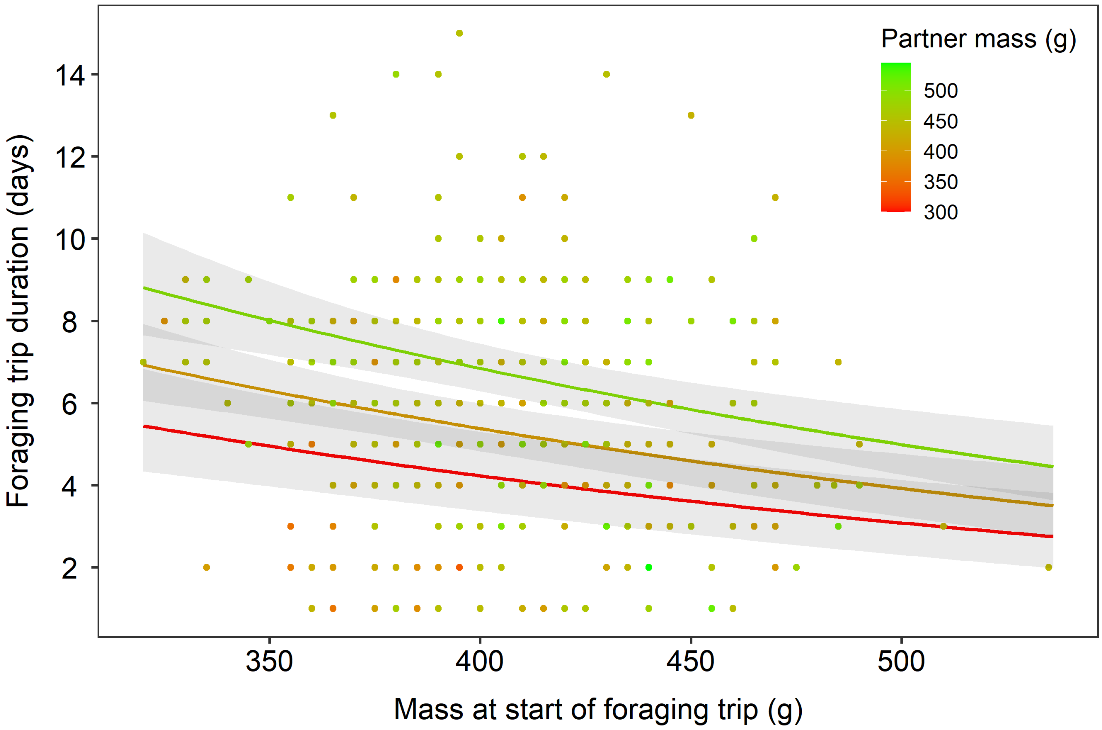

Figure 3.6: Foraging trip duration in days as a function of mass at start of the foraging trip (grams). Mass of the partner indicated by colour gradient of low (redder colours) to high (greener colours) mass. Slopes indicate predicted trip durations for given values of partner mass (grams).

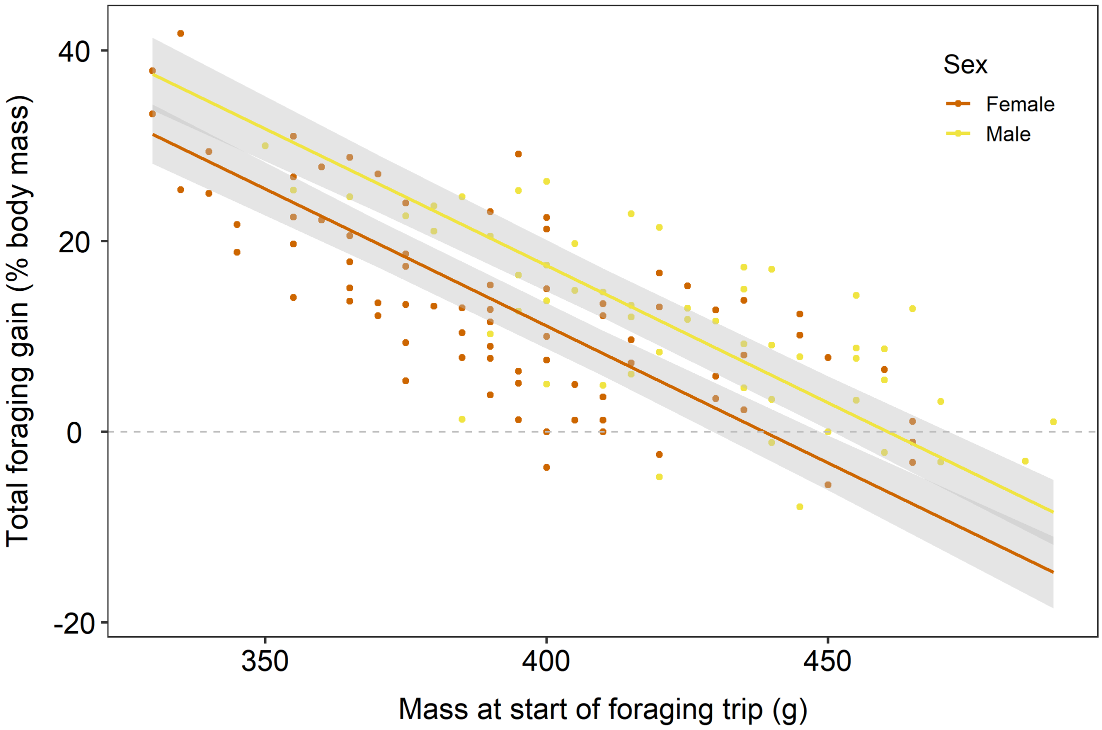

Figure 3.7: Total foraging gain as a percentage of body mass according to mass at the start of the foraging trip (grams) for females (yellow) and males (orange). Shaded areas indicate 95% confidence intervals.

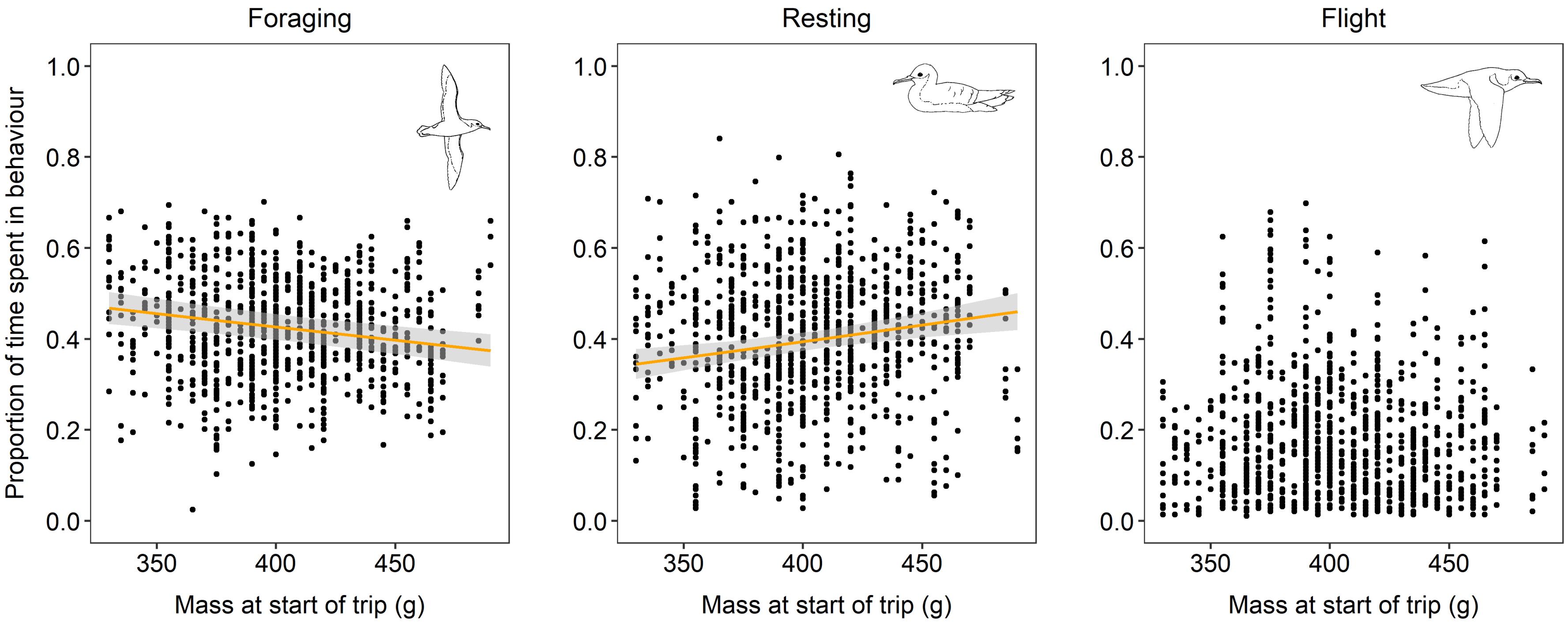

Figure 3.8: Proportion of time during the foraging trip spent in each of foraging, rest, and flight behaviour according to mass at the beginning of the trip (grams). Shaded areas indicate 95% confidence intervals.

3.5 Discussion

Here we provide the first evidence that the regulation of body mass drives decisions relating to incubation scheduling and investment in the Manx shearwater. While incubating birds appeared to respond principally to the return of their partner from sea, we found that foraging trip duration was mostly driven by the requirement of the foraging bird to recoup its lost body mass, with those birds that departed the nest at a lower mass spending a proportionally longer time at sea. Similar results have been reported for storm petrels (Bolton, 1996), little penguins *Eudyptula minor* (Kato et al., 2008), and short-tailed shearwaters (Carey, 2011), and probably reflect the importance of regulating body mass effectively during breeding for these long-lived species.

Mass losses for incubating shearwaters were substantial, with individuals losing around 2.3% of their body mass per day, corresponding to an overall decline of 11.5% over an average incubation shift. This places a significant energetic constraint on parents and highlights the importance of recouping these costs. Not unexpectedly, the amount of mass individuals gained on their foraging trips was primarily driven by how much mass they lost during their incubation shifts, with those birds that ended their shift at a lighter mass gaining more on their foraging trips, suggesting that individuals have an individual target of body mass that they try to maintain. That there was a significant correlation between the duration of the current and previous incubation shifts lends further support to the idea that foraging trip duration is driven primarily by the departure mass of the foraging parent: birds that incubate for longer will need longer foraging trips to compensate, leading to a lengthened corresponding incubation shift by the partner. Furthermore, lighter birds went on longer trips, spent more time foraging, and less time resting. The finding that better-condition shearwaters dedicated less time to foraging and more time to rest mirrors previous findings that shearwaters whose breeding investment is experimentally reduced, and who are therefore likely to be in better condition, spent more time resting during the overwintering period (Fayet et al., 2016b). It may be the case that this level of effort reflects each individual's optimal balance between foraging gains and limits to energetic expenditure incurred when foraging. If birds do not have as much condition to gain, it may be in their interest to invest less in the highly energetic activity of foraging, and instead spend more time in resting states. This may be employed strategically, so that as the bird approaches good condition it pays only to explore better foraging opportunities, and to pass up less profitable ones by resting. Shortening the duration of the trip itself may not be an optimal way to conserve energy, as longer foraging trips can themselves be beneficial by optimising the balance between commuting time and foraging time, and by allowing birds to exploit further distance foraging locations that are likely to be more productive than those closer to the colony (Dean et al., 2015; Shoji et al., 2015b).

While males were found to take a greater share in incubation, they did not differ from females in either the number of shifts they were responsible for nor the duration of these shifts, conflicting with earlier studies that found males took on longer incubation shifts (Thompson 1987) but matching findings in other species (cape petrel, Weidinger, 2008; banded stilt *Cladorhynchus leucocephalus*, Pedler et al., 2016). Instead, it is probable that this observed difference in contribution arises due to a combination of small differences between males and females, which may add up to a large effect over the scale of the entire incubation attempt, as well as the fact that when the female took the first incubation shift, it was significantly shorter than usual. This latter finding is probably driven by the energetic deficit the female has incurred from building the egg, which at 15% of her body mass (Brooke, 1990), is substantial, and has also been observed in the Laysan albatross *Phoebastria immutabilus* (Fisher, 1971) and the northern fulmar *Fulmaris glacialis* (Hatch, 1990). While males were found to be heavier than females, both sexes experienced a similar proportional daily decay in body mass over incubation, suggesting that the short-term resource costs of incubation shifts are comparable for the two sexes, as observed in wandering albatross (Weimerskirch, 1995). This may additionally explain the finding that males and females were equally likely to neglect their egg, which would be expected if the decision to leave the nest was mediated by an individual threshold of mass. The similar behaviour of males and females during incubation, and the relatively small increased contribution for males, suggests that the greater mass of males is probably not adaptive in incubation. The higher mass of males might instead be more important in pre-laying behaviours, such as securing and defending the nest, or during the chick-rearing period, during which time males provide 40-50% more food to the chicks (Hamer et al., 2006). Finally, the mass of both males and females gradually increased over the course of the incubation period. By increasing their energy reserves during incubation, birds may ensure they are prepared for the more energy-intense provisioning period ahead.

In line with previous studies (Boersma & Wheelwright, 1979), egg neglect was found to be infrequent (8% of shifts over the entire study). The mass of a bird at the start of its incubation shift predicted the probability that the shift ended in neglect, with birds that began incubation at a higher mass being less likely to neglect. We did not find consistency in the mass point at which birds chose to neglect the egg, which does not support a mass threshold for neglect; nor was there evidence of a relationship between incubation shift duration and the probability of neglect, suggesting this decision was not driven by incubating birds being forced to wait on the nest for excessively long durations when their partners spent longer at sea than usual. Rather, those birds that chose to neglect began their shifts in poor condition, suggesting they were simply unable to fast for the duration of the shift due to their insufficient body mass. For those shifts where neglect occurred, the amount of time the bird remained on the nest before neglecting was predicted by its mass, with heavier birds sustaining a longer period of incubation before ultimately abandoning the nest. Despite the remarkable resistance of Manx shearwater embryos to the chilling associated with temporary neglect of the egg (Matthews, 1954), hatching success was observed to be a decelerating function of egg neglect, with just three days of neglect being sufficient to reduce the probability of hatching by 62%, while further days of neglect did not reduce hatching probability substantially.

New pairs were found to be more likely to neglect their eggs than experienced pairs, despite showing no significant differences in any other facets of their incubation behaviour, making it difficult to identify from where this difference in probability arises. Furthermore, both new and experienced pairs had comparable hatching success. These findings contrast with many previous studies investigating the relationship between pair experience and breeding success (outlined in introduction). However, this may reflect the fact that our method for assigning pairs as ‘new’ or ‘experienced’ meant that all individuals in ‘new’ nests had necessarily been observed breeding in the previous year. Consequently, these birds had, by definition, at least one year of breeding experience. Our failure to find differences between our new and experienced nests may therefore suggest that the previously reported positive effects of experience on breeding success for Manx shearwaters (Harris, 1966; Brooke, 1978b) are probably not due to the duration of the pair bond, but rather the experience or age of the individual parents. Further research is needed to disentangle the relative contributions of individual and pair experience on breeding behaviour and success (van de Pol et al., 2006; Griggio & Hoi, 2011)

While it was found that the principle determinant of foraging trip duration was the mass of the outgoing bird, we also found that foraging birds whose partners were in good condition took longer foraging trips compared to those whose partners were in poor condition. This could provide evidence for a negotiation strategy in which foraging parents incorporate information about their partner’s body condition into their decision making process. This may be driven by short-term considerations (can my partner sustain the next incubation shift), but parents might additionally act to improve, probabilistically, their partner’s long-term survival if there is a benefit to pairing with the same individual in multiple years (Griffith, 2019). In Chapter 4, we explore this experimentally, by reducing the foraging efficiency of departing birds over the targeted duration of one trip, to observe how they adapt their behaviour in response to their own compromised condition in conjunction with the needs of the partner.

If foraging birds do account for their partner’s condition, this suggests that shearwaters might have some mechanism by which they can determine the condition of their partner and act according to this information. Previous empirical evidence does suggest that the foraging decisions of Manx shearwaters are to some extent pre-planned, with birds on long duration foraging trips being found considerably further from the colony than short duration trips on the first day of the trip, suggesting the decision has been made on or shortly following departure from the colony (Guilford et al., 2008). It is less clear how individuals would gain information about the condition of their partners. One possibility is that the vocal duets observed between partners on their reunion at the burrow might be an opportunity to exchange information about body condition. Gémard et al. (2019) found that the calls of male blue petrels and Antarctic prions *Pachyptila desolata* carry information about morphological characteristics of the caller. In other biparentally caring species, vocalisations have been found to signal need by incubating females (Boucaud et al., 2016b), indicate readiness to take over incubation (Boucaud et al., 2016a; Boucaud et al., 2017), and have been correlated with measures of parental coordination (Kavelaars et al., 2019). It is feasible then, that the vocalisations of Manx shearwaters may contain information that allows shearwaters to negotiate informed decisions about the duration of their trips based on a consideration of both their own and their partner's body mass (Johnstone et al., 2014; Johnstone & Savage, 2019).

Overall, we find evidence to suggest that the decisions underlying foraging trip duration, and consequently the duration of incubation shifts, are primarily driven by the departing mass of the foraging bird, and mediated by its partner's condition. Through this strategy, Manx shearwaters can effectively divide incubation in such a way that preserves their long-term condition both in preparation for the ensuing, energetically demanding chick provisioning period, and to preserve their future reproductive value. While our results do not support the notion that neglect is driven by a threshold mass at which the incubating bird departs the nest following a protracted fasting period, we do find evidence that neglect is driven by an inability to sustain incubation due to an insufficient starting mass. As such, the regulation of body mass during foraging is of key importance both on the short-term scale of sustaining incubation, and for the longer-term scales of the entire breeding period and beyond. While our observational results raise the prospect of a cooperative strategy, whereby foraging birds make their decisions based on their own and their partner's condition, further work is needed to determine the mechanisms by which individual birds can communicate effectively to this end.

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4

Responses to handicapping in a long-lived seabird and its implications for the coordination of care

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Contents

4.1 Abstract

Seabirds care for their offspring in remote breeding colonies where foraging sites are distant and may be unpredictable, and where chicks are left unaccompanied for extended periods during their parents' foraging trips, leaving them vulnerable to predation or starvation. One way to mitigate risks to the offspring is for individuals to coordinate parenting duties with their partner. Many biparental and cooperatively breeding species are now known to coordinate their care, though the mechanisms underlying this are not well understood. During incubation, parent Manx shearwaters *Puffinus puffinus* alternate shifts on the nest in a coordinated manner with their partner. To resolve how shearwaters determine the duration of these shifts, and to what extent this reflects an active coordination process between the parents, we imposed a wing-loading handicap on one member of the pair to reduce its foraging efficiency, forcing it to choose between an extended foraging trip or to return to the nest before its condition has recovered to optimal levels. We found that handicapped parents took significantly longer trips than normal, to which their partner responded by lengthening their incubation shift, suggesting shift durations are not pre-determined. However, the duration of foraging trips and the mass at which the foraging bird returned to the nest appeared to be mediated by the condition of the partner. These results suggest that while foraging trip duration is largely driven by the need for the foraging bird to recoup its own condition losses, information transfer between the parents may facilitate a more cooperative mechanism whereby the decisions made by foraging birds still account for the condition of their partner.

4.2 Introduction

In species exhibiting shared parental care, coordinating behaviour between all carers can increase parental investment efficiency, either by maximising benefits to offspring (e.g. through more adaptive food delivery: Raihani et al., 2010) or by minimising carer costs (e.g. by reducing predation: Foster and Treherne, 1981; Raihani et al., 2010). Behavioural coordination is apparent in a range of species exhibiting joint parental care, and manifests in, for example, synchronous nest visitation (e.g. prairie voles *Microtus ochrogaster*, Ahern et al., 2011), turn-taking behaviour (e.g. rufous hornero *Furnarius rufus*, Massoni et al., 2012), or correlation in levels of parental effort (e.g. convict cichlid fish *Amatitlania nigrofasciata*, Itzkowitz et al., 2002). However, the specific mechanisms that allow parents to divide the tasks associated with raising offspring have received little empirical attention.

The capacity for parents to exhibit coordination has been experimentally manipulated in a number of species, usually by altering levels of parental investment, for example by increasing brood size (e.g. Mariette and Griffith, 2015) or by imposing a handicap on one parent (e.g. Wright and Cuthill, 1990; Dearborn, 2001). Through such studies, coordinated care has been found to be variably flexible across species, and achieved through a spectrum of responsiveness of carers to one-another's behaviour. At one extreme, coordination is active, and may be underlain by communication or negotiation between the parents. For example, in turn-taking ceremonies, components of the display may signal individual quality (e.g. great tits *Parus major*, Boucaud et al., 2016; common guillemots *Uria aalge*, Takahashi et al., 2017), and therefore provide information that allows the partner to mediate its own behaviour, or indicate readiness to take on parental duties (e.g. zebra finches *Taeniopygia guttata*, Boucaud et al., 2017). Active coordination may also arise when carers adjust their own behaviour to coincide or synchronise with that of other individuals: for example, cooperatively-breeding pied babblers *Turdoides bicolor* wait for other carers to arrive before provisioning the nest together (Raihani et al., 2010). Elsewhere, apparent coordination is a passive consequence of, for example, limitations on inter-feed intervals due to commuting distance (e.g. chestnut-crowned babblers *Pomatostomus ruficeps*, Savage et al., 2017), individual responses to body condition (e.g. blue petrels *Halobaena caerulea*, Chaurand and Weimerskirch, 1994) or as a secondary consequence of other behaviours (e.g. Adélie penguins *Pygoscelis adeliae* select partners with similar preferred foraging trip durations to their own; Davis, 1988).

Seabirds are obligate biparental carers that provide for their offspring under extreme conditions. Long distance and often unpredictable foraging locations require parents to spend long periods away from the nest, leaving their offspring at risk of predation, exposure, and starvation. Consequently, seabirds are under especially strong selection to coordinate their parenting behaviour. Indeed, as seabirds are long-lived and primarily monogamous, the two parents' reproductive interests may be so intertwined that poor performance or 'laziness' by one could theoretically lead to complete compensation by the other, since the alternative is total reproductive failure (Jones et al., 2002). Increasing empirical evidence shows that parental coordination is widespread in seabirds (great frigatebirds *Fregata minor*, Dearborn, 2001; wedge-tailed shearwaters *Ardenna pacifica*, Congdon et al., 2005; little auks *Alle alle*, Welcker et al., 2009; little penguins *Eudyptula minor*, Saraux et al., 2011; Manx shearwaters *Puffinus puffinus*, Tyson et al., 2017). However, few studies have investigated how coordination is actually achieved.

The Manx shearwater is a Procellariiform seabird in which both males and females contribute to offspring care. During incubation, both parents take turns to alternate between incubating their single egg and foraging at sea for the total 51-day period (Brooke, 1978). To counter the commuting cost of reaching long distance foraging sites (approximately 215km, Guilford et al., 2008; Dean et al., 2015), shearwaters must spend several days foraging at sea (approximately 7; Brooke, 1990). While the ability of shearwater eggs to withstand a break in incubation of up to 11 days (Brooke, 1990) means that temporary neglect of the egg can form part of a successful breeding attempt, this still entails a cost in terms of predation and damage risk, and slowed embryonic development (Matthews, 1954). As failed eggs are not replaced (Brooke, 1978), unsuccessful incubation represents breeding failure for the entire year. The two parents are consequently faced with an intrinsically linked dilemma: while the foraging bird must spend sufficiently long at sea to recover its body condition, it must return to incubate before its partner decides to neglect the egg. The low incidence of neglect in Manx shearwaters (Brooke, 1990; Shoji et al., 2011) compared to other burrow-nesting petrels exhibiting embryonic chilling resistance (e.g. short-tailed shearwaters *Ardenna tenuirostris*, Carey, 2011) suggests that incubation is well coordinated in this species. However, the mechanisms and information underlying the decisions of incubating birds to depart the nest, or foraging birds to return from their trips, have not been explored.

It is not known where the incubation scheduling of Manx shearwaters lies on the spectrum of coordination. To investigate this, we used a classic handicapping paradigm (e.g. Sanz et al., 2000; Paredes et al., 2005; Bijleveld and Mullers, 2009; Ratz et al., 2019) to disrupt the behaviour of parents. We forced parents beyond the extremes of their decision-making processes by introducing a physical constraint on locomotion using a wing-loading handicap, forcing them to choose between extending the foraging trip to compensate, or to return before they have fully recovered their body condition. We then assessed the partner's response to a change in behaviour of the focal bird to determine the degree of responsiveness of shearwaters to their partners' behaviour. For example, if parents actively negotiate their shifts, they should form expectations about the duration of each incubation shift and corresponding foraging trip. If shift duration was therefore pre-determined, we predicted that either the incubating parent would choose to neglect the egg when its partner did not return when expected, or that the foraging parent would return to the nest well before its body condition had been sufficiently recouped. Alternatively, if shearwaters follow more individualistic rule following processes, we might expect that incubating birds simply wait indefinitely for their foraging partners to return, with apparent coordination emerging as a by-product. We aimed to determine how individuals make decisions relating to the duration of their foraging trips and incubation shifts, whether they factor their partner's condition into this, and whether this was better explained by active cooperation or individualistic behaviour.

4.3 Methods

4.3.1 Data collection

This study was carried out on Skomer Island, Wales (51°44’ N, 5°17’ W), during the incubation period between April and June of 2018 and 2019. Nests were introduced to the study as eggs were laid, and randomly assigned to the ‘control’ or ‘handicapped’ groups according to lay date, so that each nest in the handicapped group was matched to a control nest with a lay date within 1 day of its own. Adults were captured at the nest through the burrow entrance or purpose-built inspection hatches, and were uniquely identified with a permanent stainless steel ring (British Trust for Ornithology). Females were identified at the point of laying through cloacal inspection (Boersma & Davies, 1987) , and males by inference. We monitored the attendance of incubating adults at the nest continuously until the egg hatched, allowing us to determine the incubation shift duration of each adult, and the corresponding foraging trip duration of the absent parent, as parent shearwaters do not normally overlap at the nest during incubation. Where cold eggs were found in the burrow, we inspected the nest until one of the parents returned (at which point we deemed the egg ‘neglected’), the egg was depredated, or we reasoned that the burrow was abandoned. A total of 48 nests were used, comprising 23 handicapped (12 in 2018, 11 in 2019) and 25 control (12 in 2018, 13 in 2019) nests. Within experimental nests, we handicapped 10 females and 13 males.

To determine how body condition relates to the decisions made during incubation, we weighed incubating birds daily, from the day the egg was first found to the day it hatched, using a 500g Pesola spring balance precise to 5g. To account for the influence that differences in skeletal body size may have on measurements of mass, we calculated a ‘scaled mass index’ as follows (Peig & Green, 2009):

$$\widehat{M_i} = M_i \left[\frac{L_0}{L_i}\right]^{b_{SMA}}$$

Where M_i = individual body mass, L_i = individual tarsus length, b_{SMA} = scaling component estimated by the regression of M on L, and L_0 = the mean tarsus length value for the entire sample. We measured tarsus length to the nearest 1mm using digital callipers. Four individuals abandoned the nest before this measurement could be taken, and so condition was unknown for these birds.

4.3.2 Foraging behaviour

To monitor foraging behaviour during the experiment, we fitted 48 individuals in 31 nests (19 individuals in 12 nests in 2018; 29 individuals in 19 nests in 2019) with geolocators (Migrate Technology Intigeo-C250 or Intigeo-C65), with 30 fitted to birds in the handicapped group and 18 the control group. Geolocators are miniaturised (< 2.5g) archival light loggers, which were programmed to record salt water immersion data as the transition between wet and dry states and duration spent in either state. These were attached by two small cable ties to a plastic leg ring to ensure immersion when sitting on the sea (see Guilford et al., 2009). Deployment lasted from the first day individuals were captured at the nest, to the day the chick hatched, or, in the case of failure, when the bird was next found on the colony.

We used the immersion data to determine behavioural states. Data were binned into 10 minute epochs, in which immersion values represented the number of seconds the device had been immersed for, and could range between 0 (= no immersion) and 600 (= constant immersion). We applied a threshold model to these data using the criteria set out by Phalan et al. (2007) and Dean et al. (2013): values <2% of the maximum possible total were labelled as 'flight'; >98% were labelled as 'rest' and values in between as 'foraging'. This method has been validated for the Manx shearwater (Dean et al., 2013; Fayet et al., 2016). Foraging behaviour was summarised as the proportion of each 24 hour period (00:00 – 23:59 UTC) spent in each of the three behavioural states.

4.3.3 Handicapping protocol

The handicapping procedure followed a three-stage (A-B-C) experimental design (Figure 4.1). We handicapped adults following the completion of at least one foraging trip by both parents (phase 'A') since laying, and no later than 10 days prior to the expected hatch date. Drawing on handicapping methods outlined by Bijleveld and Mullers (2009), we bound together the two outermost primary feathers (P9 and P10) on both wings using 3 strips of 3mm diameter marine cloth Tesa 4651 tape (Figure 4.2), in order to increase wing loading and therefore decrease flight efficiency (Pennycuick, 1989). The handicapped bird was allowed to complete a single foraging trip (phase 'B'), and the tape was removed following its return to incubate (phase 'C').

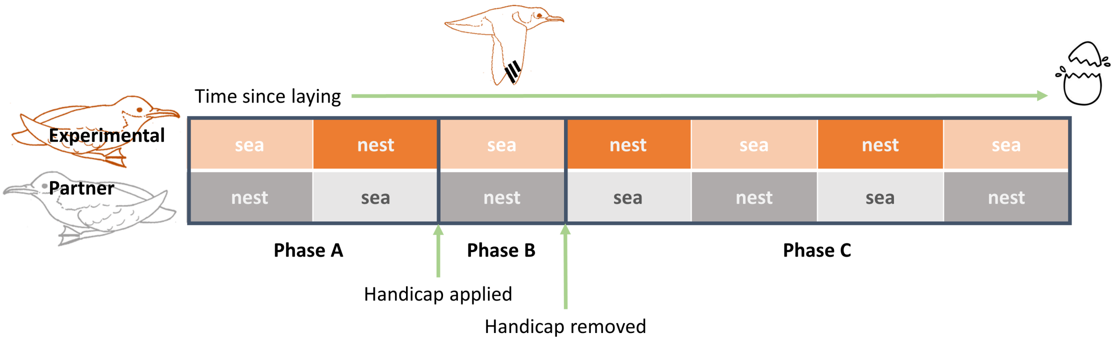

Figure 4.1: Cartoon schematic of the handicapping protocol. Both parents were observed until they each completed one complete incubation shift and foraging trip (Phase A). The handicap was then applied to the incubating experimental bird so it would be handicapped for the entire duration of its next foraging trip (Phase B). On its return from the trip, the handicap was removed, and the behaviour of the two parents was observed until the egg hatched (Phase C).

4.3.4 Statistical Analysis

All analyses and data processing were carried out in `R` version 3.5.1 (core Team, 2018). To construct linear mixed effects models (LMMs) and generalized mixed effects models (GLMMs), we used the `R` package `lme4` (Bates et al., 2015). Generalized beta mixed models were constructed using the package `glmmTMB` (Magnusson et al. 2020). Model fit was assessed through visual inspection of diagnostic residual plots. For LMMs, we obtained p-values via Sattherthwaite's degrees of freedom method using the package

Figure 4.2: Left wing of an adult Manx shearwater, showing placement of cloth Tesa tape at regular intervals along the P9 and P10 feathers.

`lmerTest` (Kuznetsova et al., 2017); for GLMMs and beta models we used a Wald test (z-test). Data are presented as means with 95% confidence intervals unless otherwise specified.

To determine the consequences of the handicapping treatment for the entire incubation period, we examined the incidence of neglect, incubation duration, and productivity as a function of experimental group (‘control’ vs ‘handicapped’). Permutation (randomization) tests were used to assess differences in the total days of neglect and incubation duration respectively between control and handicapped nests to account for their non-normal distribution. In each case, the observed values for each variable (number of days of neglect or incubation duration) were randomly assigned to the two groups, and the mean difference between the two randomised groups was calculated. This was repeated over 10,000 iterations, and two-tailed p-values were calculated as the proportion of permutations in which the calculated mean difference of the random samples was greater than the observed difference. As egg failure often results in curtailing of the incubation period, we compared the duration of the entire incubation period between only successful control and handicapped nests (n = 33). All other analyses included all nests regardless of breeding success (n = 47). Productivity was measured as the number of chicks hatched per egg laid, and was compared between the two groups using a Pearson's Chi-squared test.

We hypothesised that handicapping may lead to a change in the proportional contribution of each parent to incubation. To explore this possibility, we first examined whether males and females normally differed in their shares of incubation using a one-sample t-test that examined whether the mean difference in the proportional contributions of the two parents differed from 0 (n = 47). We then used a linear model to test whether the ratio of female to male care differed between 'control' and 'handicapped' nests.

To assess the effects of the handicapping treatment on incubation shift duration, shift number, body condition changes, and foraging behaviour, we fitted a set of GLMMs and LMMs according to the structures outlined in Table 4.1. For the purpose of analysis, we divided individuals into 4 'treatment' groups, according to the stage in the handicapping period. The 'none' group comprised all control birds throughout the incubation period, as well as both birds in handicapped nests prior to the handicapping phase (phase 'A'). The 'handicapped/partner-handicapped' group comprised experimental and partner birds respectively in the handicapped nests during the handicapping period itself (phase 'B'). During this time, experimental birds were on their foraging trips, while their partners incubated. The 'post-handicap' group comprised experimental birds in the incubation shift or foraging trip immediately following the handicap period (phase 'C'). Finally, the 'post-partner handicap' group comprises partner birds in the incubation shift or foraging trip immediately following the handicap period (phase 'C').

To control for repeat measures, we included a random intercept of either 'ring' or 'ring' nested within 'nest' in all models as appropriate. To control for potential temporal variation in our behavioural measures, we additionally included the fixed effects of number of days since laying and year. To control for any sex-related variation in behaviour, we included the fixed effect of sex. Finally, as body condition might reasonably be expected to explain variation in incubation shift duration and/or foraging trip duration, we included condition at the start of each shift or trip respectively as a fixed effect in models 1, 3, 6, 7, and 8.

If decisions about foraging trip duration are made following a negotiation process, we might expect that the observed trip duration and/or the returning body condition of the foraging bird would relate to the condition of its partner when the foraging bird left the nest. To examine this, we included the fixed effect of partner body condition (g) in models 3 and 4b.

Models 1, 2, and 3, which explored variation in incubation shift duration, incubation shift number, and foraging trip duration, were fitted as GLMMs with a Poisson error structure to account for their count-based response variables (n = 413 shifts for 82 individuals). As our measures of foraging behaviour were given as proportions of each 24-hour period, we fitted models 6, 7, and 8 using mixed-effects beta regression models to account for the proportion-based error structure (n = 132 trips for 41 individuals).

Table 4.1: Model structures used in the analysis. Model numbers referenced in the text.

Model + Type	**Response Variable**	**Explanatory Variables**	
		Fixed	***Random***
1 Poisson GLMM	Incubation shift duration (days)	Handicap + sex + start con + year + DSL	Nest:ring
2 Poisson GLMM	Incubation shift number	Handicap + sex + year	Nest:ring
3 Poisson GLMM	Foraging trip duration (days)	Handicap + sex + start con + partner con + year + DSL	Nest:ring
4 LMM	Starting condition (foraging, g)	Handicap + sex + year + DSL	Ring
4b LMM	Ending condition (foraging, g)	Handicap + sex + partner con + year + DSL	Ring
5 LMM	Starting condition (incubation, g)	Handicap + sex + year + DSL	Ring
6/7/8 Beta	Proportion time spent forage/rest/flight	Handicap + sex + start con + year + DSL	Ring

Notes – *handicap* = level of the treatment group; *sex* = male or female; *start con* = condition at the beginning of the shift or trip; *partner con* = condition of the incubating partner on departure of the foraging bird; *year* = year of the experiment; *DSL* = days since laying

4.3.5 Ethical Note

All methods were approved by the British Trust for Ornithology Unconventional Methods Technical Panel (permit number C\5311), Natural Resources Wales, Islands Conservation Advisory Committee, and University of Oxford's Local Ethical Review Process (reference number APA/1/5/ZOO/NASPA). The decision was taken to use a wing-taping protocol for the handicapping procedure due to its temporary and reversible nature. Alternative methods, including wing clipping and weighting, would last longer than the experiment or would handicap the animal indefinitely, or at least until the next moult, should it fail to return to the colony. As per a recommendation by the University's Animal Welfare and Ethical Review Board (AWERB), we conducted a pilot of the experiment on a set of 4 early-laying nests in April and May 2018. Following assessment of the impacts on these nests, which were acceptable within the experimental context, we expanded the experiment. Handling time, both during daily weighing and the deployment and retrieval of geolocators, was normally < 5 minutes.

4.4 Results

All experimental birds except one returned to incubate following the handicapped foraging trip. This remaining bird abandoned its breeding attempt during the handicapping period, but was recovered at the nest later, permitting recovery of the tape and geolocator. Three of the 48 geolocators deployed were not retrieved as the individuals carrying them abandoned the breeding attempt and were not seen again that year. Of the remaining loggers, 2 failed to collect data.

4.4.1 The entire incubation period

More days of neglect were observed in handicapped than control nests (control = 1 day, handicapped = 10 days), and 6/10 days of neglect in the handicapped group were observed at the end of an incubation shift during which the partner was handicapped. However, this difference was not significant (two-tailed p = 0.26; permutations = 10,000). The duration of the entire incubation period did not differ between the two groups (control = 49.71 [48.83, 50.60] days, handicapped = 50.53 [49.67, 51.37]; two-tailed p = 0.86; permutations = 10,000). Productivity (chicks hatched per eggs laid) did not significantly differ between control and handicapped groups (control = 0.58, handicapped = 0.82; χ^2 = 2.25, df = 1, p = 0.13; Table 4.2).

Table 4.2: Productivity by year and group.

	2018			**2019**		
	Laid	*Hatched*	*Fledged*	*Laid*	*Hatched*	*Fledged*
Control	11	7	7	13	7	7
Handicapped	12	11	11	11	8	8

4.4.2 Incubation behaviour

Males and females did not differ in their incubation shift duration (**model 1**: female: 5.86 [5.22, 6.58] days, male: 6.01 [5.36, 6.73] days; z = 0.38, p = 0.70), or the number of shifts they took on (**model 2**: females: 4.44 [3.88, 5.08] shifts, males: 4.97 [4.37, 5.65] shifts; z = 1.19, p = 0.24). Despite this, the slight differences between males and females appeared to accumulate over the incubation period, with males being found to take on a greater share of incubation overall (male share = 0.54, female share = 0.46; mean male - female difference: 0077 [0.023, 0.13], t = 2.85, df = 46, p = 0.0066). The ratio of female to male care did not differ between control and handicapped nests (control = 0.90 [0.78, 1.02], handicapped = 0.91 [0.78, 1.03]; $F_{[1,45]}$ = 0.0015, p = 0.97).

Incubation shift duration was significantly predicted by the starting condition of incubating birds; the heavier the incubating bird at the start of the incubation shift, the longer its shift on the nest, with duration (in days) increasing by 0.0042 [0.0028, 0.0056]% for each gram increase in starting mass (**model 1**: z = 6.0, p < 0.0001).

Treatment had a significant influence on the duration of the incubation shift (**model 1**; Figure 4.3). Partners of handicapped birds sustained incubation shifts that were significantly longer than those of control birds or prior to the handicapping phase (none: 4.42 [4.14, 4.75] days, partner handicapped: 9.95 [8.51, 11.63] days; z = 9.8, p < 0.0001). Following their handicapped foraging trips, experimental birds also sustained longer than normal incubation shifts (post-handicap: 6.64 [5.52, 7.98] days; z = 4.2, p < 0.0001). By their second incubation shift following the handicapping phase, partner birds incubated for as long as birds in the 'none' category (post-partner handicap: 4.23 [3.34, 5.36] days; z = -0.4, p = 0.70), suggesting a return to normal shift durations.

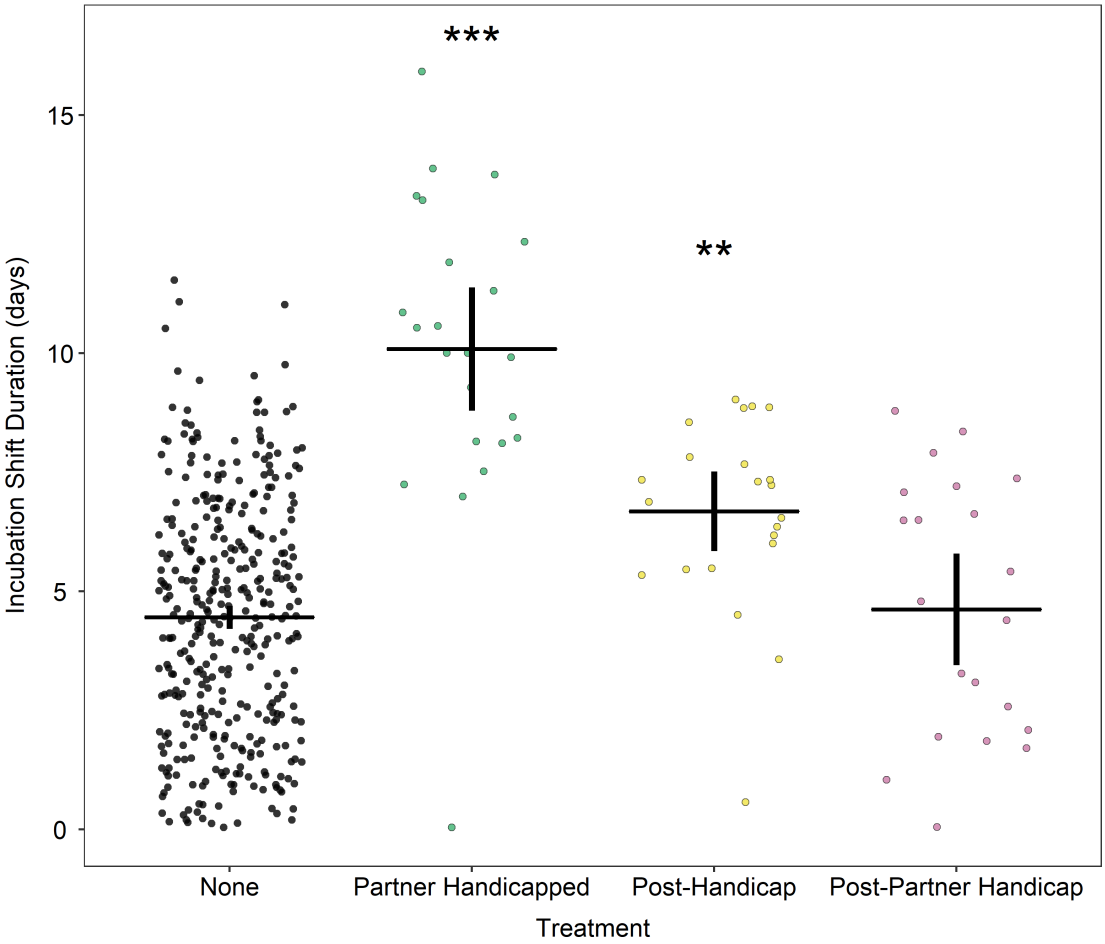

Figure 4.3: Duration of incubation shift in days according to treatment group. Horizontal line indicates mean, vertical lines indicate 95% confidence intervals. Stars indicate significant differences relative to controls where *** = $p < 0.0001$; ** = $p < 0.01$. Data points are ‘jittered’ in X axis for readability.

4.4.3 Foraging behaviour

In line with the observed effects on incubation shift duration, treatment group had a significant effect on duration of the foraging trip (**model 3**; Figure 4.4). Experimental birds took significantly longer foraging trips than birds in the 'none' category (none: 5.33 [4.99, 5.69] days, handicapped: 10.60 [9.15, 12.27] days; z = 8.6, p < 0.0001), corresponding to the increased incubation shift of their partners (see Section 4.4.2). Following their extended incubation shift, partner birds went on foraging trips that were not significantly different in duration to normal (post-partner handicap: 6.49 [5.35, 7.87] days; z = 1.9, p = 0.055), though the finding that the corresponding incubation shifts of handicapped birds were significantly longer than normal, taken together with the marginal p-value, may indicate that this could be a Type 2 error. The condition of the partner when the foraging bird departed the nest positively influenced its subsequent foraging trip duration: for each gram increase in the partner's body mass, the trip duration of the foraging bird increased by 0.0020 [-0.0019, 0.0041] days (z = 2.8, p = 0.0046).

The proportion of each day of the trip that was dedicated to foraging behaviour did not vary with treatment (**model 6**: none: 0.43 [0.41, 0.45], handicapped: 0.39 [0.35, 0.43]; z = -1.9, p = 0.054; post-partner handicap: 0.43 [0.38, 0.48]; z = 0.09, p = 0.93; post-handicap: 0.41 [0.36, 0.46]; z = -0.9, p = 0.36). During the handicapped phase, experimental birds spent more time resting compared to those in the 'none' category (**model 7**: none: 0.38 [0.36, 0.41], handicapped: 0.52 [0.46, 0.57]; z = 4.7, p < 0.0001), though returned to normal levels on their next, non-handicapped trip (post-handicap: 0.33 [0.27, 0.39]; z = -1.8, p = 0.069). On their trips following the extended incubation shift, partners did not differ in the proportion of time they spent resting (post-partner handicap: 0.41 [0.35, 0.48]; z = 0.8, p = 0.40). Experimental birds spent a lower proportion of their time in flight during the handicapping phase (**model 8**: none: 0.18 [0.16, 0.20], handicapped: 0.093 [0.071, 0.12]; z = -5.1, p < 0.0001), but spent more time flying during their trip following handicapping (post-handicap: 0.25 [0.20, 0.30]; z = 3.0, p = 0.0030). On their foraging trip following the return of the handicapped experimental bird, partners did not differ in the proportion of time they spent in flight (post-partner handicap: 0.15 [0.11, 0.19]; z = -1.5, p = 0.14). Figure 4.5 illustrates the proportion of the trip spent in each behavioural state for each treatment group.

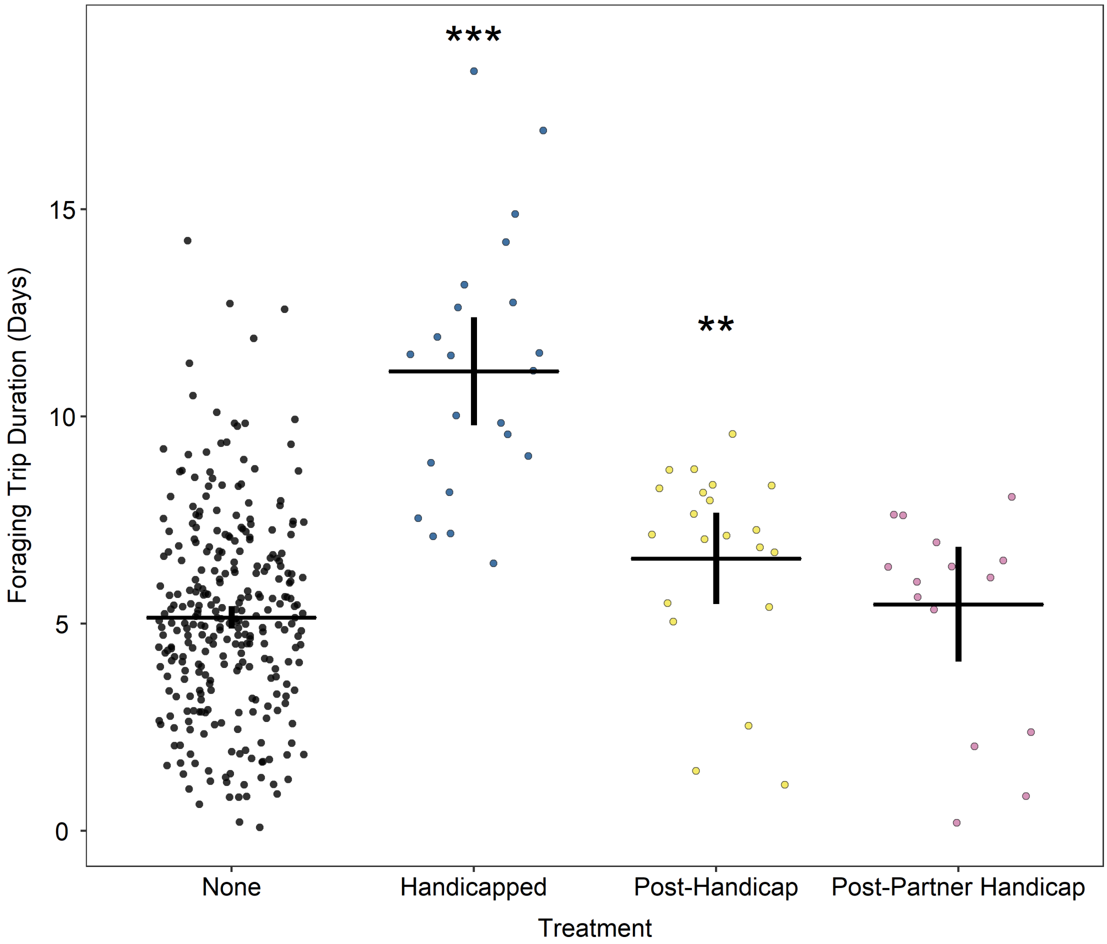

Figure 4.4: Duration of foraging trip in days according to treatment group. Horizontal line indicates mean, vertical lines indicate 95% confidence intervals. Stars indicate significant differences relative to controls where *** = $p < 0.0001$; ** = $p < 0.01$. Data points are 'jittered' in X axis for readability.

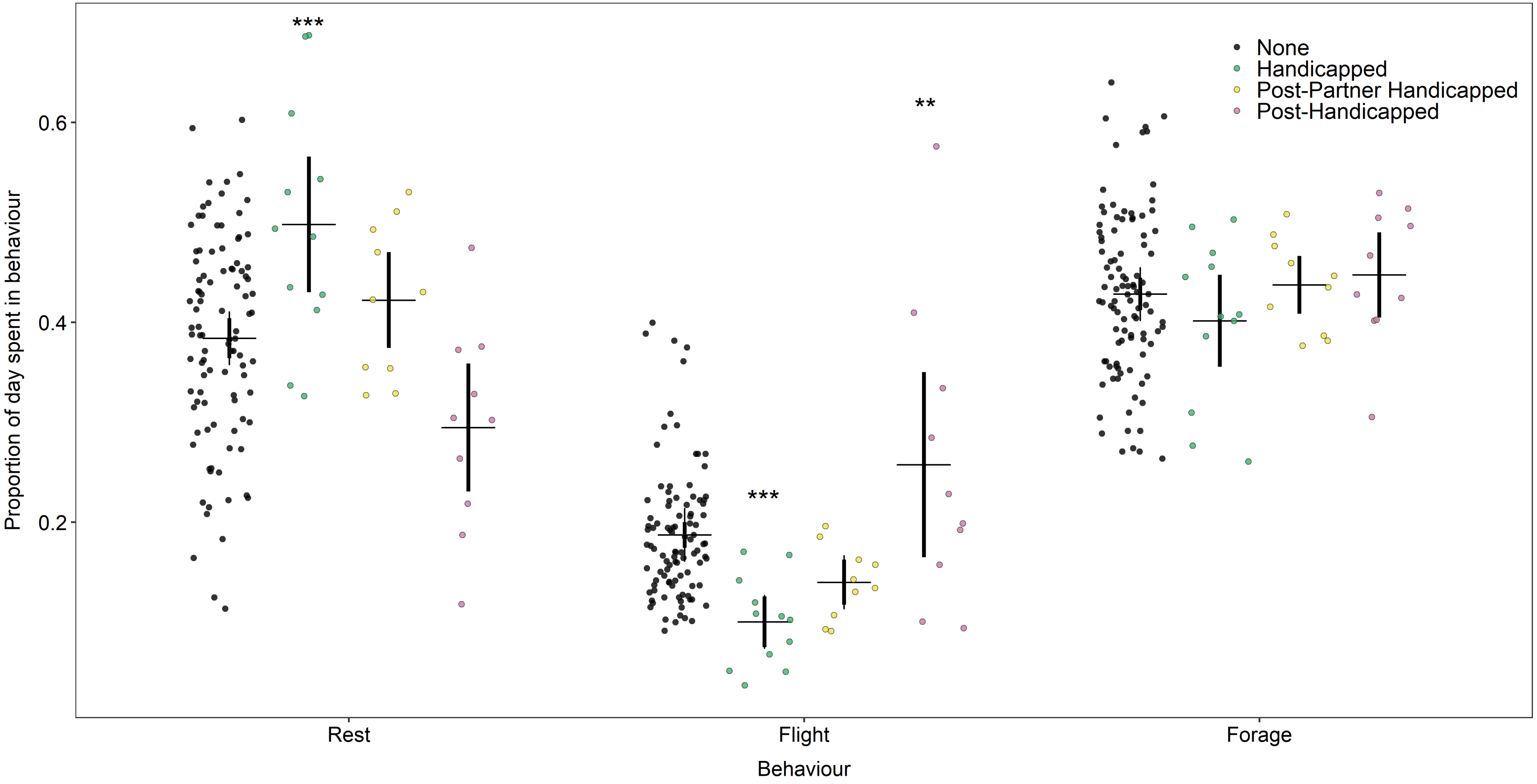

Figure 4.5: Proportion of each day of foraging trip spent in each of rest, flight, and foraging behaviours for each level of the handicapping treatment, where black points = ‘None’, turquoise points = ‘Handicapped’, yellow points = ‘Post-Partner Handicapped’ and pink points = ‘Post-Handicapped’. Horizontal line indicates mean, vertical lines indicate 95% confidence intervals. *** = $p < 0.0001$; ** = $p < 0.01$ Data points are ‘jittered’ in X axis for readability.

4.4.4 Body condition

Experimental birds began their handicapped foraging trips at a similar level of body condition, calculated as a scaled body mass, to those birds in the 'none' category (**model 4a**, *foraging start condition*: none: 411 [402, 419]g, handicapped: 406 [392, 419]g; t = -0.8, *df* = 0.03, p = 0.41). However, despite taking considerably longer trips than normal, these birds returned from their handicapped foraging trips in poorer condition (**model 4b**, *foraging end condition*: none: 453 [444, 462]g, handicapped: 433 [419, 446]g; t = -3.7, *df* = 0.02, p = 0.00024). This was further mediated by the condition of the partner: those birds whose partners were in better condition themselves returned to the nest in better condition, with ending condition increasing by 0.14g for each gram increase in the partner's condition (**model 4b**, *foraging end condition*: t = 2.4, *df* = 0.02, p = 0.019).

Experimental birds, which returned from their handicapped trips in poor condition, subsequently began their ensuing incubation shift at a low starting condition (**model 5**, *incubation start condition*: none: 450 [441, 458]g, post-handicap: 429 [416, 442]g; t = -3.8, *df* = 0.03, p = 0.00017). As these birds continued to lose mass during the incubation shift, by the start of their next foraging trip following the handicap, experimental birds were in lower condition than normal (**model 4a**, *foraging start condition*: post-handicap: 385 [369, 400]g; t = -3.6, *df* = 0.03, p = 0.00042). However, their condition by the end of this trip did not differ to control birds, suggesting increased foraging gains (model 4b, *foraging end condition*: post-handicap: 452 [436, 467]g; t = -0.2, *df* = 0.02, p = 0.83).

The partners of experimental birds began their incubation shifts during the handicapping phase in similar condition to birds in the 'none' category (**model 5**, *incubation start condition*: partner handicapped: 450 [437, 464]g; t = 0.1, *df* = 0.03, p = 0.92). These birds subsequently took on considerably longer incubation shifts (see Section 4.4.2) and so lost more mass during this time. Consequently, partner birds began their first foraging trip following the handicapping phase in worse condition than normal (**model 4a**, *foraging start condition*: post-partner handicap: 366 [352, 380]g; t = -7.5, *df* = 0.02, p < 0.0001). Partner birds appeared to compensate for this increased mass loss on the ensuing foraging trip by increasing their foraging gains, as they returned from this trip in normal condition (**model 4b**, *ending condition*: post-partner handicap: 452 [438, 467]g; t = -0.3, df = 0.02, p = 0.78). Figure 4.6 illustrates the condition values for each phase of the experiment for each of the treatment groups.

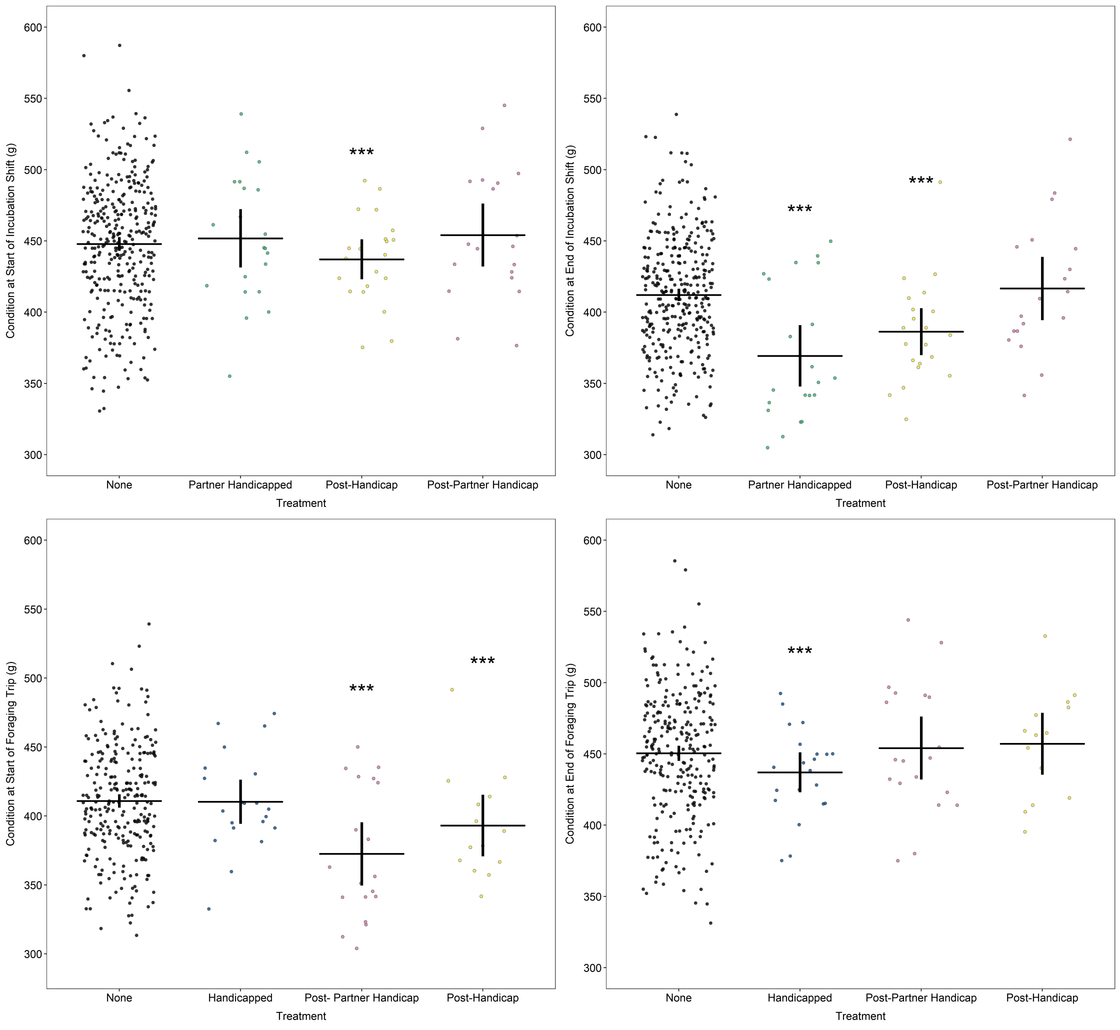

Figure 4.6: Body condition at the start (left plots) and end (right plots) of incubation (top panels) and foraging (bottom panels) according to treatment. Horizontal line indicates mean, vertical lines indicate 95% confidence intervals. Stars indicate significant differences relative to controls where *** = $p < 0.0001$. Data points are 'jittered' in X axis for readability.

4.5 Discussion

Manx shearwaters that were handicapped for the duration of one foraging trip spent twice as long at sea as prior to the manipulation, and their partners compensated for this reduced nest attendance by incubating continuously during this time. However, handicapped birds returned from their trips in poorer condition than normal, suggesting that they were returning to the nest earlier than might be optimal from the perspective of regaining lost body condition. The extent to which these birds returned early was dependent on the condition of their partners, with those whose partners were in better condition spending correspondingly longer at sea and returning at a higher mass, suggesting information transfer may facilitate the coordination of incubation in this species.

As incubating partners lost mass continuously during the protracted incubation shift, these birds ended the shift in worse condition than normal. Consequently, once the handicapped bird returned to the nest, a conflict emerged in the preferred strategies of the two parents: while the partner would benefit from a long foraging trip to recoup its lost condition, the experimental bird may not be able to sustain the corresponding lengthened incubation shift due to its own compromised condition. Foraging partners appeared to win this conflict, with post-handicapping incubation shifts averaging 1.6 days longer than normal, suggesting that incubating birds simply wait for the foraging bird to return to the nest. These results together suggest that while incubating shearwaters simply adopt a ‘sit-and-wait’ strategy for controlling their shift durations, foraging birds make use of condition-dependent information to adopt a trip duration that is optimal for the pair as a whole. Such a mechanism may permit flexibility in the behavioural responses of the two parents, while maximising fitness returns from the breeding attempt.

The observation that the incubating bird continued to wait at the nest, even when its partner was away for considerable durations of time, suggests that these decisions are unlikely to be pre-determined through a negotiation process. Instead, regulation of incubation shifts in Manx shearwaters appears to be mediated primarily by the decisions made by the foraging bird, as has been observed in short-tailed shearwaters (Carey,

2011) and great frigatebirds (Dearborn, 2001). That the condition of the foraging bird takes priority in incubation scheduling may be due to the inability or unwillingness of Manx shearwaters to adjust their foraging behaviour dynamically. While the foraging gains of experimental birds were clearly reduced, there was no associated change in effort. This contrasts with previous studies, where handicapped birds were found either to increase (Navarro & González-Solís, 2007) or decrease (Tajima & Nakamura, 2003; Jacobs et al., 2013; Serota & Williams, 2019) foraging effort. As experimental birds were observed to reduce flight time and increase time spent resting, this is unlikely to reflect a failure to identify behavioural changes. Observed foraging effort was comparable to previous studies (Dean et al., 2013), and may indicate that breeding shearwaters are already foraging at their maximum capacity and cannot upregulate this to compensate for a decrease in efficiency. Consequently, only by extending the trip duration can shearwaters increase their foraging gains. Indeed, the increased trip durations observed for partner birds post-handicapping were sufficient to recoup their condition to normal levels, despite maintaining normal foraging effort. If Manx shearwaters are constrained to increase foraging gains by increasing trip duration, this provides a rationale for the foraging bird to maintain control of trip length, further supporting the notion that incubation scheduling is mediated by the need for the foraging bird to regain lost mass, as is expected in long-lived species that are selected to prioritise their own condition (Stearns, 1992). The finding that handicapped nests exhibited similar levels of equity in the proportional contributions of each parent to care suggests that this is an effective mechanism to maintain coordination and equality in investment.

We can envisage two scenarios under which this model of decision-making may operate. In the first, foraging birds feed until their mass reaches some set threshold, at which point they return to the nest, regardless of the condition of the partner. Under this strategy, we expect that both successful (gain mass quickly) and unsuccessful (gain mass slowly) foragers would return to the nest at the same mass, but the former group would spend fewer days at sea (Figure 4.7, Panel A). The infrequency of neglect in this study, combined with the extremely long incubation shifts exhibited by partners, suggests incubating shearwaters do not normally reach a physiological limit beyond which they have insufficient energy reserves to maintain incubation. Maintaining a ‘buffer’ of condition may ensure incubating birds can sustain an unexpectedly long shift if adverse environmental conditions retain the partner at sea for longer than usual. Consequently, a ‘sit-and-wait’ strategy could be effective for incubating birds.

However, clearly parents will be unable to sustain incubation indefinitely, and an extremely protracted foraging trip by the partner will force the incubating bird to abandon the nest, either due to an extreme decline in its body condition, or because of the perceived low likelihood of its partner returning to the nest. Though no relationship could be found between incubation shift length and the probability of neglect in this study, it is possible that this was due to its low frequency. In other seabirds, neglect occurs when the body condition of the incubating bird falls below some threshold (e.g. herring gulls *Larus argentatus*, Sibly and McCleery, 1985; blue petrels, Chaurand and Weimerskirch, 1994; Ancel et al., 1998). A similar relationship may exist in Manx shearwaters. While Manx eggs are resistant to chilling, just 3 days of exposure reduces survival to 28% (Harris, 1966; Brooke, 1990). As the breeding success of the parents is intertwined, both parents should thus attempt to minimise the likelihood of neglect. We can therefore envisage a second, more cooperative decision-making strategy for foraging birds, in which the returning mass threshold decreases as the duration of the foraging trip increases (Figure 4.7, Panel B). Such a strategy would allow birds to prioritise and act on their own condition when deciding on trip duration, while implicitly taking into account their partner’s needs. That experimental birds returned from their long-duration trips in worse condition lends support to this second model, and is a common finding in seabird handicapping studies, where despite reducing parental care, handicapped individuals still suffer some reduction in condition (Navarro & González-Solís, 2007; Bijleveld & Mullers, 2009; Harding et al., 2009; Jacobs et al., 2013), suggesting this may be widespread.

The slope of this declining return mass threshold could be set by evolutionary or behavioural processes. In the former case, the rate of decline may evolve to match the average change in probability of neglect for incubating shearwaters across the population. There is clearly considerable flexibility and resilience in the amount of time the incubating bird can sustain on the nest, and so this may be an effective means to minimise the probability of neglect from the perspective of the foraging bird. Alternatively, the slope of the decline may be set by information transfer between the parents. On reunion at the nest, Manx shearwater pairs engage in conspicuous vocalisations (Brooke, 1990), which may serve as an opportunity to exchange information about body condition (Jones et al., 2002). Such information could allow the foraging bird to set the gradient of its return threshold slope according to the condition of the incubating partner, ensuring that that foraging trip duration is optimised to the needs of the pair as whole. Our finding that both foraging trip duration and return mass were mediated by the condition of the partner lends greater support to this more flexible model: birds with partners in better condition spent longer at sea, and returned to the nest at a higher mass.

Our interpretation of the reduction in foraging gains for handicapped birds observed here is that it reflects a combination of the compromised foraging efficiency of these individuals and their decision to return to the nest early to minimize the probability of desertion by the partner. However, an alternative explanation is that this reduction in body mass is adaptive: as reduced body mass reduces wing loading, this in theory could compensate for the increased energetic expenditure associated with the handicap (Blem, 1976). Adaptive mass loss has been observed in other species, and may be associated with unfavourable foraging conditions (e.g. burrowing parrots *Cyanoliseus patagonus*, Masello and Quillfeldt, 2003), or, more commonly, the switch in breeding stage from incubation to the more energetically-intensive chick provisioning period (thick-billed murres *Uria lomvia*, Croll et al., 1991; collared flycatchers *Ficedula albicollis*, Cichon, 2001; Wilson's storm petrel *Oceanites oceanicus*, Quillfeldt et al., 2006). However, our mass changes were observed over a much more restricted time period and exclusively during incubation. Existing evidence suggests that higher masses during incubation are adaptive, by providing fasting endurance (Chastel et al., 1995; Cuthill & Houston, 1997). Furthermore, incubating adults tend to gain mass when they are released from energetic constraints, for example when environmental conditions are favourable, further suggesting that higher masses are adaptive (Holt et al., 2002; Quillfeldt et al., 2006). Finally, the handicapped birds in our study returned to the nest at a much lower condition

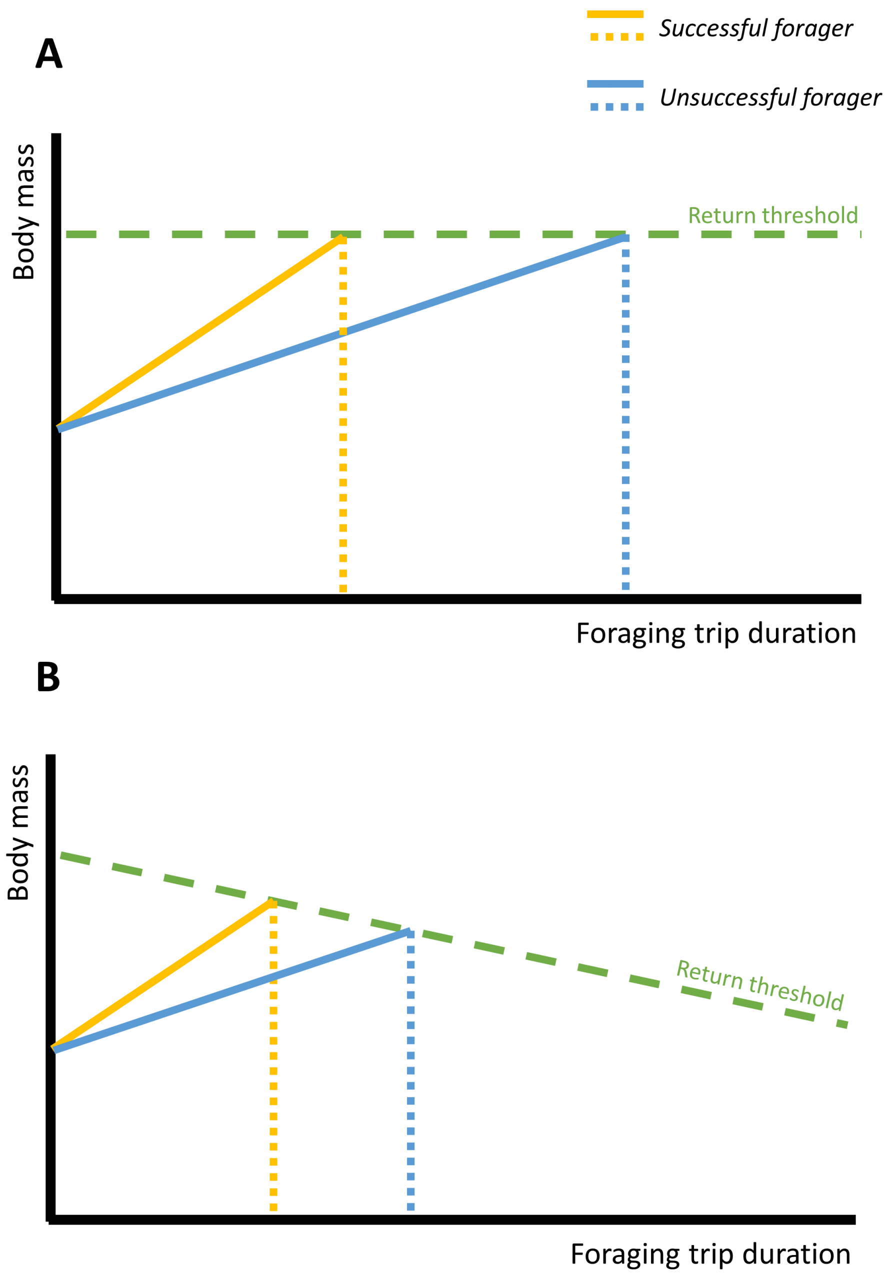

Figure 4.7: Illustrative model to demonstrate the outcome of a return mass threshold-based decision paradigm for foraging behaviour. Successful foragers, which gain mass quickly, are coloured in yellow; unsuccessful foragers, which gain mass slowly, are coloured in blue. **A)** *Fixed return threshold*. Successful foragers reach their return threshold mass rapidly and so return to the nest after a short trip. Unsuccessful foragers reach their return threshold mass more slowly, and so spend more time away from the nest. Both birds return at the same mass. **B)** *Declining return threshold*. Successful foragers reach their return threshold mass rapidly and so return to the nest after a short trip and at a relatively high mass. Unsuccessful foragers reach their return threshold mass more slowly, and so take a longer trip and return at a relatively lower mass.

than the observed range of control birds, suggesting that their reduction was beyond the natural adaptive range of mass. Given this evidence, we believe that our observed mass changes are more likely to reflect the energetic constraints imposed by the handicap, than an adaptive strategy by the handicapped bird.

The duration of incubation shifts, and their corresponding foraging trips, in the Manx shearwater appear to be primarily decided by the foraging bird. The partners of shearwaters that were handicapped for the duration of one foraging trip sustained incubation shifts that were more than double the duration of normal shifts, suggesting they simply wait for the partner to return the nest. However, the decisions made by foraging birds appear to be mediated by the state of their partner, with handicapped birds returning to the nest earlier and at a lower mass when their partners were in worse condition. This provides evidence that incubation scheduling in this species is maintained by a cooperative strategy whereby shearwaters exchange information about their metabolic needs and condition in order to optimise their foraging trip durations in a way that benefits the pair as a whole. These results suggest that simple decision-making mechanisms with some condition-dependent information are sufficient to maintain cooperation between parents without the need for pre-determined negotiation of behaviour.

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5

Exploring the mechanistic drivers of coordinated chick provisioning in Manx shearwaters *Puffinus puffinus*

With contributions from Chris Tyson, Joe Wynn, Martyna Sysposz, Cécile Vansteenberghe, and Tim Guilford.

Contents

5.1 Abstract

Many species that provide care for their offspring in tandem with a partner coordinate their activities to maximise the efficiency of their investment. However, it is not well known exactly how this coordination is achieved. Manx shearwaters *Puffinus puffinus* are Procellariiform seabirds that exhibit a dual foraging strategy during chick provisioning, in which long foraging trips to maintain condition are alternated with short, frequent trips to feed the offspring. This strategy is employed in a coordinated manner between the parents, with one parent making short trips while the other takes a single long trip. Previous work has revealed that a complimentary change in foraging trip type is initiated by the parents following a synchronous visit to the nest. We examined the mechanisms that may underlie this behaviour. Specifically, we investigated whether physical reunion of the parent, indirect cues gained from the chick's begging behaviour, or both, could inform a switch in behaviour. We took an experimental approach to manipulate the information adults had available to them: first, we removed the opportunity for parents to interact at the nest during their visits; second, we supplementarily fed chicks to alter their begging behaviour. We found neither experimental protocol induced a change in parental behaviour. We discuss the possibility that the patterns of alternated provisioning observed during chick rearing in Manx shearwaters may emerge through entrainment during the well-coordinated incubation period preceding provisioning.

5.2 Introduction

As the resources available to individuals are limited both by their distribution in the environment and by the time and energy required to obtain them (Stearns, 1992), parents should partition their investment in offspring and self-maintenance in such a way that minimises costs to their future reproductive success or survival (Trivers, 1972). This has been historically viewed to generate conflict between parents when both provide care to offspring, as each stands to gain from the benefits of increased reproductive output while only paying the cost of its own contribution (Chase, 1980). However, for species in which the reproductive output of the two partners is highly aligned, which is the case for long-lived, sexually monogamous species, the shared fitness interests of the two parents may select for more cooperative behaviour during breeding (Griffith, 2019).

In such cases, parents may benefit from coordinating their caring activities so that the cost-to-benefit ratio for the pair as a whole is minimised. Evidence for such coordination is increasingly found to be widespread across biparentally-caring species (e.g. prairie voles *Microtus ochrogaster*, Ahern et al., 2011; long-tailed finches *Poephila acuticauda*, van Rooij and Griffith, 2013; long-tailed tits *Aegithalos caudatus*, Bebbington and Hatchwell, 2016; blue tits *Cyanistes caeruleus*, Griffioen et al., 2019; *Cichlidae* fish, Lehtonen, 2017; *Nicrophorus* burying beetles, Smiseth, 2019). In seabirds, the competing demands of self-care and provisioning are particularly stark, as parents usually feed at long-distance foraging sites that are often unpredictable at small scales (Weimerskirch, 2007). To resolve this conflict, many species employ a 'dual-foraging strategy' (e.g. Congdon et al., 2005; Shoji et al., 2015; Wojczulanis-Jakubas et al., 2018; Grissot et al., 2019), in which individual parents alternate between short, frequent trips to the nest to provision young, and longer trips to feed themselves. Recent evidence suggests that parents employ this strategy in a coordinated manner with the partner, so that while one parent is out at sea for long periods foraging for itself, its partner is provisioning the offspring (Congdon et al., 2005; Tyson et al., 2017). Through such a coordinated approach to care, parents can ensure both that they replenish their own resources over the short-term, and that their offspring are provisioned efficiently.

Like many Procellariiform seabirds (Weimerskirch et al., 1994; Congdon et al., 2005; Booth et al., 2008; Wojczulanis-Jakubas et al., 2018), the Manx shearwater *Puffinus puffinus* exhibits a dual foraging strategy in which parents alternate short, approximately one-day provisioning trips with longer, condition-replenishing trips of three to four days (Shoji et al., 2015; Tyson et al., 2017). The timing of these trips is coordinated between the parents, and it has been previously observed (Tyson et al., 2017) that the switch in foraging strategy from short to long trips or vice versa follows a coincident visit of the two parents to the colony. It remains unclear, however, what the precise mechanisms guiding this coordination are.

Direct interactions between the parents may induce Manx shearwaters to switch their foraging trip type, either through negotiation between the partners, as has been observed in blue-footed boobies *Sula nebouxii* (Drummond et al., 2002) and zebra finches *Taeniopygia guttata* (Boucaud et al., 2016), or simply by directly observing the investment made by the partner (Hinde, 2006). For example, pied babblers *Turdoides bicolor* (Savage et al., 2017) and chestnut-crowned babblers *Pomatostomus ruficeps* (Raihani et al., 2010) prefer to provision the nest with other carers, and so will wait before provisioning to ensure they can feed alongside a conspecific. Manx shearwaters almost always coincide in the burrow before exchanging parenting duties during incubation, and often do so during chick provisioning also (Brooke, 1990), hinting at the possibility that physical reunion at the nest could elicit a switch in foraging trip type. However, Tyson et al. (2017) found that parents that returned to the colony on the same night, but did not overlap at the nest, were just as likely to adjust foraging strategies, suggesting physical reunion is not necessary to drive coordinated provisioning.

If parents do not physically reunite prior to provisioning, they may use indirect cues to gain the information required to initiate a switch in foraging behaviour. Chick begging, which in the Manx shearwater is thought to be an honest signal of need (Quillfeldt et al., 2004), could provide such a cue, as encountering an already satiated chick would indicate to the parent that its partner had already visited the nest that night. It has been proposed that chick vocalisations may allow parents to assess their partner's effort (Johnstone & Hinde, 2006; Bebbington & Hatchwell, 2016). Parents are known to adjust their provisioning effort in response to chick begging cues (Quillfeldt et al., 2004; Hamer et al., 2006), and as these cues reflect chick condition and therefore the partner's previous investment, it has been proposed that chick vocalisations may allow parents to assess their partner's effort (Johnstone & Hinde, 2006; Bebbington & Hatchwell, 2016), though presently explicit empirical evidence for this is lacking. Were Manx shearwaters to employ such a mechanism, then this information should only be useful to that parent returning from a short, provisioning trip, as the parent returning from a long self-maintenance trip could reasonably 'assume' that its partner was currently provisioning and switch to short trips regardless.

We took an experimental approach to determine whether 1) direct communication between the parents or 2) indirect signalling, mediated by chick begging, inform changes in foraging trip type from provisioning to self-maintenance, and vice versa. Using an automated RFID-based individual detection system, Tyson et al. (2017) explored the coordination of provisioning behaviour in Manx shearwaters. While the authors' findings did not support a role of physical reunion in this behaviour, we aimed to replicate the observational findings of that study using two further years of data and an updated experimental set-up, which should improve the accuracy of detections. Through this, we aimed to determine conclusively whether directly meeting the partner at the nest is important by removing the opportunity for partners to reunite. In a second experiment, we artificially fed chicks prior to the arrival of either parent to simulate a previous provisioning visit from the perspective of the first parent to arrive to the nest. Through this, we aimed to assess whether parents respond to satiated chicks by changing their foraging behaviour.

5.3 Methods

This study was conducted on Skomer Island (51°44’ N, 5°17’ W), Wales, U.K. during the chick rearing periods (June-August) of 2018 and 2019. During the breeding season, adult Manx shearwaters nest in underground burrows, which they visit only at night. Inside the nest chamber, shearwaters can be accessed by hand either through the burrow entrance or through a purpose-built inspection hatch. In the last few weeks of incubation, established nests were monitored daily so the identity of pairs could be identified and to determine the hatching date, taken as the first day the chick was found entirely outside of the eggshell. During these daily checks, adults were fitted with passive integrated transponder (PIT) tags (2 x 12mm EM4102 glass tag, Cyntag Cynthiana, KY, USA), programmed with a unique identification number. These were shrink-wrapped onto a 1mm cable tie, which was looped around the tarsus, above the metal British Trust for Ornithology ring, and tightened sufficiently that it could not pass over the ring or intertarsal joint, but could otherwise move freely (see Figure 5.1A). A total of 46 nest in 2018 and 55 nests in 2019 were used in the study; of these 25 nests were monitored in both years.

Radio Frequency Identification (RFID) readers were deployed at the entrance to burrows to record precisely the arrival and departure times of adults into and out of the nest. These consisted of two-loop antenna, a computer, and a RAVPOWER 26800mAh portable battery (Figure 5.1B and C). One antenna was placed at the entrance of the burrow, and the other approximately 20cm inside the tunnel to determine directionality in the detections. When a PIT tag passes within 5 cm of the antennae, the tag transmits its unique identification number, which is stored on the RFID computer with the date and time of detection.

5.3.1 Data processing and analysis

All analyses and data-processing were carried out in `R` version 3.5.1 (R core team). Means are presented throughout with 95% confidence intervals (CI), unless otherwise

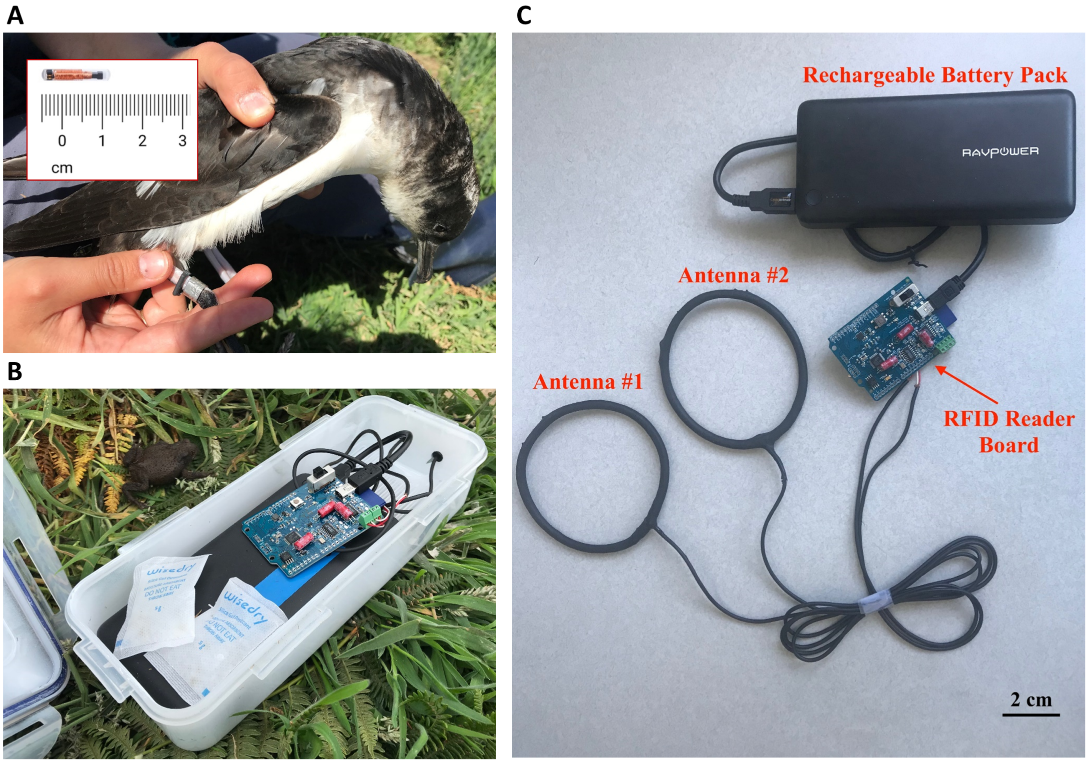

Figure 5.1: *(A)* Placement of a PIT tag on the tarsus of an adult Manx shearwater, just above the metal ring. Insert: unhoused PIT tag with scale bar. *(B)* RFID set-up in the field. The RFID reader board and rechargeable battery pack were housed in a waterproof box to protect against the weather. The two antennae were placed approximately 20cm apart in the tunnel entrance of the burrow nest. *(C)* RFID set-up laid out to show all components.

specified. Model fit was assessed through visual inspection of diagnostic residual plots. To control for multiple measurements from the same nests and in different years, all our models included a random intercept of individual ID or individual ID nested within nest ID as appropriate, nested within year.

Detections from RFID readers were used to determine the times and durations of nest visits and foraging trips. Directionality of the parents into or out of the nest was inferred based on which antenna was triggered first: if the first detection was on the antenna at the entrance, and the second on the internal antenna, the parent was moving into the burrow, and vice versa. Based on this classification, foraging trip duration was taken as the time between the departure and arrival time of each bird at the nest while the time between arrival and departure indicated time spent in the burrow. RFID readers were programmed to report their status every hour. If the RFID reader was reported as off

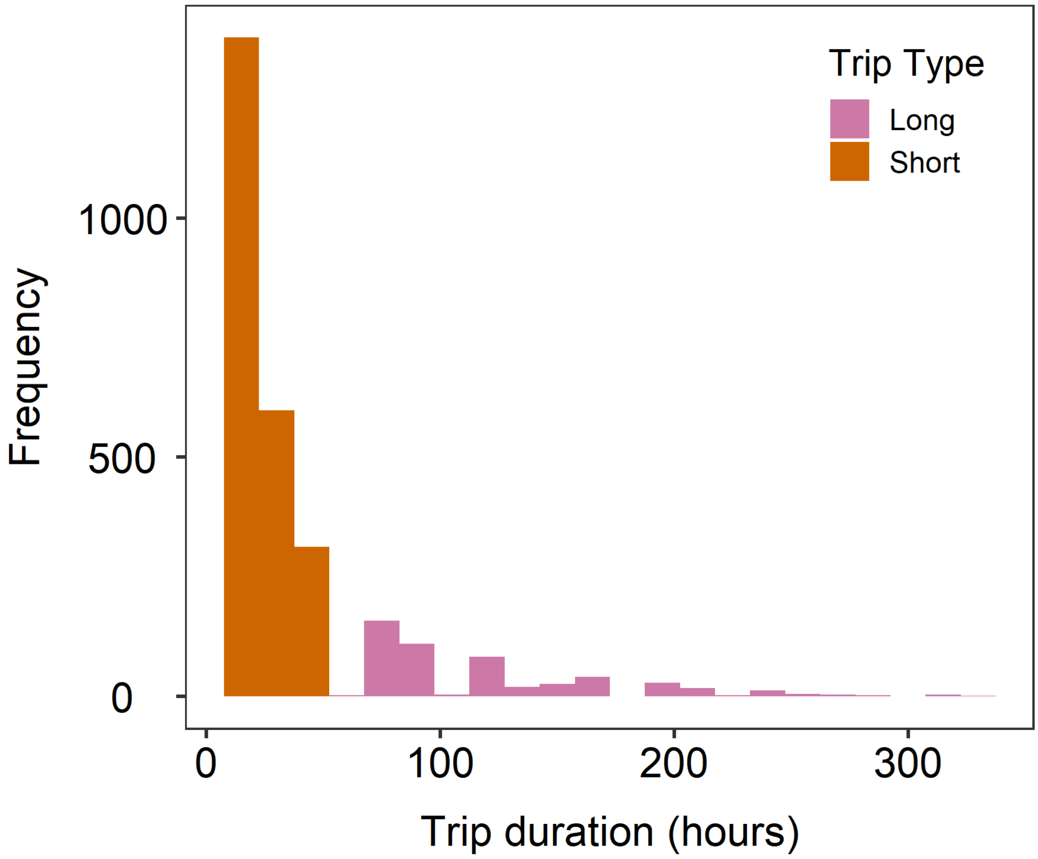

Figure 5.2: Histogram to show trip duration (in hours) across our dataset. Bars have been coloured according to our trip type assignment, where purple bars = 'long' trips, and orange bars = 'short' trips. Gaps in histogram bar are an artefact of the fact Manx shearwaters can only visit their nest at night.

for >1 hour during the night, the 2 trips adjacent to the off period were discarded. From our RFID data, we extracted 2787 provisioning visits.

We split provisioning and self-maintenance foraging trips (hereby 'short' and 'long' trips, respectively) based on methods outlined by Welcker et al. (2009). We assumed that the duration of foraging trips could be represented by a bimodal distribution in which two separate lognormal distributions of duration in hours represent short and long trips respectively (Figure 5.2). By iteratively changing the cut-off point between the two distributions, we looked for the point at which the variance in both distributions was minimised. This occurred at approximately 50 hours in our dataset.

5.3.2 Direct communication hypothesis

To test the hypothesis that the physical reunion of parents in the burrow precipitates a change in trip type, we considered observational data from our control (unmanipulated) nests, and additionally conducted an experiment in which parents were prevented from encountering one-another in the burrow.

The first evidence that Manx shearwaters actively coordinate their provisioning visits was reported by Tyson et al. (2017), who found that parents were more likely to switch from one trip type (short or long) to the other when they visited the nest on the same night as their partner, regardless of whether they physically coincided at the nest. To test his hypothesis in our dataset, we used the `R` package `lme4` (Bates et al., 2015) to construct a linear mixed effects model (LMM) to compare the absolute change in trip duration when only one parent returned to the colony versus nights where both returned (model 1; Table 5.1). Large differences would indicate a switch in foraging trip type, whereas small differences would indicate no change. For those nights where both parents returned (n = 1096 trips for 69 nests), we further examined whether the change in foraging trip duration differed depending on whether the parents overlapped at the nest (model 2; Table 5.1).

In our experimental approach, we physically prevented pairs of Manx shearwaters from meeting each other by removing one parent from the nest chamber and containing it within the lab for the remainder of the night. We then examined the subsequent behaviour of the second parent to arrive (Figure 5.3). For this protocol, nests were checked for the presence of an adult every 20 minutes from dusk until two hours before dawn; where a single adult was found, it was blocked in the burrow for 30 minutes to allow it to feed the chick. When this time had elapsed, the adult was removed and temporarily housed in an individual cardboard box within a darkened lab. All held adults were subsequently assessed every 15 minutes for signs of distress (e.g. excessive vocalisation, scratching) until their release. It was decided *a priori* that any birds that either showed extreme signs of stress or exhibited any stress-indicating responses for three consecutive checks would be released; this protocol did not need to be enacted over the course of the experiment. At dawn, all birds were released from a sea-facing cliff by placing them on flat, outstretched hands facing the sea and allowing them to take off in their own time. Holding time varied between 49 minutes and three hours 57 minutes, and all birds returned to feed their chicks as normal on subsequent nights.

The predicted behaviour of parents subsequent to the holding protocol depended on their trip type immediately prior to the night of the experiment. In normal conditions, parents who return to the nest on the same night as their partner are observed to switch foraging trip type in opposing directions, with those returning from self-maintenance trips (‘long-trip parents’) switching to short, provisioning trips (‘short-trip parents’), and vice versa. As parents usually adopt the opposite trip type to their partner, long-trip parents can reasonably ‘assume’ that their partner will be making short-trips and therefore visiting most nights. Consequently, these parents should not require additional information to inform their change in trip type. Conversely, short-trip parents do not necessarily know when their partner will return to the nest, and so require additional information, either by meeting the partner or through indirect cues, to inform when they should change trip type. Because of this dichotomy in the benefit of information, we predicted that long-trip parents should always switch to short trips on return to the nest, regardless of the experimental protocol. Conversely, we predicted that short-trip parents should only change trip type when they encounter their partner, and so under the experimental protocol they should not change trip type and would continue to make short trips. This would manifest as <50 hour change in trip duration in either direction, which marks the threshold dividing short and long trips.

We modelled the observed change in trip duration as a function of experimental group (control vs. incarcerated). We fitted an LMM to change in trip duration with the fixed effects of experimental group, trip type (short or long), and sex (model 3; Table 5.1). As the predicted effect of experimental group depends on the trip type of the parent, we included an interactive term of group * previous trip type. To account for potential individual and temporal variation that may explain variation in trip duration, when analysing the effects of our experimental treatments, we fitted our models using two datasets: one that compared focal parents on experimental versus control nights (same birds, different nights; n = 46 trips for 5 nests), and another that compared focal parents on experimental nights to control nests on the same night (different birds, same nights; n = 222 trips for 49 nests).

Thirty-five individuals from 20 nests were subject to the experimental protocol. However, we could not predict perfectly the nights on which both parents would visit the nest. Those nights where a partner was incarcerated, but its partner did not return, were excluded from the experiment, leaving 5 individuals retained for analysis. To determine whether this small sample size may have precluded our ability to find a result, we conducted a *post-hoc* power analysis to determine the probability of discovering our predicted effects, if present, given this sample size.

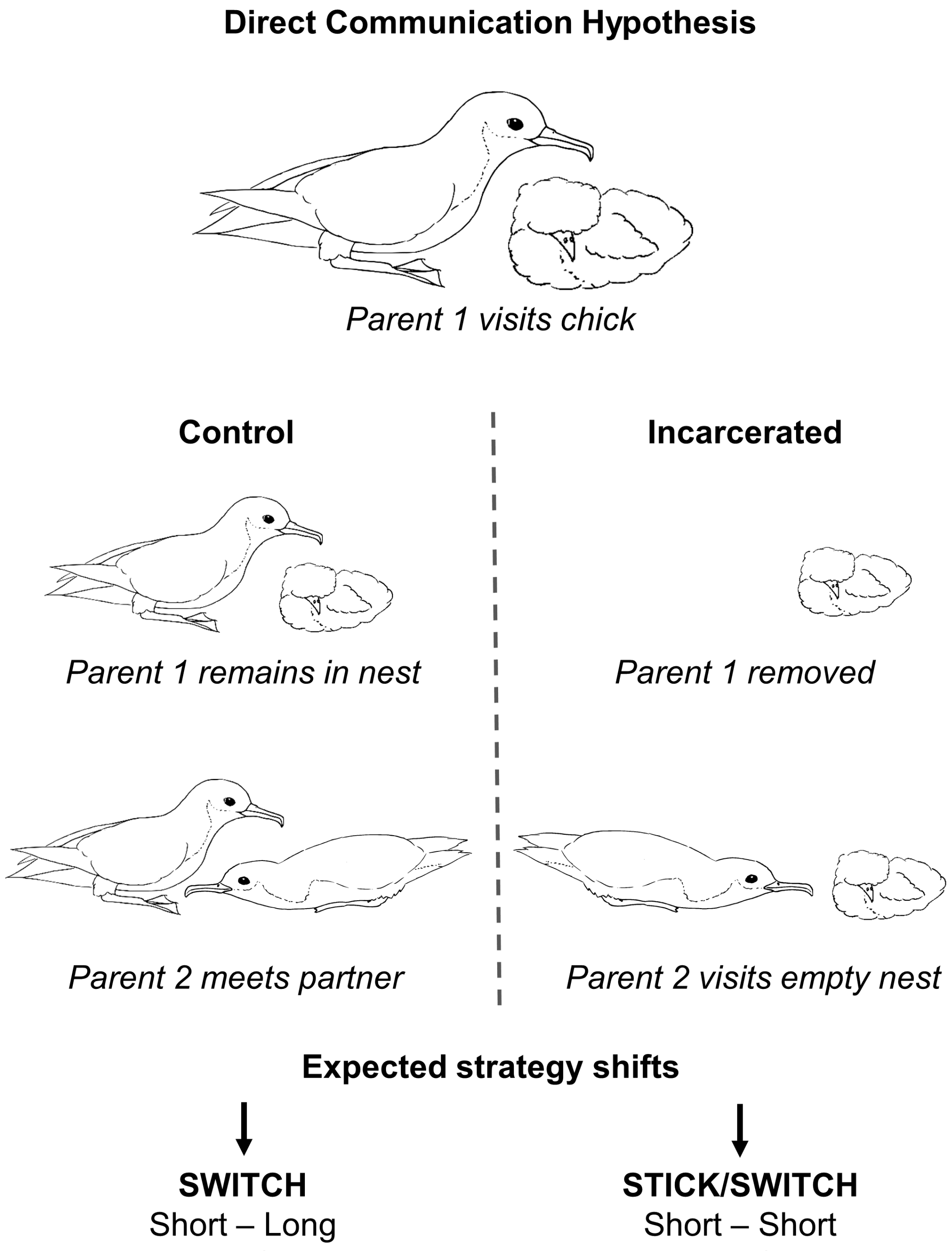

Figure 5.3: Schematic to illustrate the incarceration protocol. In control nests, parent 1 visits and feeds the chick, and is later joined by parent 2, giving the opportunity for the pair to meet. Both parents subsequently change foraging trip type. In incarcerated nests, parent 1 is removed shortly after feeding the chick. Parent 2 therefore has no opportunity to meet its partner. As outlined in the methods, this parent is subsequently expected to stick to its current foraging trip type if it has been making short, frequent trips to visit the chick, or will switch to short trips if it has just returned from a long self-maintenance trip.

5.3.3 Offspring-mediated indirect signalling hypothesis

To test whether chick-begging cues may indicate to parents that their partner has already visited the nest, we artificially fed chicks before either parent had arrived at the nest, to simulate a synchronous visit to the colony for the first parent to visit the nest (Figure 5.4). We subsequently examined the behaviour of parents that encountered satiated chicks. We predicted that this information would only be useful for parents on short trips. Consequently, we made two predictions: firstly, under natural conditions, long-trip parents would be the first to arrive to the nest, so that their short-trip partners could benefit from any indirect information available, and, secondly, short-trip parents would switch to long trips after encountering a fed chick.

Chicks were removed from the nest for feeding one hour prior to dusk (between approximately 21:00 and 22:00 UTC) to maximise the probability that parents encountered a fully satiated chick while eliminating the possibility of their returning to an empty nest, as adults do not begin to return to the colony until after dusk. Chicks were fed with whole sardines (*Clupea spp.*) in sunflower oil (60% fish by mass), which were blended with additional sunflower oil (10% by mass) and water (30% by mass), following methods by Dean (2012) and Padget (2017). The estimated energy content was 12.9KJg^{-1} (Dean, 2012). The resulting food mixture was warmed to 30-35°C just before feeding, using a water bath. Meals were administered through intubation of the proventriculus using flexible crop tubes, and delivered slowly using a plastic syringe. Chicks were fed until they stopped accepting food. Immediately prior to and following feeding, each chick was weighed on a digital scale precise to 0.5g. Total feed size was calculated as the difference between these two measures, and averaged 43.6 ± 8.8g (mean ± SD). This was approximately equivalent to the normal daily food delivery for chicks (53g per night, Hamer et al., 1998). Feeds took approximately five minutes to deliver.

Any indirect information available to the parents would only be useful for parents on short trips, because parents usually adopt the opposite trip type to their partner (Tyson et al., 2017) and so long-trip parents can reasonably ‘assume’ that their partner will be making short trips and therefore visiting most nights. Consequently, these parents should not require additional information to inform their change in trip type. Conversely, short-trip parents do not necessarily know when their partner will return to the nest, and so require additional information, either by meeting the partner or through indirect cues, to inform when they should switch trip type. Because of this dichotomy in the benefit of information, we targeted only short-trip parents for the chick feeding experiments. We fed chicks in 40 nests, and excluded any nests where both parents subsequently visited as it would be impossible to separate the effects of the experimental protocol from normal behaviour. We furthermore excluded nests where the parent visiting the nest had returned from a long trip. This left 22 nests retained for analysis.

We predicted that short-trip parents would switch to long trips after encountering an artificially fed chick. To this end, we fitted an LMM to examine whether the difference between consecutive foraging trips (in hours) differed according to whether the chick had been artificially fed or not (model 4, Table 5.1). A difference in trip duration of > 50 hours, our threshold for dividing short and long trips (see 5.3.1 Data processing and analysis), would indicate a switch in trip type. As females are known to be more responsive to chick begging behaviour than males (Quillfeldt et al., 2004; Hamer et al., 2006) and so might be expected to show a different result to the experimental manipulation, we included the interactive effect of sex and experimental group (fed or not) in our models. As with the incarceration experiment, to account for potential individual and temporal variation that may explain variation in trip duration, when analysing the effect of our feeding experiment we fitted our models using two different datasets: one that contained data on focal parents on experimental as well as all unmanipulated nights recorded for those parents (n = 234 trips for 22 nests), and another containing data on focal parents on experimental nights as well as unmanipulated nests on the same night (n = 277 visits for 65 nests).

As only short-trip parents can benefit from the indirect cues provided by chick begging behaviour, if parents use this information to decide to switch trip type, we would expect a consistent pattern in which parent arrives to the nest first. Specifically, we predicted that long-trip parents would be the first to arrive to the nest, so that their short-trip partners could benefit from any indirect information available. To examine whether this was the case, we constructed a generalized mixed effects model (GLMM) with a binomial error structure to test whether previous trip duration (in hours) predicted which parent was first to arrive at the nest for those nights where both parents visited the colony (n = 992 trips for 67 nests; model 5; Table 5.1). We predicted that parents on long trips would be more likely to be the first to arrive at the nest. We additionally included the fixed effect of sex.

To determine whether parents wait for their partners to arrive at the nest, we examined whether the duration of the nest visit differed for the first and second parent to arrive at the nest for nights on which both parents visited. To account for the fact that parents that visit the colony earlier have more night time hours available to them that they could spend waiting, we divided nest visit duration by the minutes remaining until sunrise. Because this generated a proportional response variable, we modelled differences in nest visit duration with a beta distribution using the `R` package `glmmADMB` (Bolker et al., 2012) (Bolker et al. 2012), including the fixed effect of order of arrival (model 6; Table 5.1). As the effect of order may depend on whether the parents met at the nest, we included an interactive term for nest synchrony and order. We excluded visits for which visit duration was unknown due to reader error or where data for one parent was missing, leaving 956 visits across 67 nests retained for analysis.

Table 5.1: Model structures used in the analysis.

Type	**Model**	**Parameters**		
		Response	***Fixed***	***Random***
LMM	1	Abs trip duration change (hours)	Colony synchrony + sex	Year:Nest:ID
	2	Abs trip duration change (hours)	Nest synchrony + sex	Year:Nest:ID
	3	Change in trip duration (hours)	Incarcerated group + sex	ID
	4	Change in trip duration (hours)	Fed group * sex	Nest:ID
GLMM	5	Order of arrival	Previous trip duration + sex	Year:Nest: ID
Beta mixed	6	Proportional visit time	Parental order*nest synchrony + sex	Nest:ID

Notes – *colony synchrony* = whether or not parents visited the colony on the same night; *sex* = male or female; *year* = year of data collection, 2018 or 2019. Note that the incarceration experiment was only carried out in 2019; *nest* = nest/pair identity; *ID* = individual identity; *nest synchrony* = whether parents overlapped in the nest on a given night, YES or NO; *Incarcerated group* = incarcerated or control; *fed group* = supplementarily fed or control; *previous trip duration* = duration of preceding foraging trip in hours; *parental order* = order of arrival, first or second

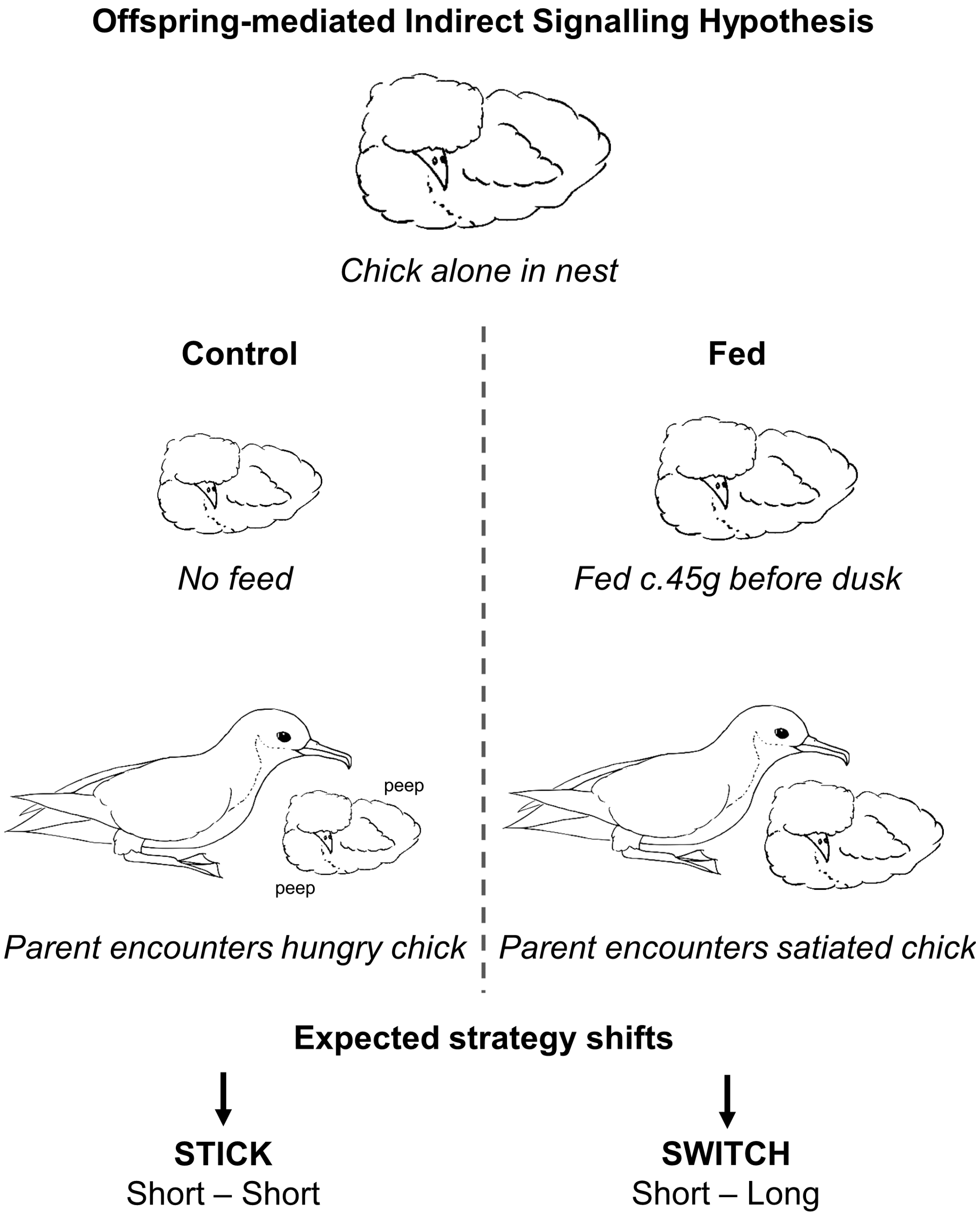

Figure 5.4: Schematic to illustrate the feeding protocol. In control nests, the parent visits an unfed chick, which subsequently begs to receive food. The parent continues to make short, frequent provisioning trips. In the fed group, chicks are fed just before the parent arrives. The parent therefore encounters a fed, satiated chick that presumably does not beg for food. It is therefore led to believe that its partner has visited the nest, and so switches to long, self-maintenance trips.

5.3.4 Ethical note

All methods were approved by the British Trust for Ornithology Unconventional Methods Technical Panel (permit number C\5311), Natural Resources Wales, Islands Conservation Advisory Committee, and University of Oxford's Local Ethical Review Process (reference number APA/1/5/ZOO/NASPA).

5.4 Results

We identified 2787 foraging trips from 76 nests; 641 trips from 46 nests in 2018 and 2146 trips from 55 nests in 2019. Mean trip duration for birds on 'short trip' strategies was 25.55 ± 9.077 hours, and for those on 'long trip' strategies was 119.076 ± 54.32 hours. The maximum visit duration recorded was 409.1 minutes (6.82 hours), and the mean visit duration was 157.93 ± 77.47 minutes.

Over the two-year period, 1057 trips were initiated following a synchronous visit to the colony. For 279 of these trips (26.4%), parents did not coincide at the nest.

5.4.1 Direct communication hypothesis

Observational

Parents that visited the nest on the same night as their partners adjusted their trip duration to a greater extent than parents who made solo visits to the nest (Figure 5.5; **model 1**: Table 5.2). Females adjusted their trip duration to a greater extent than males (female change: 39.98 [-76.68, 156.64] hours, male change: 29.73 [-90.54, 150.00] hours; Table 5.2). There was no difference in trip duration depending on whether or not the parents overlapped in the burrow (**model 2**: Table 5.2).

When parents visited the colony on the same night, but did not coincide at the nest itself (n = 354 visits for 59 nests), the time gap between their visits ranged from 0.067 to 288.32 minutes, with a mean of 58.34 ± 60.58 minutes.

Table 5.2: Coefficients and test statistics from LMM of absolute change in trip duration (hours) according to whether birds were synchronous or not at the colony and nest, and sex. P-values calculated from likelihood ratio tests comparing the full model to a null model without the effect of interest.

	Synchronous at colony			*Synchronous at nest*		
Variable	**Coefficient + 95% CI**	χ^2	p	**Coefficient + 95% CI**	χ^2	p
Intercept	24.38 [0.18, 48.42]			59.07 [33.94, 83.75]		
Synchrony(YES)	31.20 [27.00, 35.40]	202.38	<0.0001	-1.10 [-8.27, 5.93]	0.10	0.75
Sex(M)	-10.26 [-15.29, -5.35]	16.28	<0.0001	-13.67 [-20.83, -6.98]	17.03	<0.0001

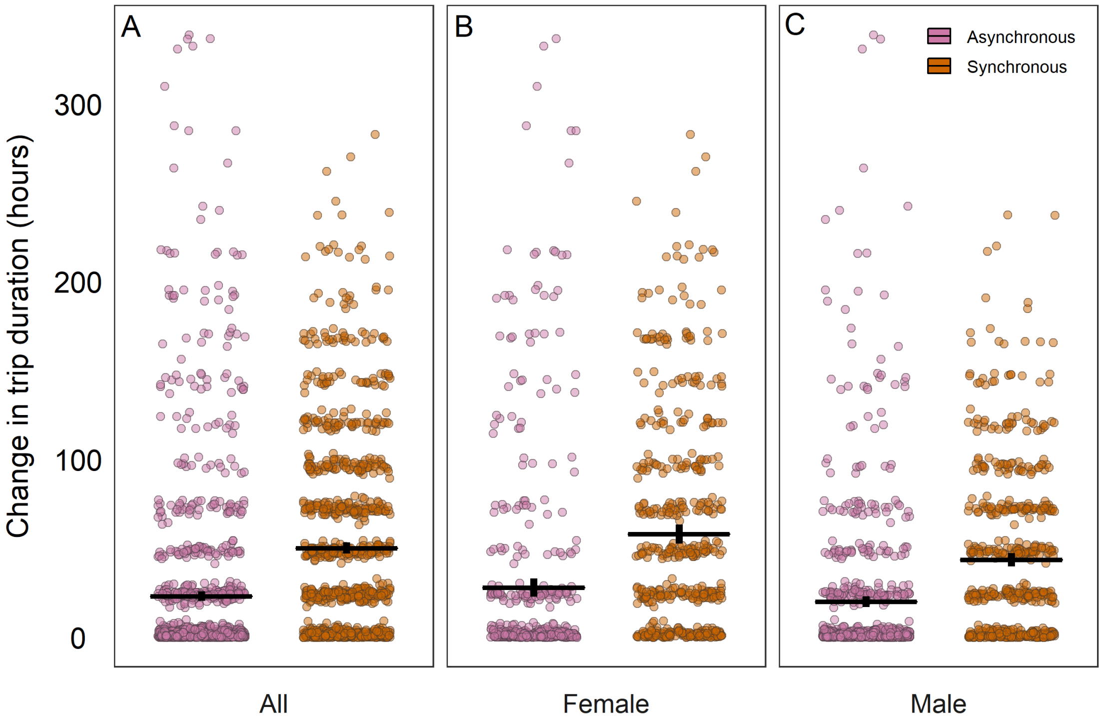

Figure 5.5: Absolute trip duration difference (in hours) between consecutive foraging trips that were asynchronous (lilac points) or synchronous (orange points) at the colony for all individuals combined (A), females only (B) and males only (C). Individuals that visited the colony on the same night as their partner showed a greater change in trip duration than those that did not overlap. Horizontal lines indicate mean, vertical lines indicate 95% CI. Data are jittered in the X axis for readability. The apparent banding in trip changes is an artefact of the fact that shearwaters only visit their nests at night.

Experimental

There was no interactive effect of experimental group and trip type on change in trip duration when comparing focal parents on experimental versus control nights, and focal parents on experimental nights to control nests on the same night (**model 3**: Table 5.3). Regardless of experimental group, birds that had been on long trips reduced their subsequent trip duration by 62.92 hours, indicating a switch to a short trip type, whereas those that had been on short trips increased their subsequent trip duration by 20.28 hours, less than the difference between short and long trips, and indicating a continuation of short, frequent nest visits (Figure 5.6; Table 5.3). Neither group nor sex had an effect on change in trip duration (Table 5.4).

With our sample size of 5, we had a power of 0.38 to detect our predicted changes in trip duration (at least a 50 hour decrease for short trip parents, and no change for long trip parents). In other words, were we to repeat our experiment 100 times, we would probably detect a real difference in trip duration 40% of the time.

Table 5.3: Coefficients and test statistics from LMM of change in trip duration (hours) according to experimental group, previous trip type, and sex. Negative values indicate a shortening of subsequent trip duration. p-values calculated from likelihood ratio tests comparing the full model to a null model without the effect of interest.

	Same birds, different nights			*Different birds, same night*		
Variable	**Coefficient + 95% CI**	χ^2	p	**Coefficient + 95% CI**	χ^2	p
Intercept	20.58 [-1.94, 43.10]			19.62 [8.71, 30.56]		
Group(expt)	-33.84 [-110.06, 42.38]	1.51	0.47	-29.66 [-98.25, 39.48]	2.40	0.30
Trip type(long)	-94.41 [-135.70, -53.11]	17.53	<0.0001	-98.51 [-114.85, -82.18]	109.1	<0.0001
Sex(M)	2.81 [-28.41, 34.04]	0.03	0.86	-4.62 [-18.10, 8.72]	0.46	0.50
Group*trip type	64.63 [-39.67, 168.93]	1.51	0.22	67.84 [-22.09, 157.16]	2.19	0.14

5.4.2 Offspring mediated indirect signalling hypothesis

Parents that visited chicks that had been artificially fed were not found to change foraging trip duration more than parents visiting control chicks, both when comparing focal parents on experimental versus control nights, and when comparing focal parents on experimental nights to control nests on the same night (Figure 5.6; **model 4**: Table 5.4). There was no interactive effect of sex and experimental group (χ^2 = 0.48, df = 1, p = 0.49).

Table 5.4: Coefficients and test statistics from LMM of change in trip duration (hours) according to experimental group and sex. P values calculated from likelihood ratio tests comparing the full model to a null model without the effect of interest.

	Same birds, different nights			*Different birds, same night*		
Variable	**Estimate + 95% CI**	χ^2	p	**Estimate + 95% CI**	χ^2	p
Intercept	2.23 [-8.012, 11.93]			6.45 [-1.403, 13.83]		
Group(expt)*Sex(M)	-8.14 [-15.09, 31.41]	0.48	0.49	15.21 [-8.48, 39.56]	1.61	0.20
Group(expt)	-1.71 [-20.10, 16.47]	2.39	0.30	-5.54 [-24.56, 13.39]	0.48	0.49
Sex(M)	4.077 [-3.77, 12.93]	0.79	0.67	-2.60 [-10.65, 5.61]	2.09	0.35

Long-trip parents are always expected to change foraging trip type on their return to the nest, and so only short-trip parents would be expected to benefit from the information gained from indirect signalling. As such, we predicted that long-trip parents would provision at the nest first, as the resulting satiated chick would indicate to the short-trip parent that its partner had returned to the colony. Contrary to these predictions, we found that parents that had been on short trips were more likely to arrive at the nest first (Figure 5.7; **model 5**: χ^2 = 4.96, df = 1, p = 0.026). The probability that a parent would be the second to arrive at the nest increased by 0.44 [0.047, 0.85]% for each additional hour that the bird had spent on its previous foraging trip. Males were more likely to arrive at the nest first than females (males: 58.1 [50.9, 64.9]%; females: 42.3 [35.1, 49.9]%; χ^2 = 5.39, df = 1, p = 0.02).

Parents spent a larger proportion of the night at the nest when they overlapped with their partner in the burrow (Figure 5.8; **model 6**: no overlap: 0.037 [0.030, 0.046]; overlap: 0.12 [0.11, 0.13]; z = 10.92, $p < 0.0001$). There was a significant interactive effect of burrow synchrony and parental order on the proportion of time spent at the nest (z = -4.12, $p < 0.0001$). On nights where both parents overlapped in the burrow, the first parent spent a larger proportion of the remaining night at the nest than the second (Figure 5.8; first: 0.17 [0.15, 0.19]; second: 0.09 [0.065, 0.10]). On nights where the parents did not overlap, parents spent the same proportion of time in the burrow regardless of arrival order (first: 0.34 [0.025, 0.045]; second: 0.086 [0.074, 0.10]). Males and females did not differ in the proportion of time they spent at the nest (females: 0.062 [0.053, 0.073]; males: 0.073 [0.063, 0.085]; z = 1.76, p = 0.078).

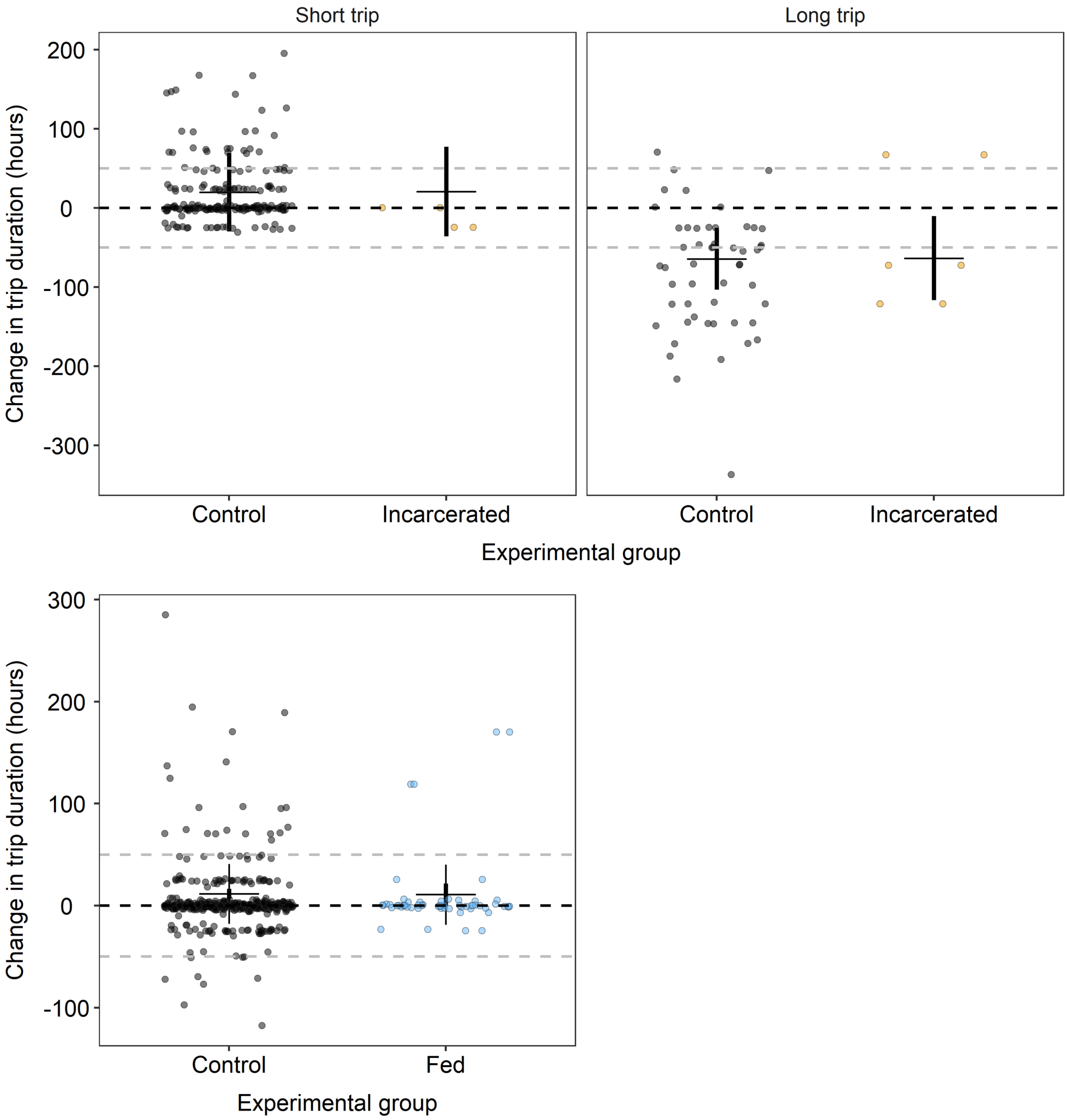

Figure 5.6: Change in trip duration in hours according to experimental group and previous trip type. Top panel: change in trip duration for control vs incarcerated birds, split according to whether parents were on short, provisioning trips (left panel) or long, self-maintenance trips (right panel). Bottom panel: change in trip duration for parents of fed chicks versus control birds. Only short-trip parents were included in this analysis. Dark grey horizontal dotted line in all panels indicates 0 change in trip duration; grey horizontal lines indicate +50 and -50 change in trip duration. Parents whose change in trip durations lay outside these margins were deemed as having changed trip type (short to long or vice versa). Horizontal line of crosshairs indicates mean, vertical lines indicate 95% CI. Data are jittered in X axis for readability.

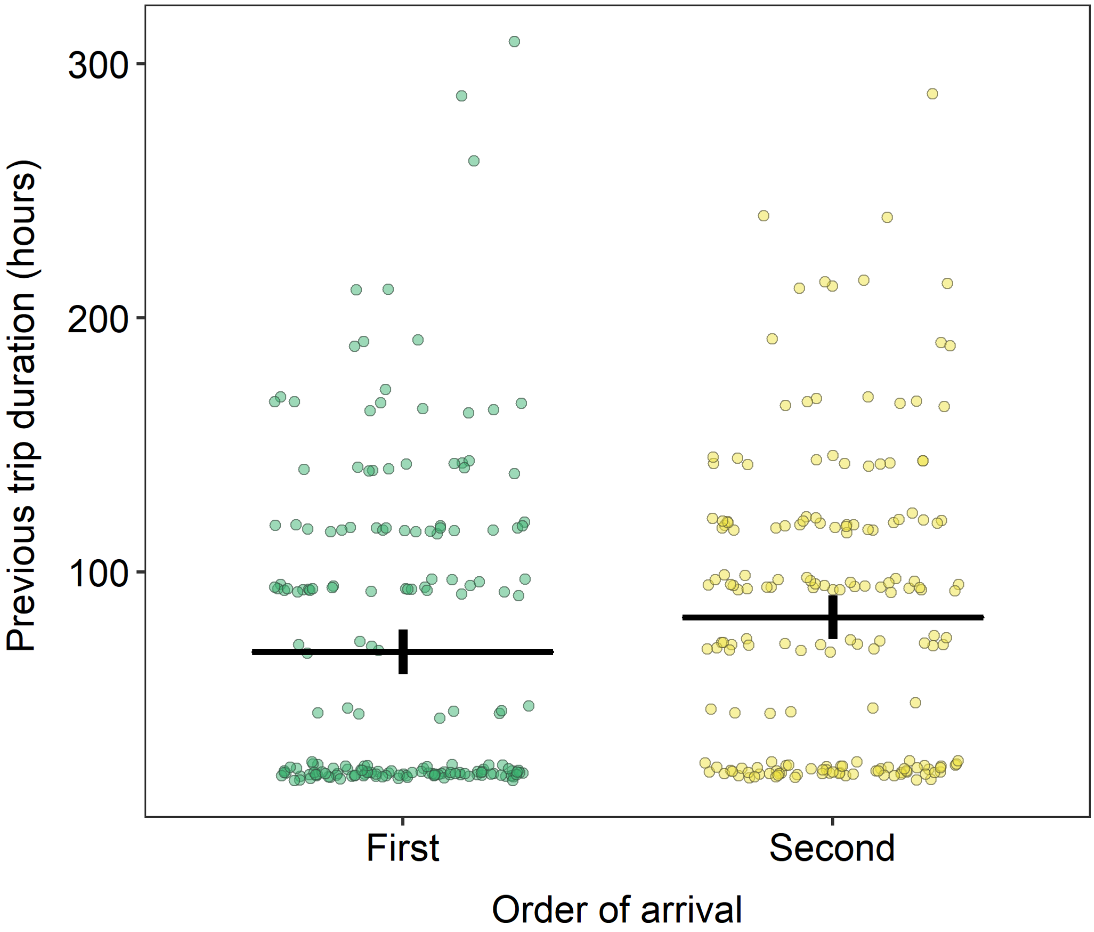

Figure 5.7: Previous trip duration in hours according to whether the parent arrived first or second to the burrow. Parents that had been on shorter trips were more likely to be the first to arrive at the nest. Horizontal line indicates mean, vertical lines indicate 95% CI. Data are jittered in X axis for readability.

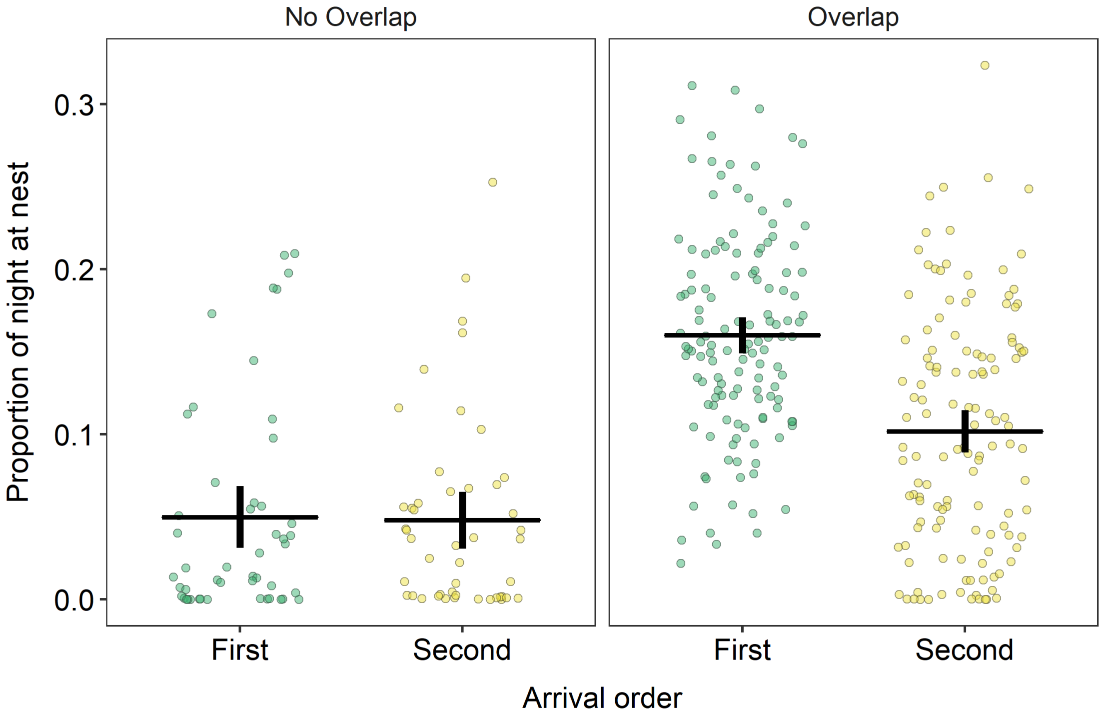

Figure 5.8: Proportion of time spent at the nest (adjusted for the number of hours of night available to birds following arrival) as a function of arrival order of the parents, and split by whether the parents coincided at the nest itself (Overlap) or not (No Overlap). Parents that were the first to arrive to the nest spent more time at the nest when they overlapped with their partner. Horizontal line indicates mean, vertical lines indicate 95% CI. Data are jittered in X axis for readability.

5.5 Discussion

The coordination of care between parents is a major example of cooperative behaviour between non-related individuals. Through such coordination, individual parents can maximise the benefit to cost ratio of their parental investment, both for themselves and, for those species where pairs have highly aligned fitness interests (Griffith, 2019), for the pair as a whole. Yet despite its widespread occurrence, the mechanisms underlying this coordination are not well understood. By experimentally manipulating the information that parent Manx shearwaters can access during provisioning, and following their subsequent behaviour using an automated nest-monitoring system, we investigated whether direct communication between parents or indirect signalling from the chick may facilitate the coordination of care. Despite replicating the finding that care is coordinated (Tyson et al., 2017), neither our observational findings nor experimental results provided support for the role either mechanism in the maintenance of provisioning coordination.

We experimentally manipulated the information that parent Manx shearwaters had access to while provisioning their offspring, and assessed whether this precipitated any change in their behaviour. For parents visiting the nest on the same night as their partners, we removed the opportunity for physical interaction between the pair at the nest. For shearwaters visiting alone, we artificially fed chicks so that parents encountered satiated young, which may indicate a visit by the partner. Neither manipulation resulted in a change in behaviour: parents in both treatments behaved as would be expected under natural conditions, switching trip type in a complimentary direction to the partner on nights where they both visited the colony, or continuing on their original trip type when they did not. These results suggest that neither physical reunion at the nest nor indirect cues from the chick are necessary to generate the coordinated provisioning strategy observed in Manx shearwaters.

Manx shearwater pairs almost always reunite at the nest prior to exchanging incubation duties (except during temporary neglect), and often overlap in the nest during provisioning (Brooke, 1990), which may present an opportunity for communication between the pair.

Although we did not find that parents were more likely to change trip strategy depending on whether they overlapped at the nest or not, only 25% of partners did not meet at the nest. Furthermore, we observed that the first parent to arrive at the nest tended to spend longer waiting at it, even accounting for night time hours available, which could indicate parents were waiting for their partner to return to the nest. Parents that were the first to arrive at the nest were furthermore more likely to encounter their partner the longer they waited, though we recognise the circular nature of this result. However, as reported by Tyson et al. (2017), while we found that parents adjusted trip duration considerably more when they visited the colony on the same night as their partner, the magnitude of this adjustment did not depend on parents overlapping at the nest itself. We further found that parents that were experimentally prevented from encountering their partners adjusted their trip durations in the same direction and by the same amount as expected under normal conditions. While the small sample size in our experiment meant we had limited power to detect an effect and therefore reduces the certainty in our conclusions, the alignment of our experimental findings with observational results suggests a role for physical reunion is unlikely.

Alternatively, it is possible that parents physically reunite prior to entering the nest, which would not be detected by our RFID detection system. It has been previously suggested (Congdon et al., 2005) that parents may reunite while at sea. Manx shearwaters form large rafting aggregations in the hours before dusk, which may present an opportunity for such interaction between partners (Brooke, 1990; Richards et al., 2019). However, these rafts form for only a few hours and consist of many thousands of shearwaters, and there is no evidence that individuals raft in consistent locations (see Section 5.6), making this hypothesis unlikely. Furthermore, it has been previously observed that shearwaters returning from long, self-maintenance trips tend to return to the nest immediately following their commute, rather than spend any time rafting (Padget et al., 2019). This may additionally explain our observation that short-trip parents were more likely to arrive at the nest first. Consequently, it is unlikely that parents on opposing trip strategies raft at the same time at all.

Male shearwaters have been observed to be less responsive to changes to chick begging, maintaining similar provisioning rates regardless of chick state (Quillfeldt et al., 2004; Hamer et al., 2006; Dean, 2012) and in both our and Tyson et al.'s (2017) study, altered foraging trip duration to a lesser degree than females, a finding that would be expected if chick begging cues underlie the observed changes in trip duration. This may reflect differential energetic constraints between the sexes: females, which have paid the high energetic cost of producing the egg, may experience an energy deficit during chick rearing (Quillfeldt et al. 2004), which means they experience more constraints on their behaviour. As such, they might be selected to exhibit more responsiveness to chick begging so they can make a more careful trade-off their self-maintenance and provisioning behaviour. This may further explain our finding that males were more likely than females to arrive to the burrow first; if males are under less energetic constraint, they may be freer to return to the colony than females, who may need to maximise their foraging time. However, we could not induce a change in behaviour through our artificial feeding paradigm alone. Similar amounts of food provided at a similar time in previous experiments (Hamer et al., 1998; Hamer et al., 2006; Dean, 2012) have induced changes in parental behaviour, so it is unclear why our feeding manipulation was insufficient to alter parental provisioning rates. However, a key difference between our and previous experiments is that we fed chicks for only a single night. If parents integrate information about the chick over a longer period of time and use this to make decisions about their provisioning behaviour, then this single night of supplementary feeding may have had little influence on parents' perceptions of their chick's hunger state.

Although we did not find evidence for the importance of chick hunger state as a source of information for shearwater parents, other cues may serve as indirect signalling cues. For example, olfaction is known to be ecologically significant to procellariforms (Nevitt, 2008), and may play a social function in some seabirds (Hagelin et al., 2003). It is possible that odour cues provide information on partner visitation to provisioning parents, which our experimental set-up would not emulate. The role of a tactile stimulus, whereby the adult may assess the condition of its chick through, for example, preening, was not explicitly investigated here, however any physical changes to the chick associated with feeding that might be detected through tactile assessment would probably be sufficiently replicated through the supplementary feeding paradigm. However, a mechanism for coordination that involved indirect signalling would require that the long trip parent was the first to return to the nest, so that its partner could infer its return without directly encountering it. Our results did not support such a pattern in parental visitation: conversely, short trip parents were more likely to visit the burrow first. This is perhaps unsurprising, given that parents that are feeding their chick forage closer to the colony, and therefore have less distance to cover (Guilford et al., 2008). Taken together, these results suggest that neither physical reunion at the nest or indirect cues from the chick are necessary to generate the coordinated provisioning strategy observed in Manx shearwaters.

Given these findings, it becomes plausible to consider that apparent coordination during provisioning might actually be the result of some kind of entrainment that develops during incubation and persists into the chick rearing period. This may occur when parents respond in similar ways to environmental variation or changes in their body condition. In Chapters 3 and 4, I found that incubating Manx shearwaters largely sit at the nest until their partner returns, meaning shift duration is ultimately set by the foraging bird, which determines how long to spend at sea based on a combination of its own and its partner's body condition. Over the entire 51-day incubation period, the interdependent contribution of both parents' condition to determining foraging trip duration might give rise to a consistent pattern of alternating incubation and foraging shifts. If similar decision-making processes are employed with regards to parental body condition during chick provisioning, then these patterns may carry over into this period. For example, a pair in which one parent always incubates for 4 days, and the other always incubates for 5, might later be observed to alternate 4 and 5 day shifts of frequent provisioning visits when feeding the chick. This may additionally present an alternative explanation for findings by Tyson et al. (2017) that coordination within pairs decreases with chick age. As parents do not always feed nightly, especially as the chick grows older and is less dependent on frequent provisioning (Hamer et al., 1998), then this could lead to a breakdown in this rhythm over time, as provisioning visits are not subject to the same constraints as incubation shifts. Such a mechanism could be an effective way for parents to maintain largely well-coordinated provisioning visits when the opportunities for direct interaction are reduced by the limitations of chick feeding.

While we were unable to find a role for chick begging cues or parental reunion at the nest in the coordination of provisioning behaviour in the Manx shearwater, it is not clear whether this is because parents use alternative mechanisms to regulate their care, such as olfactory cues or reunion outside of the nest, or because they do not actively coordinate their provisioning behaviour at all. Though the coordination of parental behaviour is clearly widespread (e.g. Johnstone et al., 2014; Bebbington and Hatchwell, 2016; Mariette, 2019; Savage and Hinde, 2019), demonstrating conclusively that this is an active process is not straightforward. Similarities in individual behaviour may lead to synchrony in parental care if, for example, parents respond to environmental or physiological cues in the same way (Schlicht et al., 2016; Savage et al., 2017; Lejeune et al., 2019). The possibility that behavioural coordination at one stage in a breeding attempt may carry over into subsequent stages has not previously been explored. To determine whether this may occur in Manx shearwaters, future work should investigate the relationship between provisioning coordination and adult body condition, and whether the timing of parental shifts on the nest and at sea during incubation translate into similar patterns during the provisioning period.

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5.6 Appendix

To determine whether reunion at sea might be a plausible mechanism by which parents are induced to change foraging trip type, we analysed a long-term dataset of GPS data to examine whether there is individual consistency in rafting locations within years. We hypothesised that if physical reunion occurs outside of the nest, it is most likely to happen during pre-dusk rafting. As the two members of a pair were never GPS tracked simultaneously, it was not possible to examine the rafting overlap of partners. Instead, we used individual repeatability as a proxy: if individuals are consistent in their rafting location, then this presents an opportunity for partners to reliably encounter each other.

GPS loggers were attached to the dorsal feathers of birds using 5 strips of marine Tesa tape (see Guilford et al., 2008 for details). Loggers were programmed to take location fixes every five or ten minutes; for the latter group, five-minute fixes were interpolated to ensure comparability between the tracks. Rafting behaviour was isolated by fitting a mixture model to log(speed) using the `R` package `mixtools` and following methods by Dean et al. (2013) and Richards et al. (2019). This model identified rafting versus other behaviours (such as flying or foraging) based on a threshold of speed.

For each individual foraging trip, we calculated the utilisation distribution (UD) of GPS fixes taken during rafting behaviour. This parameter quantifies the locations used by animals as well as the proportion of time spent in these (Fieberg and Kochanny 2005). We estimated UDs using the `R` package `adehabitat` (Calenge, 2006), and then calculated the overlap between UDs of multiple trips within the same year for each individual using Battacharyya's affinity (Fieberg & Kochanny, 2005), a measure of the similarity between two probability distributions, which ranges from 0 (no overlap) to 1 (complete overlap).

To explore whether there was individual consistency in rafting locations, we used a randomisation to test the null hypothesis that individuals were as likely to overlap with their own rafting locations as the locations of random birds in the population. The null distribution of rafting overlap was calculated by randomly reassigning bird identity within each year without replacement, and calculating the mean overlap across the random population sample. We used 10000 permutations, and calculated the proportion of permutations in which the calculated mean population-level overlap exceeded the observed value.

Individual Manx shearwaters did not appear to show consistency in their rafting ranges. The mean individual overlap in rafting location within years was 0.0086 as measured by Battacharyya's affinity. Individual spatial consistency did not differ from a null expectation of random foraging locations (p = 0.92).

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6

Allopreening in the black-browed albatross *Thalassarche melanophris*: an exploration of patterns and possible functions

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Contents

6.1 Abstract

The functions of display between breeding pairs of animals have been given little attention outside of sexual selection. Yet evidence suggests that display between partners is in fact most commonly observed following mate choice, and is often just as elaborate. In many bird species, allopreening, when one member of a pair preens the other, is a major component of display both pre- and post-pair formation. Despite this, there has been little investigation into its functions. Explanations that have been put forward tend to focus on its role in feather hygiene, which has limited phylogenetic support, or its function in the maintenance of the pair bond, though how this might occur or indeed what this actually represents has not been adequately explained. Phylogenetic evidence reveals that allopreening is most commonly observed in those species exhibiting high levels of partner retention and biparental care, and it appears to be functional in maintaining cooperation in parental behaviour in at least one species. In our observational study, we explored the patterns and putative functions of allopreening during the nest-relief displays of breeding pairs of Black-browed Albatross during incubation and chick-provisioning. Allopreening was an important feature of displays, constituting 30% of display time. We found that the bird returning from its foraging trip usually initiated allopreening, and preened more than its partner prior to changeover of nesting duties. We further found a positive relationship between the amount of time the pair spent in display and the duration of the subsequent foraging trip, providing tentative support for a function in maintaining cooperative parental behaviour between the parents. While we cannot be conclusive in its exact functions, we add to a limited literature the first exploration of functions for this conspicuous behaviour in albatrosses.

6.2 Introduction

Despite more than a hundred years having passed since Huxley's first observations that intra-pair display is more commonly observed after than before pair formation (Huxley, 1914), pair display often remains viewed through the lens of sexual selection (Griffith, 2019). Consequently, the functions of displays occurring after mate choice has been made (hereby post-pair formation display) remain poorly understood. Post-pair formation displays can be every bit as elaborate as those seen during mate choosing, from the post-nuptial displays of great crested grebes *Podiceps cristatus* that initially piqued Huxley's interest, to the private duets of zebra finches *Taeniopygia guttata* as they exchange incubation duties (Elie et al., 2010). While such displays have historically been explained with reference to the intangible 'maintenance of the pair bond' (Harrison, 1965), this in itself requires ultimate explanation, and few authors have attempted to explain exactly how display contributes to this maintenance, or indeed what the bond actually represents (Wachtmeister, 2001).

In birds, one of the more common forms of post-pair formation display is the nest-relief ceremony (Wachtmeister, 2001), in which one parent returns to the nest to relieve the other of its parenting duties. These displays are common in socially monogamous, biparentally-caring species, and may include bouts of allopreening (common guillemot *Uria aalge*, Takahashi et al., 2003), vocalisation (Manx shearwater *Puffinus puffinus*, Brooke, 1990), and 'dance' postures, such as ritualised bowing (pied avocet *Recurvirostra avosetta*, Makkink, 1936) or wing-flapping (wandering albatross *Diomedea exulans*, Jouventin and Lequette, 1990). For such species, in which pair bonds persist over long time periods, the breeding success of parents is largely interdependent, ultimately leading to highly aligned lifetime reproductive output (Griffith, 2019). Consequently, parents may benefit from coordinating their behaviour to maximise the benefit to cost ratio of providing care from the perspective of both parents (Mariette & Griffith, 2015; Pilakouta et al., 2018). Intra-pair communication can help parents achieve this coordination, and may manifest in post-pair formation display. Through such displays parents may, for example, signal their state to the partner to stimulate a change in its behaviour. This appears to be the case in great tits *Parus major*, where the incubating female vocally communicates her hunger to the male to stimulate him to feed her more, so that she can reduce her own foraging effort (Boucaud et al., 2016b). Communication may also facilitate direct negotiation: blue-footed boobies *Sula nebouxii* ultimately come to a collaborative decision on where to lay their eggs by negotiating their nesting site preferences through ‘nest-pointing’ displays (Drummond et al., 2002). Finally, displays may stimulate individuals into reproduction or caring tasks (Wachtmeister & Enquist, 2000), which may facilitate coordination by ensuring synchrony in breeding activities.

Allopreening, in which one individual preens the feathers of another, is often incorporated into displays both pre- and post-mate selection (Wachtmeister, 2001). Allopreening may play a hygienic role through the removal of ectoparasites, as has been experimentally investigated in some species (e.g. rock pigeons *Columba livea*, Villa et al., 2016; *Eudyptid* penguins, Brooke, 1985), or help maintain feather condition by protecting against breakage and facilitating the distribution of preen oil (Clayton, 1991). However, its restricted phylogenetic distribution suggests any such function must be secondary to its ancestral purpose (Harrison, 1965). Furthermore, phylogenetic analysis (Kenny et al., 2017) reveals no association between allopreening and colonial living, which would be expected if allopreening had originally evolved to fulfil a hygienic function. Both allopreening and its mammalian counterpart, allogrooming, have been found to reduce stress in a variety of taxa, including Brunnich’s guillemot *Uria lomvia* (Kober & Gaston, 2003), ravens *Corvus corax*, (Stöwe et al., 2008), horses *Equus caballus* (Feh & de Mazierès, 1993), and crested black macaques *Macaca nigra* (Aureli & Yates, 2010). However, it is not clear how or why allopreening would evolve to elicit such a response. Social functions for allogrooming in mammals have been well-explored, particularly in the primates (Dunbar, 1991), and increasing evidence is emerging for the importance in birds of its counterpart, for example when forming and maintaining social bonds (Morales Picard et al., 2020), establishing dominance (e.g. large-billed crows *Corvus macrorynchos*, Miyazawa et al., 2020), forming pairs (e.g. Eurasian wren *Troglodytes troglodytes*, Gill, 2012), and as an appeasement behaviour (e.g. common guillemots, Birkhead, 1978). However, the possibility that allopreening functions in maintaining cooperation in behaviour has been little explored. A study of allopreening in common guillemots revealed the first evidence that it may serve a cooperative function (Takahashi et al., 2017). Parent guillemots that return to the nest without food for the chicks spent more time preening the partner, and birds whose partners took longer to take over nesting duties delayed allopreening, suggesting it may serve a dual appeasement and punishment function. Allopreening has additionally been linked to partner retention between breeding seasons (Gill, 2012) and high levels of parental cooperation (Kenny et al., 2017), further hinting at a social and potentially cooperative function of this behaviour.

Allopreening is a common behaviour in the black-browed albatross *Thalassarche melanophris* that can be observed during initial pair formation, between paired individuals throughout the breeding season, and between parents and offspring (Tickell, 1984). While allopreening albatross tend to focus on the head and nape of their partners, as is the case in other species (Harrison, 1965), direct observations conducted by Tickell (1984) did not report any evidence of individuals removing lice or ticks from their partners during allopreening, suggesting this is not its primary function, though this is yet to be experimentally tested. As is characteristic of the Procellariiforms, albatross are long-lived, have stable, long-term pair bonds, and care for their offspring cooperatively with their partner (Tickell, 2000). That paired individuals continue to allopreen following their reunion at the beginning of the season and throughout breeding raises the prospect that allopreening may function to encourage or facilitate parental care. While some evidence from other species points to mechanistic explanations for how this could operate, for example by stimulating the productions of hormones such as oxytocin or prolactin (Keverne et al., 1989), or by reducing stress levels (Schino et al., 1988), functional hypotheses have been less explored, particularly in birds.

During incubation and brood guarding, parent black-browed albatross engage in conspicuous nest-relief ceremonies displays as they exchange parenting duties with the partner. While these displays comprise many other behaviours, such as vocalisation and ritualised dance postures, the predominant behaviour is allopreening, on which this study is focused. Previous phylogenetic analyses reported that allopreening is associated with cooperative parental care (Kenny et al., 2017). Using a field-observation approach, we investigated the possibility that allopreening may serve such a function in black-browed albatross, which as long-lived, socially monogamous birds, should be selected to care cooperatively with their partners (Griffith, 2019). We describe the patterns of allopreening observed between reuniting parent albatross during late incubation and early brood guarding, and between parents and offspring following hatching, and consider the potential drivers and functions of its observed variation. We additionally consider allopreening observed between adults and chicks, and investigate whether this may form part of the nest-relief display. Levels of allopreening have been found to vary with sex (Zolnierowicz et al., 2016; Miyazawa et al., 2020), have been linked to partner retention (Gill, 2012; Kenny et al., 2017), and may vary with age and breeding experience (Lanctot et al., 2000; Perrot et al., 2016). In this observational study, we investigated whether these factors predict the duration of allopreening bouts and nest-relief displays in the black-browed albatross. We additionally explored whether these displays may facilitate information transfer, which may ultimately indicate a cooperative function, by investigating the relationship between display time and foraging trip duration.

6.3 Methods

6.3.1 Study site

This study was carried out on New Island, Falkland Islands (51°43’32”S, 61°17’55”W), where individually marked black-browed albatross have been monitored since 2003. Between 6th December 2019 and 10th January 2020, encompassing late incubation and early chick rearing, which in this species lasts 68-71 and 120-130 days respectively (Tickell, 2000), adult attendance was monitored daily in 114 nests in which both parents were marked with a coloured plastic ring, permitting identification at a distance. The sex of birds had been previously identified through the observation of sex-specific pre-incubation behaviours or through molecular techniques using DNA from blood samples. For 74 nests, pairs had been monitored for multiple years and so their pair experience, taken as the number of years both birds had been observed breeding together, could be determined. The age of eggs and chicks was taken as the number of days since laying and hatching respectively.

6.3.2 Observations

A total of 99 nest-relief displays were observed. Observations were conducted between the hours of 09:00 and 20:00 (Falkland Islands Standard Time) by a single observer. Approximately 6 hours of observation was conducted per day, usually split into two shifts; a mean of 2.8 displays were observed per day. Due to the small size of the colony and its sloped topography, all nests could be observed from a single viewpoint. Behavioural data were collected during the nest-relief displays of pairs, when the previously foraging parent returns to the nest to relieve its partner from parenting duties (incubating the egg or brooding the chick). Data collection began from the moment the incoming bird was sighted near to the nest to the moment its partner was deemed as departed from the colony, either because it had taken off into flight or because it had walked out of sight. The time between the arrival of the incoming bird at the nest and the point at which the departing bird ceased interaction with its partner was recorded as ‘total display time’. Whenever the incoming bird arrived at the colony, the observer commenced data collection while simultaneously changing position to be within 1-2m of the target nest for the duration of the recording period. At this distance, pairs did not respond to observer movements (*pers. obs.*). This movement took less than one minute and observation was possible throughout, so important behaviours were unlikely to be missed. Allopreening was identified as any preening directed at either the partner or chick. For any bout of allopreening, the duration and recipient was manually recorded in real time using a pencil and notepad, and a stopwatch to record duration, for both parents simultaneously. Any switch or pause in behaviour that lasted longer than a second indicated the end of a single bout. The time at which parents physically exchanged duties (indicated by swapping positions on the nest) was recorded, and is henceforth referred to as the ‘changeover’.

The duration of foraging trips was determined as the number of days between sequential sightings of an individual albatross at the nest, i.e. the total number of consecutive days that that individual was not seen on the nest. Mean foraging trip duration is 5.2 days (range: 0.3-11.3 days) during incubation and 1.9 days (range: 0.1-6.3 days) during chick provisioning (Granadeiro et al., 2018), and so while it is possible that adults returned to the nest outside of the observation window, and so the duration of the trip in hours would not be known, number of days is a valid proxy for trip duration (Weimerskirch et al., 1994).

Allopreening between adults and offspring was observed during nest-relief displays and sporadically when parents were alone with the chick during brooding. We investigated whether there are qualitative differences in chick-directed allopreening between these contexts that may indicate a role for this behaviour in the display. To this end, we collected data on the number of chick-directed allopreening bouts during nest-relief displays. We additionally estimated the frequency at which chick-directed allopreening occurs when parents are alone during brooding, using an instantaneous scan sampling method. Between the 1st and 10th January 2020, we scanned the entire colony opportunistically in three-to-five-minute bouts per day during the observation window, and counted the number of brood guarding parents that allopreened their chicks in this time. We converted the resulting number of parents observed allopreening to a proportion of total nests in the colony where the adult was brood guarding. These frequency data were collected over 31 bouts.

6.3.3 Environmental data

Wind conditions at sea are likely to affect the duration of foraging trips in albatross (Wakefield et al., 2009), and so we accounted for this in our models of trip duration. Crosswind and tailwind components were reasoned to be the most important components of the wind, based on an *a priori* expectation as to effects of the interaction between wind and a shear-soaring flight mechanism (Pennycuick, 2002; Sachs, 2004; Paiva et al., 2010; Ventura et al., 2020). Estimated wind data for the colony location were downloaded from the NOAA Global Forecast System at a spatial resolution of 0.5 degrees and a temporal resolution of 3 hours using the `R` package `rWind` (Fernández-López & Schliep, 2019). For each bird a likely crosswind and tailwind component was calculated for its at-sea duration assuming travel to the most likely feeding locale around Staten Island (southern Argentina; Catry et al., 2013). It was further hypothesised that weather conditions at the colony may affect display behaviours. To this end, qualitative data on weather were collected each morning and afternoon of observations, using the simple categorisation of ‘overcast’, ‘sunny’, ‘showers’ or ‘fog’.

6.3.4 Statistical analysis

Statistical analyses were completed in `R` version 3.51 R Core Team, 2018. The `R` package `lme4` (Bates et al., 2015) was used to construct linear mixed effects models (LMMs) and generalized linear mixed effects models (GLMMs), and p-values were obtained by comparing full models containing all variables to null models without the effect of interest, using a likelihood ratio test. Visual inspection of residual plots was used to assess model fit. For categorical variables with more than two levels, least squares means for each level of the factor were calculated using the `R` package `emmeans` (Lenth et al., 2018). Data are presented as means ± standard error. For brevity, model structures are presented in Table 6.1. All models were fitted with a random intercept for individual (Ring), pair identity (Pair), or individual nested within pair identity (Pair:ring) as appropriate, to control for repeated measures. We additionally included the fixed effects of sex, age, and breeding experience (in years) which we identified as factors possibly influencing behaviour.

We investigated which variables explain the amount of time spent allopreening by individuals (Table 6.1, model 1), by the pair as a whole (Table 6.1, model 2), and between parents and offspring (Table 6.1, model 3).

To investigate whether sex or the breeding experience (in years) of individuals influenced the amount of time they engaged in allopreening, we fitted a binomial GLMM to the time an individual spent allopreening its partner, calculated as a proportion of the total allopreening time in the display, as a function of sex and breeding experience (Table 6.1, model 1). Individuals for which any of these variables were unknown were excluded from the analysis, leaving n = 320 observations for 104 individuals. Allopreening time may differ depending on whether the bird is arriving to or departing from the nest, and might additionally vary before and after physical changeover on the nest. We accounted for this by including the fixed effects of 'position' (incoming vs outgoing bird) and 'timing' (pre- or post-changeover).

'Total allopreening time' was taken as the summed duration (in seconds) of all allopreening bouts by both parents in a single display. We investigated whether total allopreening time varied with breeding experience of the pair (in years), historical breeding success (chicks fledged per breeding attempt) or sex of the outgoing bird by fitting an LMM (Table 6.1, model 2) that included these variables as fixed effects. Nests were excluded from the model dataset if these variables were unknown, giving a total n of 78 observations for 50 nests. To account for differences between incubation and chick provisioning, we additionally included 'breeding stage' as a fixed effect.

We investigated whether and which factors predicted the number of chick-directed allopreening bouts instigated by each parent. We fitted an LMM to the number of bouts using the predictors of sex and whether the bird was arriving at or departing from the nest (‘position’; Table 6.1, model 3) for nests in which we had data on displays during chick rearing (n = 168 observations for 43 nests). We included ‘total display time’ as a fixed effect to account for the amount of time available to parents to allopreen their chicks.

We were further interested in what factors predict variation in total display time (Table 6.1, model 4) and foraging trip duration (Table 6.1, model 5). We hypothesised that if nest-relief displays facilitate information transfer between the pair, then we would observe a relationship between the duration of the display and the duration of either the preceding or subsequent foraging trip. A relationship with the duration of either trip might indicate a negotiation process between the parents, where each signals its condition to allow a decision to be made on optimal trip length. For example, departing parents in poor condition could signal this to their partner to indicate that they require a longer stint at sea. Evidence for prior ‘planning’ of foraging trip duration has been reported for Manx shearwaters *Puffinus puffinus* (Guilford et al., 2008), where parents that embarked on long foraging trips were already found further from the colony than those on short trips on the first day of foraging.

For models 4 and 5, we included only those nests for which previous trip duration was known (n = 49). As only 16 nests had more than one observation, we randomly selected one observation from each of these nests, so that each of the 49 nests was represented in the dataset only once. We first fitted a linear model (LM) to total display time (minutes) as a function of the duration of the previous foraging trip in days (‘previous trip’; Table 6.1, model 4). As display time may also vary with breeding experience of the pair, historical breeding success, breeding stage, offspring age, and sex of the outgoing bird, we included these variables as fixed effects. The effect of age may differ between eggs and chicks, and so we included an interactive effect between age and breeding stage. We then fitted an LM to subsequent foraging trip duration (days) as a function of total display time (minutes) and total allopreening time (seconds; Table 6.1, model 5). As before, we controlled for experience, breeding stage, historical breeding success, offspring age, and sex of the outgoing bird. As consecutive foraging trips are likely to be correlated in length, we also included the fixed effect of previous trip duration. Finally, environmental conditions are known to affect foraging trip duration in black-browed albatross (Wakefield et al., 2009). To control for this, we included the environmental variables of crosswind, headwind, and qualitative weather (see Methods, Environmental Data).

Table 6.1: Model structures used in the analysis.

Type	**Model**	**Parameters** ***Response***	***Fixed***	***Random***
Binomial GLMM	1	Individual proportion of time spent allopreening	Position*timing + sex + breeding years	Pair:Ring
LMM	2	Total preening time (sec)	Years + success + stage + sex	Pair
	3	Number of chick-directed preening bouts	Position + age + sex + total display time	Pair:Obs ID
LM	4	Total display time (mins)	Years + success + stage*age + sex + previous trip	
	5	Foraging trip duration (days)	Years + success + stage*age + sex + total display time + total allopreen time + previous trip + stage*total display time + crosswind + headwind + qual	

Notes – *position* = whether the bird was 'incoming' or 'outgoing' from the nest; *timing* = timing in the display, either pre- or post- changeover; *sex* = male or female; *breeding years* = years individual observed breeding; *years* = years pair observed breeding together; *pair* = pair identity; *ring* = bird identity; *success* = historical breeding success, number of chicks fledged per breeding attempt; *stage* = breeding stage, incubation vs chick brooding; *total display time* = time from arrival of incoming bird to cessation of pair interaction; *age* = age of offspring relative to hatch date in days; *obs ID* = unique identity for each changeover display; *previous trip* = duration of foraging trip that ended in changeover; *total allopreen time* = total time spent preening during display; *qual* = qualitative weather. Foraging trip duration refers to the trip immediately following the nest relief display

6.4 Results

Displays in which the exact timings of changeover were not known or where foraging trip duration was unknown were excluded from the analyses, leaving 91 displays across 63 nests. Across all displays, the incoming bird was female in 49% of observations, and male in 51% of observations.

Of the 91 nest reliefs observed, 90 involved display, which lasted for an average of 23.3 ± 19.0 minutes (range: 3 – 101 minutes). In the single nest relief that did not involve display, the sitting bird left the nest immediately following its partner's arrival at the colony. Allopreening was observed in all 90 of these displays, and constituted a mean of 26.7 ± 16.2% of display time (range 0.26 – 79.33%). Anecdotally, it was observed that this tended to focus on the head or neck of the bird, but it was not clear that any birds attempted to target ectoparasites specifically; in some cases, parasites visible by an observer at a 1-2m distance were on occasion seemingly ignored by the allopreening bird (*pers. obs.*). Individual bouts of allopreening lasted 16.1 ± 23.4 seconds, and each display comprised 27.1 ± 26.2 bouts.

In 62% of displays, the incoming bird initiated allopreening, in 26% the outgoing bird initiated, and in 12% both birds began allopreening simultaneously. Following the changeover, the incoming bird resumed allopreening first in 64% of displays, the outgoing bird resumed in 28% of displays, and both birds simultaneously resumed in 8% of displays.

6.4.1 Model 1 – Individual allopreening time

The proportion of time individuals spent allopreening during the display was best predicted by an interaction of whether the bird was incoming to or outgoing from the nest, and whether allopreening occurred before or after changeover (Figure 6.1; $\chi^2 = 12475.05$, $df = 1$, $p < 0.0001$). Prior to changeover, incoming birds spent a greater percentage of the display allopreening than departing birds (incoming: 5.27 ± 0.84%, outgoing: 0.24 ± 0.042%). This reversed following changeover, when outgoing birds were found to spend more time allopreening than incoming (incoming: 2.41 ± 0.39%, outgoing: 4.44 ± 0.72%). Females spent a greater proportion of their time engaged in allopreening than males (female: 2.97 ± 0.63%, male: 1.26 ± 0.28%; $\chi^2 = 8.29$, $df = 1$, $p = 0.0040$). The number of years an individual had been observed breeding had no effect on the time they spent allopreening ($\chi^2 = 0.92$, $df = 1$, $p = 0.34$), and allopreening times were not repeatable at the level of individual (104 observations across 44 individuals, $r = 0 \pm 0.022$, $p = 0.50$).

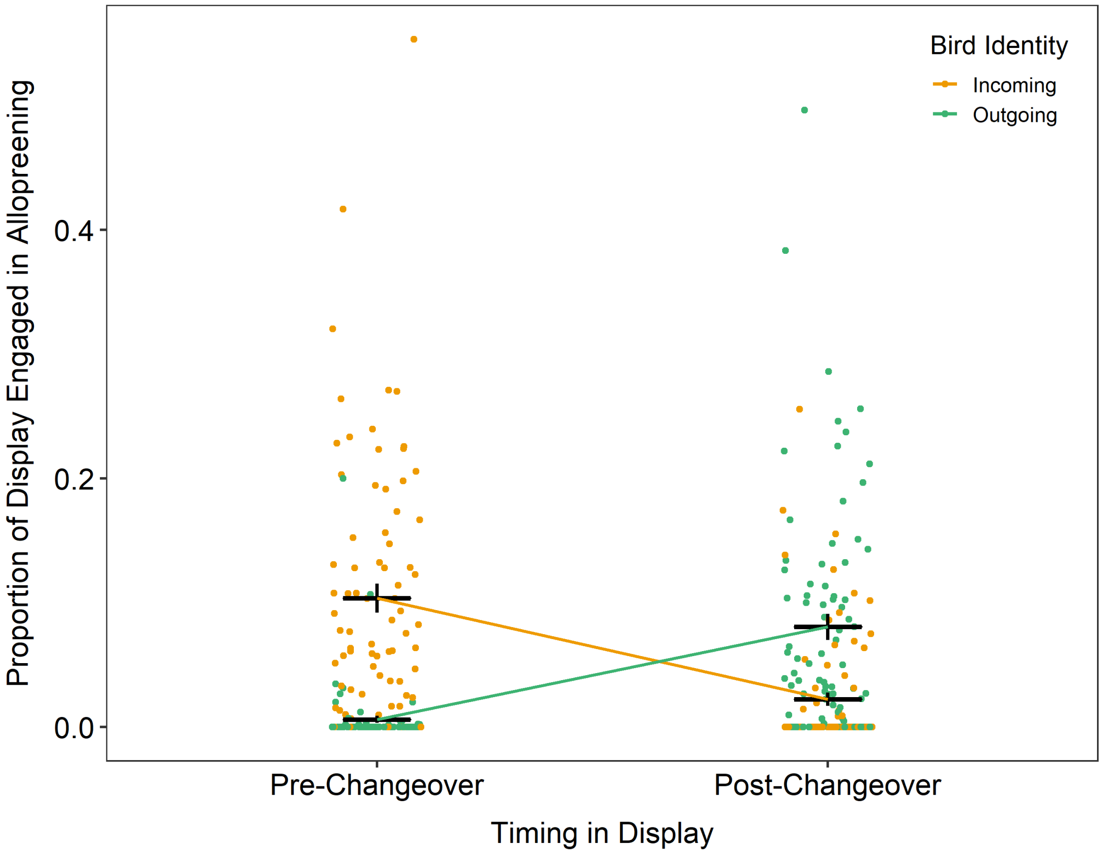

Figure 6.1: Proportion of total display time spent allopreening prior to changeover and following it for the incoming (orange) and outgoing (green) parents. Black crosses indicate mean (horizontal line) and standard error (vertical line). Data points are ‘jittered’ horizontally for readability.

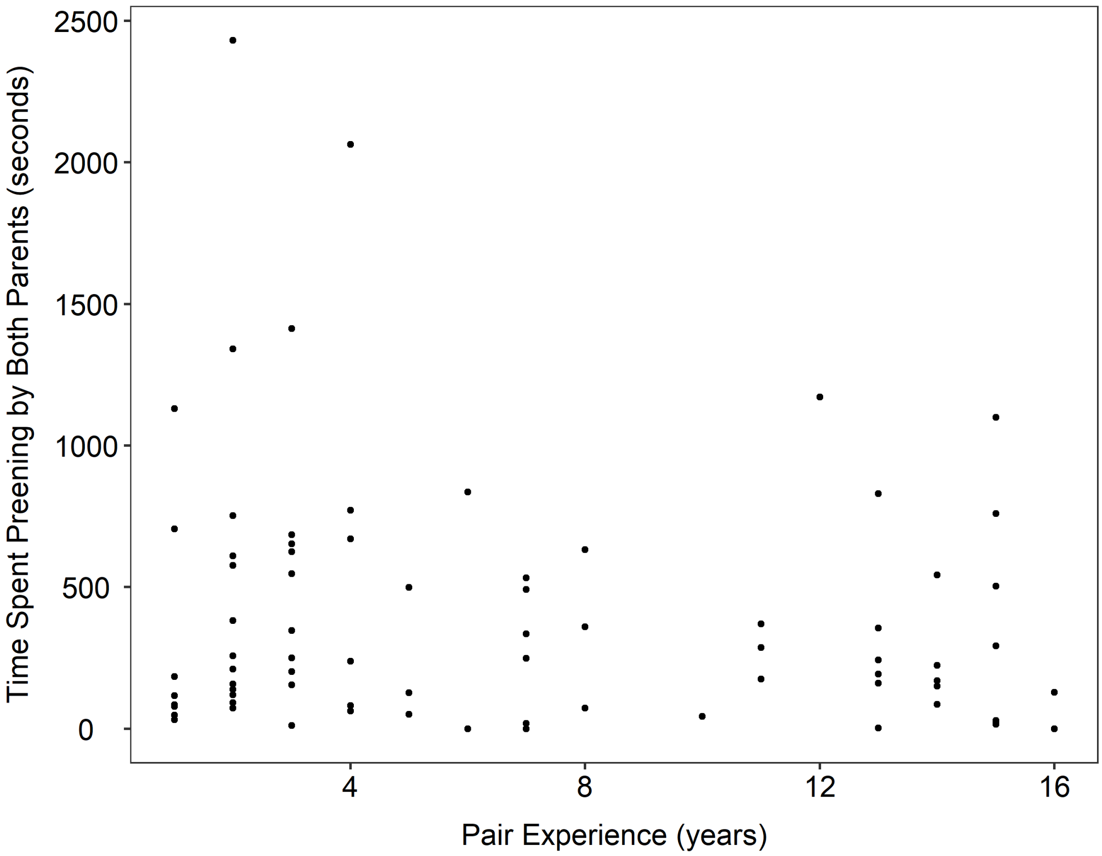

Figure 6.2: Total time spent preening by both parents in seconds according to pair breeding experience (years). Shaded area gives confidence intervals.

6.4.2 Model 2 – Total allopreening time

The amount of time pairs spent allopreening did not vary with the length of time the pair had been together (Figure 6.2) nor historical breeding success, and there was additionally no effect of sex of the outgoing bird (Table 6.2). Incubating pairs spent significantly more time allopreening than brooding pairs (incubating: 872 [700, 1044] seconds; brooding: 236 [139, 333] seconds).

Table 6.2: Test statistics and coefficient estimates from likelihood ratio test on LMM estimating predictors of total allopreening time (seconds). Significant variables in bold.

Variable	χ^2	*df*	p**-value**	**Estimate**	**Std. Error**
years	2.57	1	0.109	-12.63	8.067
success	0.33	1	0.56	-106.24	189.93
stage (egg)	**36.57**	**1**	**< 0.0001**	**636.34**	**96.29**
outgoing sex (M)	0.35	1	0.35	-48.30	83.99

Notes – *years* = number of years pair observed together; *success* = historical breeding success, chicks fledged per breeding attempt; *stage* = breeding stage, incubation vs brood guard; *outgoing sex* = sex of departing parent

6.4.3 Model 3 – Chick-directed preening

Of the 68 displays that took place during chick rearing, 83.3% involved some allopreening of the chick. The amount of preening varied significantly depending on whether it was provided by the incoming, outgoing, or both parents (Table 6.3), with incoming birds providing more bouts of allopreening than outgoing parents (incoming: 5.68 ± 0.37 bouts; outgoing: 0.35 ± 0.37 bouts) and simultaneous allopreening by both parents making up the fewest number of bouts (0.32 ± 0.37 bouts). There was no effect of sex, age, or total display time on the number of bouts (Table 6.3).

Parents were frequently observed to preen chicks when alone during brood guarding. During our daily preening observations, the number of nests in which the chick was being brood guarding varied between 19 and 79 with a median of 43. On each day in any 5 minute interval, a median of 14.1% of adults could be observed to preen their offspring (range = 8.5 – 18.4%).

Table 6.3: Test statistics from likelihood ratio test on LMM to investigate significance of fixed effects on number of chick-directed allopreening bouts. Significant variables in bold.

Variable	χ^2	*df*	p-value	Estimate	Std. Error
position (incoming)	**106.49**	**1**	**<0.0001**	**5.36**	**0.49**
position (outgoing)				**0.033**	**0.49**
sex (M)	0.22	1	0.64	-0.18	0.40
age	3.61	1	0.057	0.070	0.037
total display time	0.43	1	0.51	0.015	0.023

Notes – *position* = driver of chick allopreening, either incoming, outgoing, or both parents; *sex* = male or female, for simultaneous preening represents sex of incoming bird; *age* = offspring age; *total display time* = total duration of display in minutes

6.4.4 Model 4 – Display duration

There was no effect of sex of the outgoing bird, previous foraging trip duration, pair experience, or the interaction of breeding stage and offspring age on display duration (Table 6.4). Displays during incubation were significantly longer than during chick rearing, at 59.61 ± 20.8 minutes versus 15.98 ± 2.69 minutes for chick rearing.

Table 6.4: Test statistics and coefficient estimates from ANOVA to investigate significance of fixed effects on total display time. Significant variables in bold.

Variable	t	p-value	Estimate	Std. Error
years	0.057	1.0	0.027	0.47
success	0.92	0.37	9.39	10.27
stage (egg)	**3.38**	**0.0016**	**36.16**	**10.71**
age	-0.50	0.62	-0.19	0.38
stage*age	0.61	0.55	0.92	1.52
outgoing sex (M)	1.88	0.067	8.82	4.69
previous trip	-0.71	0.48	-0.89	1.25

Notes – *years* = number of years pair observed breeding together; *success* = historical breeding success, chicks fledged per breeding attempt; *stage* = breeding stage, incubation vs brood guard; *age* = offspring age; outgoing sex = sex of departing parent; *previous trip* = duration of preceding foraging trip

6.4.5 Model 5 – Foraging trip duration

There was a significant effect of the interaction between offspring age and breeding stage on the duration of foraging trips (Table 6.5). Mean trip duration for incubating birds was 4.17 ± 1.89 days versus 1.68 ± 0.39 days for brood guarding birds (Figure 6.3a). For each day increase in age, trip duration decreased by 0.58 ± 0.14 days for incubating birds and by 0.0016 ± 0.030 days for brood guarding birds (Figure 6.3b). Total display time significantly predicted foraging trip duration during incubation (Figure 6.4; Table 6.5), with trip duration decreasing by 0.085 ± 0.025 days for each one minute increase in display time for incubating birds, and increasing by 0.0034 ± 0.027 days for brooding birds. There was no effect of sex, pair experience, previous trip duration, total allopreening time, or any of the three weather variables, on trip duration (Table 6.5).

Table 6.5: Test statistics from likelihood ratio test to investigate significance of fixed effects on foraging trip duration (days). Significant variables in bold.

Variable	t	p-value	Estimate	Std. Error
years	0.72	0.48	0.031	0.043
success	0.86	0.40	0.74	0.86
stage (egg)	**4.06**	**0.00040**	**4.46**	**1.10**
age	0.045	0.96	0.0016	0.035
stage*age	**-4.24**	**0.00025**	**-0.58**	**0.14**
outgoing sex (M)	1.14	0.27	0.49	0.43
total allopreen time	1.18	0.25	0.00091	0.00077
previous trip	1.78	0.086	0.21	0.12
total display time	-0.32	0.75	-0.0087	0.027
stage*total display time	**-3.0**	**0.0061**	**-0.076**	**0.025**
headwind	1.79	0.087	0.0034	0.0019
crosswind	0.63	0.54	0.00082	0.0013
qual (showers)	-2.0	0.060	-1.6	0.81
qual (sunny)	-1.41	0.17	-0.79	0.56

Notes – *years* = number of years pair observed together; *success* = historical breeding success, chicks fledged per breeding attempt; *stage* = breeding stage, incubation vs brood guard; *age* = offspring age; *outgoing sex* = sex of departing parent; *total allopreen time* = total time spent preening during display; *previous trip* = duration of preceding foraging trip; *total display time* = total duration of display in minutes

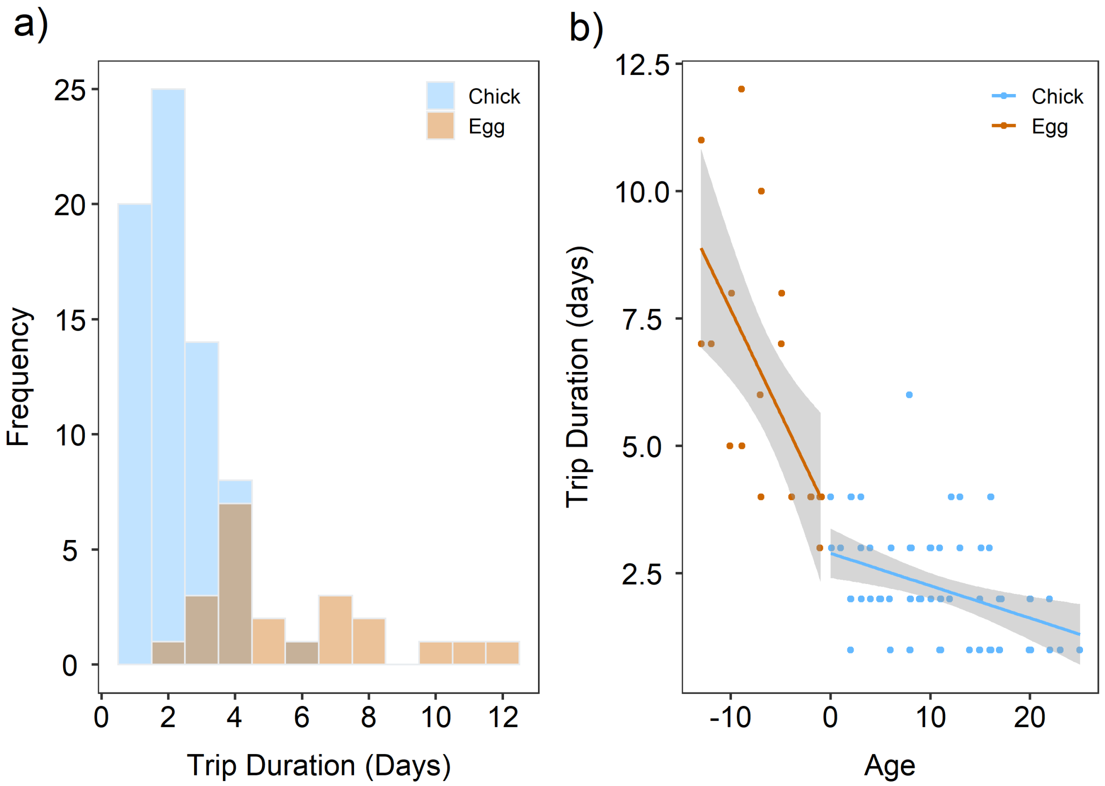

Figure 6.3: (a) Frequency of foraging trip durations for incubating (orange) and chick-brooding (blue) birds. Colours are set with transparency to make all bars visible; darker colours indicate overlapping bars. (b) Relationship between foraging trip duration (days) and offspring age (days) for incubating (orange) and chick-brooding (blue) birds. Shaded areas give confidence intervals.

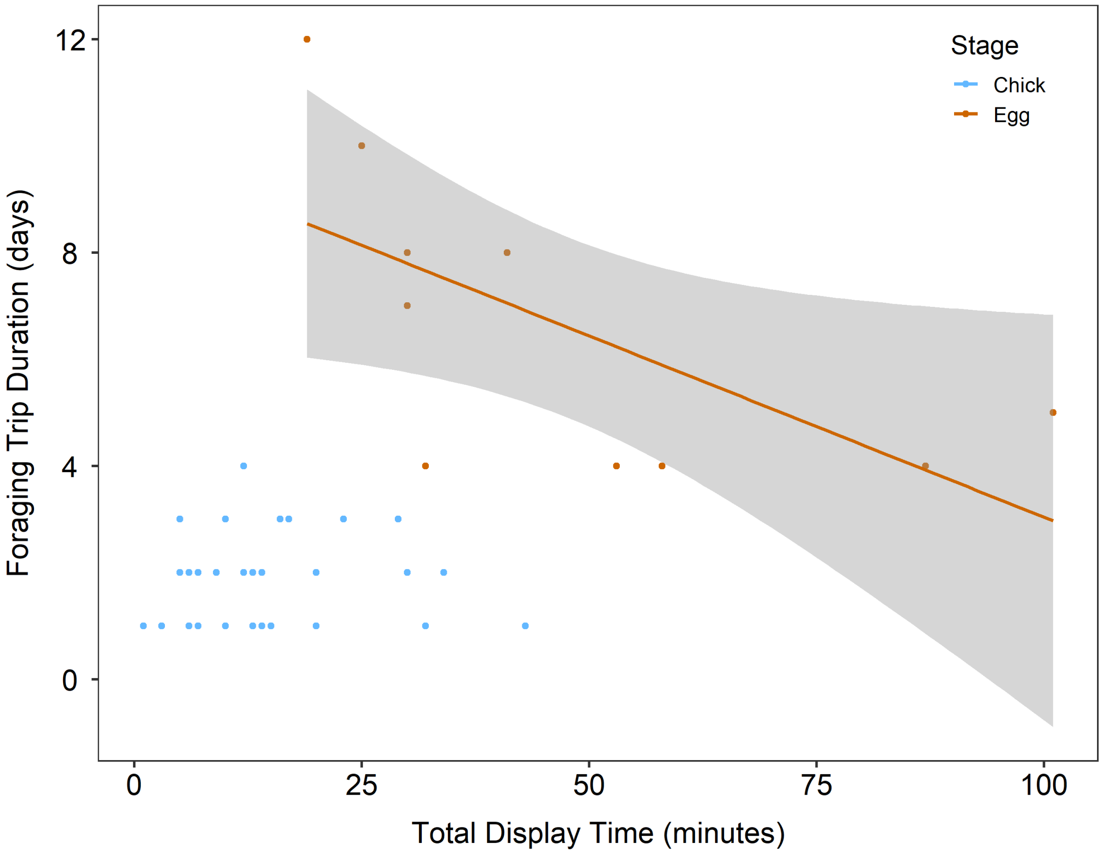

Figure 6.4: Relationship between total display time (minutes) and foraging trip duration (days) for incubating (orange) and chick-brooding (blue) birds. Shaded area gives confidence intervals.

6.5 Discussion

We report tentative evidence that allopreening, which was observed to be a conspicuous feature of nest-relief displays in black-browed albatross, may facilitate parental cooperation over care. For incubating birds, the amount of time spent in display was negatively correlated with the duration of the subsequent foraging trip, but not related to the duration of the foraging trip preceding the changeover. This relationship might indicate that display behaviour facilitates information transfer that may relate to subsequent decisions about foraging trip duration. Both parents directed bouts of allopreening at one-another, sometimes simultaneously, for variable amounts of time. The parent returning from its foraging trip tended to initiate allopreening both during the display and following the switching of parents ('changeover') on the nest. Further, this incoming bird allopreened its partner the most overall, though there was a divide between the pre- and post-changeover periods: following changeover, the outgoing bird allopreened relatively more than its now-sitting partner. Most allopreening focused on the head and neck of the partner, areas that are inaccessible during self-directed preening (autopreening). However, this did not seem to be specifically targeted at ectoparasites, matching previous observational accounts of allopreening in black-browed albatross (Tickell, 1984).

As albatrosses are long-lived and highly socially monogamous (Bried et al., 2003; Burg & Croxall, 2006), pairs are expected to share a large proportion of their reproductive output over their breeding lifespan (Griffith, 2019). Consequently, the benefit to either bird of exploiting its partner by reducing its own care, for example by taking an excessively long foraging trip, is limited, as any costs imposed on the partner are likely to be subsequently shared with the foraging bird. Such costs may be incurred either when the partner takes its own, long foraging trip, which *in extremis* could lead to an increased risk of desertion (Weimerskirch, 1995), or in future breeding attempts if the partner's condition is reduced substantially. As such, conflict between the parents is reduced, and so optimal foraging trip duration is likely to reflect a compromise between the needs of both parents, as has been previously reported for Antarctic petrels *Thalassoica antarctica* (Tveraa et al., 1997) and in Chapters 3 and 4 of this thesis. However, establishing such a compromise requires exchange of information between the two partners.

Recent evidence suggests that nest-relief displays may facilitate such a process in other species. In common guillemots, long nest-relief ceremonies, which are largely made up of bouts of allopreening, are associated with poor body condition of the incoming bird (Takahashi et al., 2017). Conversely, zebra finches *Taeniopygia guttata* that are delayed in their return to the nest engage in shorter changeover duets with the partner and shorter subsequent foraging trips (Boucaud et al., 2016a). Nest-relief displays may serve a similar function in black-browed albatross, allowing the outgoing parent to decide on its optimal foraging trip duration by assessing the status of its partner. That most allopreening observed was delivered by the incoming bird may suggest that behavioural information, such as the incoming partner's ability or willingness to allopreen, is key to assessing partner state, as a physical assessment would probably be reflected in more preening by the outgoing bird. Furthermore, it is unclear how allopreening directed at the head or neck would facilitate physical assessment of condition, as if this were the function, then it may be more logical for the outgoing bird to focus on the body of its partner, which may allow assessment of, for example, fat reserves. Instead, allopreening by the incoming bird may be explained as a mechanism of 'reassurance', whereby the arriving bird signals to its partner a strong confirmation that it is motivated and able to take over incubation duties, reducing the risk of egg abandonment and therefore nest failure. Through this, the outgoing parent can make an assessment of its partner's commitment to engage in parental care.

This may explain the observed inverse relationship between display duration and the length of the subsequent foraging trip. Long-lived species are expected to prioritise future survival and reproduction (Stearns, 1992), and so outgoing parents that are in poor condition would be expected to make decisions that favour their own condition, even at the expense of the current breeding attempt. Consequently, such poor condition parents might have less to gain from assessing the condition of their partner, and will spend less time displaying so they can leave to forage more quickly. These birds will subsequently spend more time foraging while they replenish their lost condition. Conversely, sitting birds that are in good condition are less constrained by this resource trade-off, and so might be less motivated to leave the nest without strong persuasion from the partner that it is ready to take over caring duties. This might manifest in a longer period of display as the incoming bird attempts to convince its partner to exchange places on the nest, followed by a shorter foraging trip as the departing parent does not need to spend as much time at sea to regain mass. Indeed, incubating, and to a lesser extent brooding, adults, were often observed to be extremely reluctant to leave the nest, with changeovers occasionally being initiated when the incoming bird physically pushed its partner off the nest (in our study, such behaviour was observed in 11 of 99 displays). While data on adult body condition were not available in our study, support for this may be seen in the finding that females tended to allopreen more than males. Males are larger than females (Ferrer et al., 2016) and probably in better overall condition as they have not borne the cost of producing the egg (Astheimer et al., 1985). Consequently, they are more likely to be capable of sustaining incubation for longer, which could manifest in greater reluctance to leave the nest. Males and females did not differ in their foraging trip durations, and so would be likely to experience differential costs of incubating that could manifest in such differences in motivation.

Besides behaviour, outgoing birds might make an assessment of their partner using their well-developed olfactory sense, which is an important part of the sensory system of seabirds (Hagelin et al., 2003; Nevitt, 2008). Outgoing birds may use olfactory cues gathered from the head and neck of their partners to detect cues that may indicate foraging success, such as the type or quality of food, and therefore its probable condition. One hypothesis for the functional significance of signal repetition is that it serves to reduce error in the assessment of the receiver (Enquist & Leimar, 1983; Mowles & Ord, 2012). It is possible that the inverse correlation between trip duration and total display time observed here reflects the outgoing bird taking longer to assess the partner when it is in poor condition, and therefore soliciting further allopreening from the partner. If the outgoing bird determines that the partner is in a worse state than normal, then this may encourage it to spend less time at sea and thus to return and relieve its partner earlier, reducing the risk of egg abandonment, which condemns the breeding attempt to failure due to predation in this species (Warham, 1980, *pers. obs.*). However, it is probable that if allopreening functioned in this way, more allopreening would be observed by the outgoing bird. Further research is needed to determine whether behavioural or olfactory cues actually relate to body condition, which would provide the necessary evidence that such a role for allopreening could exist.

For brood-guarding birds, the effect size of the relationship between foraging trip duration and preening time was slightly positive, but small and not statistically significant. Foraging trip durations were considerably shorter during chick rearing, a common strategy observed in seabirds that can help to balance the costs of commuting and the risks of chick starvation when delivering food (Cuthill & Kacelnik, 1990). This may consequently mean less time is available to the parents for display and, by extension, allopreening. Brood-guarding albatrosses experience higher energetic expenditure than incubating adults (Bevan et al., 1995), and so despite their shorter spells on the nest are probably subject to similar constraints as during incubation. Furthermore, if the returning adult arrives with little food available for the chick, it is important that its partner does not subsequently spend long at sea. As such, trip duration may be more constrained due to the competing demands of self-maintenance and chick provisioning, meaning both ‘reassurance’ of a commitment to caring by the partner and assessment of partner condition are probably less important. Indeed, displays were considerably shorter during chick rearing than incubation, and brooding pairs spent significantly less time allopreening than during incubation, suggesting limited value of an information transfer function, if it exists.

Following hatching, allopreening of the chicks by either or both parents became a common component of the nest-relief display. Bouts of chick-directed preening were most commonly observed by incoming birds, which were reuniting with the chick (and partner). Similarly, for parents visiting lone chicks, several minutes of chick-directed allopreening were observed before the parent either began brooding or commenced feeding. This may suggest chick allopreening has a role in reunification, evidence for which has been observed in primates, where temporary separation of mothers and offspring leads to a subsequent increase in grooming behaviour following reunion in a wide range of species (Anderson & Chamove, 1979; Gunnar et al., 1981; Taylor et al., 2015). However, the function of this sort of behaviour is not clear, and, furthermore, brood-guarding parents regularly preened their chicks sporadically during the day, and with no obvious initiating cue.

The functions of offspring-directed allopreening in birds have not been well explored. While evidence for a stress-reducing function of allopreening has been reported for primates (Anderson & Chamove, 1979; Gunnar et al., 1981; Taylor et al., 2015), it is less clear why this would be necessary here. It is possible that allopreening in this case serves a stimulating role or is a way for parents to assess chick need. In some cases, parents arriving to the nest were observed to allopreen the chick for some time, but ultimately did not feed it, generally following a lack of begging response by the chick. As parents brood chicks for several days in some instances, this could be a mechanism to maximise the efficiency of food provisioning by providing it over several days according to chick hunger levels, rather than loading the chick with more food than it can efficiently digest in one go (Cuthill & Kacelnik, 1990; Wright et al., 1998). In this case, therefore, allopreening may serve an assessment function, whereby parents encourage begging from the chicks to determine their hunger levels and ensure optimal food delivery (Weimerskirch et al., 1997). Alternatively, allopreening of the chick may serve a hygienic function. High tick load within black-browed albatross colonies has been found to be associated with increased mortality of chicks (Bergström et al., 1999). While chicks autopreen regularly, allopreening by the parents, to whom more of the chick's body is exposed and which are probably more adept at preening, is likely to be a more effective mechanism of plumage maintenance. However, there is limited evidence that adults are successful at removing ticks either from their partners (Tickell, 1984) or their offspring (Catry, *pers. comm.*). Finally, chick-directed allopreening could in theory provide information to displaying parents, for example by indicating willingness of the allopreening bird to engage in parental care. While the tendency of incoming birds to allopreen the chick the most during displays supports this, that parents continued to allopreen when alone with the chick means this must also play some role outside of display, which is as-yet unclear. Future work should examine how patterns of offspring-directed allopreening change as the chick ages, whether allopreening reduces measures of stress, and whether it correlates with reduced tick load.

In many bird species, reproductive success is seen to increase with duration of the pair bond, even when controlling for possible confounding variables such as age (Emslie et al., 1992; Pyle et al., 2001; van de Pol et al., 2006; Leach et al., 2020). However, the mechanistic basis of this is not well known. Earlier laying (van de Pol et al., 2006), reduced time spent courting (Sanchez-Macouzet et al., 2014), and improved behavioural coordination (Griggio & Hoi, 2011) of more experienced pairs have all been invoked to explain this improvement in breeding success over successive years of mating. We examined whether allopreening varied with pair experience, which might suggest that increased pair bond duration enhances parental coordination. Our results did not support this: the total amount of allopreening observed during the nest-relief display showed no relationship with the number of years that a pair had been observed breeding together. This further suggests that 'maintenance of the pair bond', which would be expected to precipitate some relationship between pair duration and allopreening, is not a satisfactory explanation for the function of this behaviour. Alternatively, a relationship may exist between allopreening and the amount of time parents remain together in the future. To this end, future studies could consider whether pairs that allopreen more are less likely to divorce in subsequent years.

Our observations provide tentative evidence that intra-pair displays between parent black-browed albatross, in which allopreening behaviour is a key component, may facilitate cooperation over parental care. Allopreening by incoming parents may be a mechanism by which arriving birds try to 'convince' their partner to allow them to take over parenting duties, or alternatively might allow the departing parent to assess its partner's condition or success at sea, so it can adjust its foraging trip duration accordingly. To determine which, if either, hypothesis is more likely, future work should investigate how body condition of the parents relates to the amount and patterns of allopreening observed. The phylogenetic distribution of allopreening, as well as previous observations of black-browed albatross (Tickell, 1984) do not support an ancestral role in plumage maintenance, and so we do not suspect this as its primary role. However, we did not investigate this directly and so further experimental work would be needed draw conclusions on the putative hygienic or feather maintenance benefits of this behaviour. The function of other facets of the nest-relief display not investigated here such as vocalisation and dance postures have not been explored. These aspects of display may supplement the reassurance or assessment functions of allopreening suggested here, or may serve altogether different purposes. Many aspects of the nest-relief display incorporate elements seen also in displays between newly-forming pairs. Whilst ultimately allopreening is likely to be multi-functional, our findings suggest for the first time that in this species, it may serve a cooperative function.

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7

Discussion

Contents

Early models seeking to explain the evolution of biparental care systems struggled to reconcile the widespread incidence of this form of parental investment with the prediction that such an approach to caring for offspring would inevitably entail sexual conflict, which would ultimately compromise parent and offspring fitness. A key step towards solving this problem was the development of conditional cooperation models (Johnstone et al., 2014), in which parents took turns to make their investment decisions, allowing them to base their decisions on the prior investment and behaviour of their partner. Such responsiveness of the parents might give rise to emergent behaviour within the pair, which has come to be known as ‘coordination’ (Ihle et al., 2019). In the years following the development of these models, many empirical studies have sought to identify evidence for coordination of parental activities in a range of species.

In this thesis, I investigated the evidence for and potential mechanisms of coordinated parental care in two long-lived seabird species that are presumably under strong selection to cooperate with their partners. In **Chapter 2**, I explored how parenting behaviour can be disrupted by the deployment of GPS, but not GLS, confirming that the latter device is appropriate for the collection of data pertinent to this thesis and providing the first evidence for partner compensation in response to a reduction in care by one parent. In **Chapter 3**, I examined the natural patterns of incubation shifts within a pair and related this to individual and pair behaviour, which was then followed by an experimental approach in **Chapter 4**, where I used a handicapping paradigm to disrupt natural incubation rhythm in a controlled and targeted manner in order to elucidate the specific mechanisms underlying the establishment of this routine. In **Chapter 5**, I investigated coordination during the chick provisioning period. My experimental approach manipulated the information available to provisioning parents in order to determine what cues are important when making investment decisions. Specifically, I explored the possibility that chick begging signals or physical meeting of the parents could underlie the coordination of chick-provisioning behaviour in Manx shearwaters. Finally, in **Chapter 6**, I explored whether intra-pair displays during breeding might function in the coordination of care. Through an observational study of allopreening behaviour in black-browed albatross, I investigated whether this conspicuous, yet poorly understood, behaviour could underlie parental coordination.

In this closing chapter, I integrate the findings of my previous chapters, and discuss the wider implications of my results for our understanding of parental care systems. I explore whether the data presented here support the existence of coordinated care in these birds, what mechanisms may underlie the patterns of care observed, and what might be inferred from this about the maintenance of biparental care more widely. Throughout this discussion, I also note potential extensions or refinements to the work I undertook that could fill the outstanding gaps in our knowledge. Finally, I discuss the limitations of my approaches to this topic, what key outstanding questions remain, and some potential future directions that could help us answer them.

7.1 Do parents coordinate?

Coordination through individualism

Published literature makes a great many references to putative examples of coordinated parental care across a range of species. However, demonstrating that individuals are actually actively responding to the behaviour of their partner (or other carers) is not straightforward, as seemingly coordinated patterns of care may also emerge through the independent behaviour of the two parents. In particular, when considering one of the most commonly observed forms of coordinated behaviour, that is, alternation of nest visits, apparently synchronous alternation can also be driven by purely individual constraints. For example, the need to commute to foraging areas at some distance from the nest may give rise to a refractory period in individual nest visitation that places a limit on inter-visit intervals, which if similar between the parents may lead to apparent synchronicity in behaviour (Ihle et al., 2019). Likewise, parents may respond to environmental conditions in the same way, which could lead to similarities in their behaviour (Lejeune et al., 2019). Indeed, a major criticism of Johnstone et al's (2014) first empirical exploration of conditional cooperation was that similar patterns might be observed if individuals were visiting the nest at random, but are constrained to do so with an inter-visit interval set by their foraging dynamics (Schlicht et al., 2016, though see Johnstone et al., 2016), making it difficult to prove that active coordination occurs in the first place.

Biparental incubation represents a prime example of apparently coordinated care that might actually result from constraints on individual behaviour. As one bird must always be sitting at the nest to ensure the continuous warming of the embryo, coordination may emerge as a by-product of a ’sit-and-wait’ strategy, whereby the sitting bird simply remains at the nest until its partner returns. My results in Chapter 3 lend support to this possibility: I found that the duration of foraging trips was set by the requirement of the departing bird to gain mass, with lighter birds spending longer away from the nest than their heavy counterparts. While foraging birds embarked on these excursions for as long as they needed to recoup their condition, their incubating partners largely continued to sit at the nest and wait for their return. The amount of time that incubating birds were capable of remaining at the nest was found in Chapter 4 to be substantial: despite their being left at the nest for almost twice as long as normal, the partners of handicapped birds did not neglect the egg any more than would be expected under natural conditions. Similarly, the partners of GPS-tracked individuals in Chapter 2 appeared to compensate for their partners' reduced care, leading to comparable breeding success for all device deployment groups. These findings suggest that Manx shearwaters are capable of considerable flexibility in their incubating behaviour, and perhaps indicates that they are not normally driven to their physiological limits of incubation under normal conditions. This may reflect an adaptive strategy whereby parents maintain a 'buffer' of condition that means they are able to sustain an extended period of time at the nest should their partner be detained at sea, due to, for example, adverse environmental conditions or, as was the case in Chapters 2 and 4, an energetic handicap.

That foraging birds are largely in control of the decision-making process is perhaps to be expected, as the duration of foraging trips is probably under more constraint than that of incubation shifts. In many seabirds, it appears that short-duration foraging trips are not optimal for parents who are trying to recoup lost condition. The best evidence for this comes from the widespread employment of a 'dual-foraging' strategy during chick rearing, whereby provisioning parents alternate short, frequent trips to the nest to feed offspring with longer, condition-replenishing trips of several days (Weimerskirch et al., 1997; Congdon et al., 2005; Magalhães et al., 2008; Welcker et al., 2009; Shoji et al., 2015; Wojczulanis-Jakubas et al., 2018; Grissot et al., 2019). The commonly invoked explanation for this behaviour is that spatial heterogeneity in resource availability makes it more energy-efficient for parents to make use of predictable, low-energy patches close to the colony when they need to make frequent visits to the nest to feed their young, then switch to long-distance, less predictable, but richer foraging locales to replenish their own condition when released from the constraint of provisioning. That parents do not use closer patches to the colony to feed themselves suggests there is a benefit to travelling further to exploit more productive locations (Weimerskirch, 2007). Indeed, species for which conditions at sea do not vary considerably in space, including the black-browed albatross (Phillips et al., 2009), often do not exhibit a dual-foraging strategy as there is no spatial dichotomy in resource availability to exploit (Elliott et al., 2009; Karris et al., 2018; Bennet et al., 2019). As such, for most seabirds there is probably a constraint on minimum foraging trip duration that arises because the energy and time costs of the commute would outweigh the foraging gains to be made at nearby sites. Consequently, foraging birds may be limited in the plasticity of their behaviour.

This suggests that a simple and sufficient way to coordinate incubation in many central-place foraging species might be for incubating birds to simply wait at the nest until their partners return, so that the foraging parent has sufficient time to replete its reserves and hence sustain the next bout of incubation. In Manx shearwaters, this might be an effective means to maintain the division of parental labour, exemplified by the low incidence of neglect observed both during my studies and in others (Matthews, 1954; Harris, 1966; Brooke, 1990), in contrast to, for example, the short-tailed shearwater *Ardenna tenuiostris*, in which incubation shift duration is determined by the sitting bird independently of the partner, and where the incidence of neglect is very high (Carey, 2011). Consequently, provided foraging conditions are good and so the excursion of the foraging partner is short enough that the incubating bird is not pushed to its physiological limits, apparently coordinated behaviour could in theory arise without the need for explicit communication or negotiation.

However, a purely-individualistic 'sit-and-wait' strategy for determining incubation shift duration may not be sustainable long-term. Incubation entails high energetic expenditure and a period of fasting, which consequently leads to declining mass for the sitting bird (Vleck, 1981). Even temporary desertion of the egg, which is survivable in some taxa, including the Procellariiforms (Brooke, 1978), imposes costs on the breeding attempt in the form of slowed embryonic growth and increased risk of predation (Ronconi & Hipfner, 2009). Indeed, in Chapter 3, I found that temporary neglect significantly reduced the probability of hatching in Manx shearwaters, as has been reported for other species (Boersma & Wheelwright, 1979; Anderson & Fortner, 1988; Chaurand & Weimerskirch, 1994; Harris, 1997; Fayet et al., 2020). However, no bird will continue to incubate until its energy reserves are so depleted that its survival is materially at risk, and long-lived species in particular should be selected to preserve their own survival above that of the egg, which represents a tiny fraction of its lifetime reproductive output (Ricklefs, 1993). This additionally reduces the benefit to the foraging partner of exploiting the sitting bird by spending more time foraging than it needs to: the longer it spends at sea, the more likely it is that its partner will desert the nest, jeopardising the breeding attempt. Consequently, it is in the interest of the foraging bird to account for the risk of desertion by its partner, as it has a shared stake in the success of the breeding attempt. It is for these reasons that a more cooperative system might be expected to be at play.

Evidence for cooperation

While individualistic rules appear, to some extent, to be sufficient to give rise to the patterns of parental alternation observed during incubation for Manx shearwaters, and possibly other birds, my results in Chapters 3 and 4 hint at the possibility of more nuanced systems of cooperation. While evidence from Chapters 2 and 4 shows that shearwaters can exhibit considerable flexibility in the amount of time they can withstand incubation, it is clear that they will eventually reach a point at which they can no longer sit, and so will desert the egg. The exact determinants of the decision to temporarily neglect the egg appear to vary across species, but there is considerable evidence that it relates to body mass reserves (Dee et al., 1979; Gaston & Powell, 1989; Chaurand & Weimerskirch, 1994; Tveraa et al., 1997; Blight et al., 2010). In Chapter 3, I found that, in Manx shearwaters, the incidence of neglect was best predicted by the starting mass of incubating birds, suggesting that the decision to desert the nest is related to energetic constraints underlain by mass loss. Consequently, the foraging bird, which has the same stake in the breeding attempt as its incubating partner, may benefit from factoring the probabilistic behaviour of its partner into its decision-making processes. I found some support for this idea in Chapter 3, where foraging trip duration was found to be best predicted by a combination of the condition of both the departing bird and its sitting partner. While the gradient of the relationship between trip duration and departure mass was largely constant - all foraging birds take shorter trips the heavier they get - the intercept of this line was determined by the incoming mass of the partner. In other words, foraging birds that left the nest when their partners were heavier would take longer trips than birds of the same mass whose partners were lighter. This key finding suggests that the decisions made by foraging birds as to how long to spend at sea are modulated by the state of their partner.

Further evidence for such a strategy comes from Chapter 4, where I imposed a wing-loading handicap on the foraging ability of Manx shearwaters as they departed the nest. While handicapped birds were observed to take considerably longer foraging trips, probably because the presence of the handicap meant they struggled to gain mass at sea effectively, they still returned to the nest at a lower mass than would be expected, despite having been at sea for more than twice as long as usual. If foraging trip duration (and therefore incubation shift duration) was dictated purely by the energetic requirements of the departing bird, we would expect these birds to forage until they regained their condition to some threshold of mass. Under this mechanism, foraging shearwaters would return from every foraging trip they undertake at approximately the same mass, regardless of the time they have spent at sea. Were birds to employ such a strategy, we would probably expect them to take even longer foraging trips than observed in my study, and for neglect by the partners to be more common, as they are eventually driven to their energetic limits of incubation.

My results did not support the existence of this individualistic strategy, and this led me to describe an alternative hypothesis to explain how foraging birds can make decisions as to how long to spend at sea. In this second mechanism, handicapped individuals do largely forage for as long as it takes to regain their condition, but the threshold of mass that they aim to attain declines over time. In other words, foraging shearwaters gradually reduce their expectations about the gains they can afford to make from the trip as the amount of time they have been away from the nest increases. This would allow parents to take into account the increasing probability of nest desertion by the partner. If such a mechanism were employed by departing birds, we would expect foraging birds to spend more time at sea when they are in poorer condition, but to return to the nest at a lower mass than they would on a shorter trip. These predictions match my findings in Chapter 4.

If foraging shearwaters base their decision as to how long to forage for based at least partially on the condition of their partner, this may suggest that these decisions are made in advance of their departure from the nest. Indeed, previous observations of Manx shearwaters using GPS (Guilford et al., 2008) support the notion that trip duration is decided on departure: the authors found that birds on longer foraging trips were already found considerably further from the colony than those on shorter excursions on the first day of their trip. Taken together, this evidence might support the proposed, more cooperative, mechanism whereby foraging birds consider both their own and their partner's condition when deciding how long to spend at sea: spending longer on their trips (if needed) when their partners are in good condition, and returning earlier if they are not. The evidence so far presents both a rationale and a means by which foraging birds can factor the condition of their mate into their decision-making processes. However, this raises an important point: if this strategy is employed, then this requires information exchange between the parents about metabolic needs and condition. In the following section, I discuss how this might be achieved.

7.2 How is coordination achieved?

The role of information exchange

When individuals behave cooperatively, information exchange about the state or intended behaviour of other collaborators can be a useful way to ensure the optimal coordination of behaviour from the perspective of all involved (Bell et al., 2010). For pairs of animals in which both contribute to the care of their offspring and where parents expect to reproduce again in the future, information exchange can additionally be an effective way to resolve sexual conflict by coordinating joint investment in a way that is beneficial to both parents (Kokko et al., 2001). To ensure its honesty, this is most likely to occur in species where there is a high fitness value to retaining the partner: either because the cost of divorce is high (Culina et al., 2015), repairing is difficult (Choudhury, 1995), or because pairs that have been together for longer enjoy higher reproductive success (Coulson, 1966;

van de Pol et al., 2006; Naves et al., 2007; Sanchez-Macouzet et al., 2014). Where there is little mutual overlap in fitness interests between the parents, there is a risk that information exchange will evolve to cheat the partner into contributing more than its fair share of parental investment, which could ultimately lead to the evolution of a manipulative or coercive system (Dawkins & Krebs, 1987).

Information exchange is particularly important when individuals make decisions about their behaviour in advance (Bell et al., 2010). When parents make decisions reactively based on the previous actions of their partner, such as in the previously-discussed 'tit-for-tat' system of alternation (Johnstone & Hinde, 2006), this may be more effectively achieved by directly monitoring the behaviour of the partner, as this is inherently honest and does not require bidirectional communication. For decisions that take place before individuals actually express their behaviour, this may not be an option. For example, blue-footed boobies *Sula nebouxii* undertake long intra-pair displays when selecting a site to nest at, in which each parent takes turns to indicate its preferred site, and apparently negotiate over this until a mutual decision is reached (Drummond et al., 2002). Similarly, when short-term changes in state are likely to affect individual behaviour, it may be useful for carers to communicate this in advance. Such is the case for hungry pied babblers *Turdoides bicolor*, which signal their state to members of the group so that other group-mates can take over sentinel behaviour when they need to forage (Raihani et al., 2010). Intentional signalling is particularly beneficial when synchrony in the two actors' behaviour is paramount. For example, the speed at which male bluehead wrasse *Thalassoma bifasciatum* move their pectoral fins during their pre-spawning circling displays provides information to females as to when he is about to spawn, ensuring that she can release her eggs at the most opportune moment (Dawkins et al., 1994). While these examples consider mostly short-term behaviours, information transfer may also facilitate decision-making on a longer-term basis. In species where bouts of care tend to be prolonged - for example because incubation shifts are long or because parents take it in turns to provision the chick alone for several consecutive days - such pre-emptive decision-making is probably especially useful because parents will have little opportunity to monitor their partner's behaviour in real time.

Display as a means for information transfer

The function of pair display in long-term monogamous species is a largely neglected area of research, and those studies that have attempted to explore its adaptive significance have primarily focused on its role in achieving physiological synchrony, mate guarding, or territory guarding (Hall, 2004; Dahlin & Benedict, 2014). Yet intra-pair display in such species is particularly interesting, as high mate fidelity can lead to highly aligned fitness interests, which may select for honesty in the signalling system. For species that are likely to breed together for many years, any individual that misrepresents its own condition to induce extra investment by its partner will do so at a cost to its partner's future investment, and therefore both parents' future reproductive attempts. As such, it is possible that these displays serve more cooperative functions. Some evidence suggests that display may facilitate coordinated parental behaviour. In zebra finches *Taeniopygia guttata*, a species in which incubation is highly synchronised, structured duets allow parents to coordinate their shifts effectively (Boucaud et al., 2016a). Similarly, in common guillemots *Uria aalge*, complex relief ceremonies at the nest allow parents to communicate their physiological status so that they can negotiate parenting duties in their own and their mate's interest (Takahashi et al., 2017).

Vocal duets are a form of display commonly occurring in birds in which two individuals make temporally coordinated sounds (Farabaugh, 1982; Hall, 2004). The functions of duets are varied, and may include mate selection, territory and resource defence, and mate guarding (Hall, 2004). Vocal duets commonly occur in mated pairs, and particularly appear to be associated with long-term monogamy (Farabaugh, 1982), which has led some authors to investigate their potential role in cooperative pair behaviour (Elie et al., 2010; Boucaud et al., 2016a). Limited evidence now exists implicating vocal duets in coordination: in great tits *Parus major*, accelerated vocal signals from the incubating bird encourage its partner to return to the nest more quickly (Boucaud et al., 2016b). Similarly, in zebra finches (Boucaud et al., 2016a) and lesser black-backed gulls *Larus fuscus* (Kavelaars et al., 2019), the amount of vocalisation observed within a pair seems to correlate with how equally they share in incubation.

In Chapters 3 and 4, I found that the decision made by foraging birds as to how long to spend at sea depended on the condition of both the foraging bird and its partner. Such a mechanism requires information exchange between the two parents. When parent Manx shearwaters encounter one another at the nest, which almost always occurs during incubation changeovers and often precedes the switching of foraging trip strategy during provisioning (see Chapter 5), they are observed to exhibit prolonged and energetic vocal duets (James, 1985; Brooke, 1990). While males and females show consistent differences in the structure and context of their vocalisations (for example, males are largely responsible for defensive calling from the nest), which suggests it may serve sexual and territorial functions (James, 1985), the function of pair duets that occur in the privacy of the nest chamber are not known. Acoustic communication is a commonly observed behaviour between family members, and it is feasible that it may play a role in the negotiation and coordination of parental care (Mariette, 2019). While I was not able to examine this possibility over the course of this thesis, evidence in other species supports the potential of Manx shearwater duetting in such a role. In the closely related blue petrel *Halobaena caerulea* and Antarctic petrel *Pachyptila desolata*, the structural qualities of male vocalisations convey information about body mass, condition, and identity (Genevois & Bretagnolle, 1994; Gémard et al., 2019). If Manx shearwaters can vocally communicate their physiological state to the partner, this would provide to the departing bird the information that it appears to use to make decisions about foraging trip duration, based on my findings in Chapters 3 and 4. To investigate to what extent Manx shearwater duetting represents direct communication that facilitates information transfer between pairs, future work could utilise recordings of duetting behaviour taken from known pairs during breeding, and relate this to behavioural facets of incubation.

Allopreening is another conspicuous feature of intra-pair display, characterised by the preening of another individual's feathers by a focal bird. Allopreening can aid in ectoparsite removal and feather maintenance (Villa et al., 2016; Goodman et al., 2020). However, it is difficult to reconcile this as an ancestral function with its restricted phylogenetic distribution (Kenny et al., 2017). Allopreening in birds appears to be largely restricted to family or pair members (Gill, 2012; Miyazawa et al., 2020; Morales Picard et al., 2020), which could indicate a social or affiliative function. The mammalian counterpart to allopreening, allogrooming, has been much more thoroughly investigated in terms of its social function, and has been linked to tension reduction (Schino et al., 1988; Aureli et al., 1999), appeasement of dominant individuals (Kutsukake & Clutton-Brock, 2006), and stress reduction (Feh & de Mazierès, 1993; Aureli & Yates, 2010). However, these are all proximate, rather than functional, explanations. Some treatment has been given to the potential function of allopreening in avian social behaviour. However, this has been largely restricted to discussion of the ambiguous yet oft-used phrase ‘maintenance of the pair bond’ (Black, 1996). More recent phylogenetic analyses investigating covariates of the incidence of allopreening behaviour have linked its occurrence to species in which the parents cooperate to raise their offspring (Kenny et al., 2017).

As a species that exhibits extensive allopreening behaviour, in Chapter 6, I investigated the potential social functions for this in breeding pairs of black-browed albatross. I found evidence that the duration of nest-relief displays was inversely related to the duration of the ensuing foraging trip: in other words, departing birds which spent longer displaying with their partner subsequently went on shorter foraging trips. I proposed two key hypotheses to explain this finding: first, that allopreening by the incoming parent serves as a means to convince or reassure the partner that it is willing or able to take over caring duties, and that increased allopreening reflects a sitting parent who is unwilling to leave the nest and requires increased coercion to depart. Secondly, I proposed that allopreening could facilitate instantaneous information exchange about metabolic needs and condition between the pairs. Outgoing birds may use the time spent allopreening to make an assessment about the state or condition of their partner, which could help inform trip duration using a similar mechanism to that proposed to exist in Manx shearwaters. To more conclusively explain my observational findings, data on adult condition would be necessary, as this would allow investigation of the relationship between foraging trip duration and resource availability, which would inform on whether such a mechanism could be at play here.

Indirect cues for information

Where parents have little opportunity to directly communicate, explicit information transfer between the partners may not be possible and so alternative mechanisms of collecting information must be used. This is more likely to be the case during the chick provisioning period, when, despite returning to the colony more frequently, parents spend less time at the nest and so might have less opportunity to interact. To gain information that might be pertinent to coordinating care, parents may in these cases be required to use alternative sources of information. This may be achieved by directly observing the partner as it provides care (e.g. Wright and Cuthill, 1990; Markman et al., 1995; Hinde and Kilner, 2007; Jenkins et al., 2021); by monitoring the behaviour of the partner, parents can make an accurate judgement of their effort and set their own investment accordingly. Alternatively, information can be gained indirectly: Johnstone and Hinde (2006) first proposed that partner effort could be used as an indicator of brood value or need, but the opposite may be true, too: parents may determine the effort of their partner based on the condition or status of the brood (Hinde, 2006). For example, an increase in begging levels from a brood may indicate a reduced work rate by the partner. The provisioning rates of parents are widely reported to be responsive to offspring begging rates, with increases in begging usually (but not always, see Caro et al., 2016) precipitating an increase in feeding. Some studies have addressed this relationship from the perspective of this indicating something about partner contributions (e.g. Hinde, 2006; Hinde and Kilner, 2007; Lendvai et al., 2018), but it is difficult to disentangle whether parents are responding to the behaviour of their partner or the need of their brood, which are highly correlated. One possibility that has not yet been explored in any species is whether offspring cues could facilitate the alternation or synchrony of parental behaviour by informing parents on when their partner has last visited the nest when they otherwise have no opportunity to directly interact.

This is a possibility I investigated in Manx shearwaters in Chapter 5. During the chick-provisioning period, shearwaters employ an alternating foraging strategy, whereby a series of short trips to gather and provide food to the offspring is followed by a long, self-provisioning trip to recoup condition (Shoji et al., 2015; Tyson et al., 2017). This strategy is coordinated between the parents, such that while one parent is away on a condition-replenishing trip, the other continues to feed the chick, reducing the risk both of chick starvation and of over-feeding, which could be sub-optimal to chick growth (Weimerskirch et al., 1994; Tyson et al., 2017). While a switch between the two foraging strategies is initiated following a coincident visit of both parents to the colony on a given night (Tyson et al., 2017), both previous observational results by Tyson et al. (2017) and my experimental findings in Chapter 5 suggest that this does not require parents to coincide in the burrow: parents that are physically prevented from reuniting at the nest still exhibit this switching behaviour on nights where their partner also visited. Instead, I hypothesised that chick begging cues could provide parents with the necessary information to initiate this switch in strategy: parents that encountered satiated chicks, which should therefore not beg (Quillfeldt & Masello, 2004; Hamer et al., 2006), could infer that their partner had made a visit to the nest and adjust their behaviour accordingly. My experimental approach did not support this hypothesis. I found that the parents of fed chicks did not switch foraging trip strategy more than natural controls. Previous experiments invoking supplementary chick feeding have found that artificial feeding is sufficient to induce changes in parental behaviour (Dean, 2012; Fayet et al., 2016; Padget, 2017). Consequently, my failure to find a change in parental behaviour following supplementary feeding is unlikely to reflect a failure of the protocol itself. Instead, other indirect cues may play a role in the decision-making of parents. For example, olfactory cues play an important role in the sensory ecology of seabirds (Nevitt, 2008; Bastos et al., 2020), and, as such, it might be the case that parents can simply smell whether their partner has paid a recent visit to the nest. Future experimental work could investigate whether eliminating the potential to make use of odour cues can disrupt normal patterns of chick provisioning.

Coordination through entrainment

Finally, it is possible that the active patterns of coordination established earlier in a reproductive attempt might extend into other phases of breeding through a process of entrainment. During incubation, the interdependence of the alternating shifts of males and females may lead to consistent shift durations and associated mass changes being exhibited by both parents. If this established pattern were to continue to influence behaviour during chick-provisioning, then apparently coordinated behaviour may emerge as the parents continue to behave according to their pre-established routine. A relationship between levels of coordination during incubation and chick-rearing has been previously reported for Herring gulls *Larus argentatus* (Morris, 1987), which could indicate the existence of such a process. Furthermore, this system could provide an alternative explanation for Tyson et al.'s (2017) findings that the degree to which parents are coordinated in their behaviour declines over the course of the provisioning period: if coordination is a by-product of pre-established behaviour, the lack of active maintenance means we would expect it to break down as time goes on.

A combination of empirical and modelling approaches could help to elucidate this possibility. Firstly, metrics of coordination could be compared between different phases of the breeding season: in birds, this would be most easily captured as coordination during incubation versus chick-rearing. If coordination does emerge through a process of entrainment, then we would expect that individuals that are more coordinated during incubation would continue to be so during chick provisioning. Of course, such a relationship does not necessarily indicate a passive continuation of coordination, and could alternatively reflect some intrinsic quality of the pair. Indeed, it is logical that parents who are better coordinated during one part of breeding should continue to be so later on. To determine with more confidence whether this coordination might emerge as a by-product of entrainment during incubation, a simulation approach could be used whereby the nest-visitation patterns of pairs are simulated using data collected during incubation, and the emergent patterns observed to see how well these map onto real behaviour. If coordination during provisioning is a consequence of coordinated incubation, then these simulated behavioural patterns should largely match the real patterns of provisioning parents.

7.3 Limitations

Characterising at-sea behaviour

A key aim of this thesis was to relate the decisions made by individuals at the colony to their behaviour at sea. To achieve this goal, I therefore required a method of collecting data remotely on the behaviour of individuals on their foraging trips. The use of small, long-lasting geolocator devices for this purpose was a strategic choice to maximise the amount of consistent data that could be collected from a single animal over the relatively long duration of its entire breeding period. These were further selected as my primary method of collecting at-sea data due to my findings in Chapter 2 that the attachment of GLS to Manx shearwaters during the breeding season does not appear to have easily-detectable negative effects on the expression of normal behaviour. When remotely collecting data on behaviour, it is difficult to assess whether animals are behaving normally, especially for seabirds, which cannot be observed directly during their trips at sea. By examining the facets of foraging behaviour - specifically, trip duration, mass gains, and effort - that I was most interested in, according to device deployment, I found that there were no differences between GLS-tracked and untracked birds, suggesting that this is an adequate method to collect relevant data about at-sea behaviour. However, the major strength of these devices - that they are small and unlikely to disrupt normal behaviour - also gives rise to their greatest weakness: the data they produce is very coarse.

While the behaviours output by geolocators (rest, flight, and foraging) have been found to correlate strongly with finer-scale measures of behaviour, such as diving (Dean, 2012; Freeman et al., 2013; Shoji et al., 2015), these classifications only give an indication of time investment, and do not provide detailed information on foraging. In this thesis, I used a simple threshold classification method to distinguish each of these three behaviours. Though previous authors have taken more complex approaches that do not assume independence of time points, such as applying Hidden Markov Models to the data (Dean, 2012; Fayet et al., 2016), these still only produce three behavioural states and so provide similar levels of information to this threshold approach.

In Chapters 2 and 4, I found that birds that were handicapped, either by the deployment of a GPS or experimentally using wing tape, did not exhibit differences in their foraging behaviour on their prolonged foraging trips, despite exhibiting changes to rest and flight behaviour. In both cases, the reduced mass gains observed in instrumented or handicapped animals suggests that foraging was in some way affected, but this was not captured by our temporal measure of ‘time spent foraging’. It is possible that these birds exhibited alterations to foraging, such as reduced dive incidence, depth, or duration, that were not captured by our geolocators. To measure these variables, accelerometers, GPS, or time-depth recorders could be used to garner a picture of finer-scale behaviour. However, as my results in Chapter 2 show, these devices must be used with care, as the deployment of large (in mass or profile) devices clearly has significant effects on normal behaviour that may not be easily identified. However, differences in at-sea behaviour were observed that were associated both with instrumentation or handicapping and differences in individual state: for example, in Chapter 3 it was observed that heavy birds spent less time foraging during incubation. That we could find biologically-relevant differences in behaviour using geolocators suggests that even these broad behavioural categories are sufficient to capture variation in individual behaviour, and so their utility should not be underestimated.

Environmental drivers of coordination

The environmental context in which care is provided can influence the fitness benefits of cooperation for pairs (AlRashidi et al., 2010), and therefore the degree to which parents may be selected to coordinate at all (Ihle et al., 2019). When environmental conditions are harsh, parents may be under especially strong selection to coordinate their behaviour, as even minor failures to synchronise behaviour could spell disaster for the breeding attempt: for example, because gaps in incubation in environments subject to extreme temperatures could cause rapid embryo death (e.g. emperor penguin *Aptenodytes forsteri*, Le Maho, 1977; Kentish plover, AlRashidi et al., 2010), or because offspring and parents are subject to significant predation pressure at the nest (e.g. blackcaps *Sylvia atricapilla*, Leniowski and Wegrzyn, 2018). Conversely, if parents are released from environmental constraints, the increased contribution of sexual conflict to the division of parental labour may lead to the evolution of less coordinated behaviour and possibly even uniparental care (Bulla et al., 2019). Furthermore, if parents respond to environmental conditions in similar ways then this could lead to the emergence of apparently coordinated care through coincident expression of synchronous behaviour (Ihle et al., 2019). It is therefore important to disentangle active coordination processes between individuals in a pair from passive processes that may emerge due to similarity in responses to environmental conditions. Consequently, understanding the influence of environmental conditions on behaviour is an important step in explaining the evolution of and diversity in parental care strategies across the Animal Kingdom.

There is extensive evidence that levels of parental coordination covary with natural variation in environmental conditions. When conditions are poor, parents may be selected for increased coordination: this is observed in both Kentish plovers *Charadrius alexandrius* (AlRashidi et al., 2010) and semipalmated plovers *Calidris pusilla* (Bulla et al., 2019), where parents exhibit greater levels of incubation coordination during the hotter parts of the day. The habitat in which animals breed may also contribute to the levels of coordination they express: Lejeune et al. (2019) report differences in coordination for great tits depending on their breeding site, with parents nesting in open habitats, which exhibit higher predation pressure, showing greater levels of coordination than those nesting in dense forest. Finally, parents may also show individual-level responses to environmental conditions that could lead to inadvertent coordination with the partner when they respond to these in the same way. For example, Manx and streaked shearwaters *Calonectris leucomelas*, which visit their breeding colonies nocturnally, are less likely to visit the colony to provision their chicks on moonlit nights (Riou & Hamer, 2008; Van Tatenhove et al., 2018).

However, these strategies have been fixed over evolutionary time, and there has as yet been little investigation into how rapid changes in climate could impact parental behaviour (Vincze et al., 2017), despite evidence from theoretical models that many facets of life history will be impacted by increasing climate variability (Carlisle, 1982; Bonsall & Klug, 2011; Tökölyi et al., 2012). Therefore a secondary, increasingly relevant reason to investigate the influence that environmental variables have on parental coordination is that this relationship might have important conservation implications. Some species already exhibit considerable flexibility in their parenting behaviour, which may be an adaptation to cope with environmental fluctuations. For example, it has been proposed that nestling obesity observed in many Procellariiform seabird chicks is an adaptation to reduce the risk of starvation when conditions at sea are poor and so parents are unable to visit the nest as frequently (Hamer et al., 1998). For seabirds that facultatively employ a dual-foraging strategy, bimodal trip durations are often favoured in response to poor conditions at sea (Pinaud et al., 2005; Cecere et al., 2014; Ochi et al., 2016; Besel et al., 2018). Species that are unable to coordinate their caring behaviour dynamically may struggle to respond flexibly to rapid and substantial changes in environmental conditions, which could ultimately lead to widespread breeding failure and, over a longer time period, population decreases. For these reasons, climate change could have important consequences for breeding behaviour. Yet our understanding of the behavioural plasticity that parents are able to employ to respond to these changes is limited, making it difficult to gauge the probable impacts of climate change on the breeding success of populations (Vincze et al., 2017).

In this thesis, my treatment of the role of environmental variables in parental coordination was limited. In my analyses of the relationship between foraging trip duration and the incidence of allopreening in black-browed albatross, I considered the roles of wind direction and wind speed, as these variables probably have an influence on the amount of time individuals spend at sea (Pennycuick, 2002; Sachs, 2004; Paiva et al., 2010; Ventura et al., 2020). However, I did not find evidence in support of this. Furthermore, I examined whether Manx shearwaters exhibit cross-colony synchrony in nest visitation during incubation, which may indicate a population-level response to environmental variables, such as moon phase. Again, I found no evidence for such an effect, which is in contrast to previous findings (Riou & Hamer, 2008), but may be explained by my focus on the incubation, rather than chick-provisioning, period. Both Manx shearwaters and black-browed albatross are clearly equipped to deal with considerable variation in at-sea foraging conditions, given their extended trip durations and breeding adaptations such as embryonic resistance to chilling and nestling obesity, and so may be less affected by variability in foraging conditions. An alternative explanation for my failure to find an effect of environment, however, is that I may not have been examining the most appropriate data, and future work may consider a different set of environmental variables.

Prey availability is one of the best indicators of the external resources available to individuals to invest in care (Grissot et al., 2019), and future analyses investigating how care is provided in different environmental contexts may start by investigating this covariate. While prey availability is difficult to measure directly, many proxies have been successfully used to monitor seabird resource use, including chlorophyll A, net primary productivity, and zooplankton distribution (e.g. Morel and Berthon, 1989; Hunt et al., 1998; Waggitt et al., 2018; Mills et al., 2020; Phillips et al., 2021). Similar proxies may be correlated against measures of coordination to test the hypothesis that there is greater selection on parents to coordinate their behaviour when conditions at sea are poor. Furthermore, ample evidence exists that suggests that wind may be an important variable in determining foraging trip duration in shear-soarers such as Procellariiforms (Pennycuick, 1982; Spear & Ainley, 2008), and so my failure to find a relationship in black-browed albatross is surprising. A major limitation of this analysis was that parents did not carry GPS, and so their probable foraging destination was inferred only. Consequently, the likely pertinent characteristics of wind (both headwind and crosswind components) were calculated by assuming departure direction. To examine this putative relationship more thoroughly, high-resolution locational data, collected from GPS, would be required to determine the actual direction of travel of focal birds.

7.4 Concluding remarks

While understanding the coordination of parental behaviour has important implications for the evolution of biparental care, mate choice decisions, and non-kin cooperative behaviour, these results show that both demonstrating the existence of coordination in the first place and explaining its occurrence is a difficult problem to pin down. Parental care encompasses a huge breadth of behaviour that exhibits considerable variation both within and between species. Explaining this variation is vitally important to understanding the evolution of biparental care, the selection for and expression of different life-history strategies across species, and how sexual conflict between breeding individuals might be resolved. In this thesis, I have identified examples of parental coordination in two species of seabirds, and begun to elucidate the mechanisms by which this cooperative behaviour is achieved. In particular, I show that while coordinated care can to some extent be explained with reference to individual behaviour, particular nuances in the way this is employed indicate that more complex cooperative mechanisms are probably at play. This gives exciting insight into the communicative world of animals and may even support the existence of cooperative functions for the breadth of display exhibited across the Animal Kingdom. As developments in biologging technology continue, and in particular the size of devices available for tracking continues to decrease (Kays et al., 2015), the amount and detail of the data we can collect about behaviour will continue to grow, with increasingly less impact on the animals studied. By relating this fine-scale behaviour to the decisions made by individuals at the breeding site, we can begin to fully appreciate the ecological and evolutionary origins of diverse parental care strategies. Such information will not only fill important gaps in our understanding of the evolution of one of the most fundamental aspects of animal behaviour, but could also inform our understanding of the likely prospect for many species now struggling to adapt to our rapidly changing climate.

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