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Aspects of coordinated parental care in several seabird species

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Aspects of coordinated parental care in several seabird species

By

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DISSERTATION

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2021

7,991,554 RFID detections
662 PIT tagged birds
280 RFID readers
14 Months in the field
3 Islands
1 Dissertation

TABLE OF CONTENTS

ABSTRACT

Sexual conflict occurs when males and females do not maximize reproductive success in the same way. Conversely, when the fitness prospects of each sex are aligned, there is greater advantage to cooperate and to coordinate. This situation, where breeding partners share a higher proportion of their lifetime reproductive output, is most likely to be realized when pairs remain together for multiple breeding attempts. As a group, seabirds are notable for the number of species that maintain long-term pair bonds and display biparental care across a protracted breeding period. Consequently, in this group behavioral cooperation and coordination is expected to be critical. Behavioral coordination between breeding partners may also improve with the experience of the pair, further incentivizing the maintenance of long-term pair bonds. The scope for coordination, however, is likely to be constrained by various intrinsic extrinsic factors, which may differ between species.

This dissertation is an examination of the causes and consequences of behavioral coordination between breeding partners in three allopatric seabird species with contrasting foraging strategies. Specifically, I studied the Cassin's auklet (*Ptychoramphus aleuticus*), the Leach's storm-petrel (*Oceanodroma leucorhoa*), and the Manx shearwater (*Puffinus puffinus*). While all of these species share many similar life-history traits, they display markedly different foraging routines, ranging from consistent day-long trips in Cassin's auklets, to multi-day trips of variable duration in Leach's storm-petrels, to trips with a bidmodal duration, ranging from one day to more than 10 days in Manx shearwaters. The distinct foraging routines displayed by each species are expected to create different possibilities and incentives for coordination. Additionally, coordination may be influenced by a variety of intrinsic factors, such as individual

age and pair experience, or extrinsic factors, such as environmental conditions. By monitoring parental care across the breeding period and combining these behavioral observations with demographic data, this dissertation aims to extend our understanding of behavioral coordination during parental care in seabirds.

In Chapter 1, I evaluate the causes of sex-specific parental care in a monomorphic seabird, the Leach's storm-petrel. While there are many reported cases of sex-specific parental care in monomorphic species, the drivers of this behavior are not well-understood. I examine several of the hypotheses that have been proposed to account for sex-specific provisioning rates in monomorphic species by combining extended observations on provisioning rates and chick growth from a large number of pairs (n = 74). I find the strongest support for energetic constraints limiting the female contribution to chick provisioning. These findings are important for understanding how investment in parental care fluctuates throughout the breeding season.

In Chapter 2, I assess the functional benefits of a unique form of coordinated provisioning displayed by Manx shearwaters and whether the degree of coordination changes with pair-bond duration. Previous work demonstrated that during chick rearing, individuals will alternate between short and long foraging trips and that partners coordinate the timing of long trips. In this chapter, I show that this coordination benefits chick provisioning and growth. I also examine whether the degree of coordination is related to pair bond duration, but find no evidence for increased coordination in more experienced pairs.

In Chapter 3, I examine the 'mate familiarity effect' in Cassin's auklets using a long-term dataset on breeding success in known-age individuals. I find evidence for both direct and indirect benefits of pair experience on hatching success, suggesting that beyond laying earlier in

the year, more experienced pairs also differ in breeding competence. Moreover, this effect was strongest during environmentally poor years. To evaluate behavioral differences between pairs, I monitored nest attendance during three breeding seasons. I find no differences in the rate of egg neglect between new and experienced pairs, suggesting that coordination during incubation does not drive differences in hatching success in this species.

ACKNOWLEDGMENTS

The first-person pronoun “I” doesn’t occur in the remainder of this document, which is to say the majority of the written dissertation. Instead, I use the third-person pronoun ‘we’ and this reflects the fact that this work was the result of the indispensable support from a large number of people. Aside from the many advisers and collaborators that helped make this research possible, I am also indebted to the many friends that helped make it all enjoyable.

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Chapter 1. Energetic constraints give rise to sex-specific provisioning in a monomorphic seabird, the Leach's storm-petrel

ABSTRACT

Sex-specific parental care in dimorphic species may be unsurprising, but why this occurs in monomorphic species is more puzzling. To date, however, there have been few examinations of the causes of this prevalent phenomenon. Here, we evaluated possible explanations of sex-specific provisioning in a monomorphic seabird, the Leach's storm-petrel (*Oceanodroma leucorhoa*). We tracked the chick-rearing behavior of 74 mated pairs using an automated nest monitoring system and collected daily measurements of chick growth. We found that males provisioned more frequently and made a larger overall contribution to chick feeding than females. Within-individual trip duration was more variable for females, suggesting that they were alternating to a greater degree between short, energetically taxing trips that prioritize chick care, and longer, recovery trips that prioritize self-care. Moreover, females were more likely to embark on longer trips after completing a short trip and after encountering a chick in good condition. Males, however, appeared better equipped to perform repeated short trips that result in greater rates of food delivery to their chick. These findings are consistent with the explanation that energetic constraints on females give rise to male-biased, sex-specific provisioning in a monomorphic species and are likely to explain similar patterns in other long-lived species where adult survival is high.

1.1 INTRODUCTION

Animals have evolved a diversity of traits to benefit offspring fitness. Any such trait, morphological or behavioral, which increases offspring fitness is considered parental care. The degree and forms of parental care are the product of ecological constraints and coevolve with a species' life-history traits (Balshine, 2012; Wedell, Kvarnemo, Lessells, & Tregenza, 2006). For example, general factors such as high egg mortality, slow egg maturation, low juvenile survival, or low adult death rates are all expected to incentivize the evolution of increased parental care (Table 2, Klug and Bonsall 2010). As such, there are broad patterns in the forms of parental care observed across vertebrate taxonomic groups. In most groups, female-only care or no care are most commonly observed (Reynolds, Goodwin, & Freckleton, 2002). Birds, however, are the exception where biparental care is found in over 85% of species (Cockburn, 2006).

Yet even in avian species with biparental care, sexes often contribute care in varying degrees and ways (Wesolowski, 1994). One explanation for this variation is sexual conflict, which leads each partner to manipulate their level of care in order to maximize long-term fitness, potentially at the expense of their partner (Houston & Davies, 1985). The relative level of care invested by each sex may depend on a variety of factors including individual quality, residual reproductive value, and degree of extrapair paternity (Wedell et al., 2006). Thus, the amount invested by each sex is dynamic and will vary with the individual characteristics of each parent. Differential investment by each sex may also be more systematic with one sex adopting particular breeding duties, e.g. in raptors, females typically incubate while males hunt (Sonerud et al., 2014). In fact, some degree of role specialization is observed in most avian species (Barta, Székely, Liker, & Harrison, 2014) and is typically linked with sexual size dimorphism. One of the most widely documented sex-specific parental roles is provisioning, which is common in dimorphic species. Sex-specific provisioning has been most widely studied in seabirds where improved foraging capabilities of the larger sex are thought to lead to competitive exclusion of the smaller sex at foraging grounds (Lewis et al., 2002; Phillips, Lewis, González-Solís, & Daunt, 2017). Sex-specific provisioning, however, may also occur in the absence of size dimorphisms, indicating that other explanations are necessary to account for this phenomenon (Burke, Montevecchi, & Regular, 2015; Lewis et al., 2002; Thaxter et al., 2009).

Four non-mutually exclusive mechanisms may explain the occurrence of sex-specific provisioning in monomorphic birds (adapted from Peck and Congdon 2006). The *nest attendance rhythms hypothesis* states that differences in the timing of nest visits may lead to sex-specific levels of care. This could be caused by differences in daily foraging rhythms (Casaux, Favero, Silva, & Baroni, 2001) or perceived predation risk if one sex is more risk averse (Expósito-Granados, Parejo, & Avilés, 2016). If one sex is more responsive to offspring condition, then the *offspring condition hypothesis* may explain varying levels of care (Kilner, 2002). Sex-specific responses to offspring condition might be caused by selection for one sex to more precisely allocate care due to higher overall investment, sexual conflict, or as a mechanism for partial compensation of parental care. The *cryptic dissimilarities hypothesis* proposes that even species categorized as sexually monomorphic may be sufficiently different morphologically to create unequal foraging abilities between males and females, which may in turn lead to competitive exclusion of one sex while foraging, and ultimately divergent parental roles (Peck & Congdon, 2006). Lastly, the *energetic constraints hypothesis* posits that energetic limitations or nutritional requirements may require one sex to devote more time to self-provisioning or to selectively target particular prey, resulting in longer foraging trips and reduced food delivery to offspring (Gray & Hamer, 2001; Welcker, Steen, Harding, & Gabrielsen, 2009). Energetic constraints may arise from asymmetric investment early in the breeding period, such as nest construction and defense (Harris, 1966) by one sex or egg production by females, resulting in differential energetic or nutritional demands that are carried over to later breeding stages. Though some studies have explicitly explored a subset of these hypotheses in monogamous species with sex-specific parental care, few studies have simultaneously explored all of these hypotheses.

Among birds, seabirds are notable for displaying obligate biparental care (Cockburn, 2006), which is maintained over extended incubation and chick-rearing periods (Burger, 1980). Most seabirds are visually monomorphic (E. A. Schreiber & Burger, 2001), which historically made it challenging for human observers to assign sex-specific behaviors in the field. The proliferation of light-weight tags and molecular sexing has enhanced our ability to collect detailed behavioral observations from a large number of known sex individuals. In this study, we employed these methods to investigate parental care in the sexually monomorphic Leach's storm-petrel (*Oceanodroma leucorhoa*), which displays traits typical of seabirds, such as long life, delayed sexual maturity, social monogamy, and low rates of extra-pair paternity (Ingrid L. Pollet et al., 2019). This species has previously been described as having male-biased care (Mauck, Zangmeister, Cerchiara, Huntington, & Haussmann, 2011), but this finding came from a single colony and a small number of individuals, so whether this strategy is widespread within the species is unknown. Here, we focused on the extended 55-day provisioning period, during which both sexes undertake long-distance foraging trips to collect food for dependent offspring waiting at the nest. After evaluating whether male-biased care occurs in this population, we explored the four previously described hypotheses, explicitly testing the three (offspring condition, nest attendance, energetic constraints) that apply to Leach’s storm-petrels, in order to identify the mechanisms that underlie sex-biased parental care in this monomorphic species.

1.2 METHODS

Study site and field methods

Fieldwork was conducted on Bon Portage Island, Nova Scotia, Canada (43°26'N, 65°45'W), which is home to approximately 39,000 breeding storm-petrel pairs (Ingrid Louise Pollet & Shutler, 2018). A colony of 550 marked burrows has been monitored on Bon Portage Island since 2010. Each year, we conducted a census of marked burrows to identify and band breeding pairs. From each adult, we collected morphometrics (mass, flattened wing chord, and tarsus length) and 75 µL of blood from the brachial vein for molecular sexing. Blood samples were stored at room temperature in 0.5 mL of Queen’s lysis buffer. DNA extraction and molecular sexing were conducted using the methods described in Hoover et al. (2018).

During the 2016 breeding season, we inspected occupied burrows every three days until hatching, which allowed hatch dates to be estimated to within two days. Once brooding ceased, typically within a few days after hatching, chicks were weighed each day between 1000 and 1300 using a 100 ± 1 g Pesola scale. Morphometrics (tarsus, head bill, and wing chord) were taken every three days. Sampling was conducted under the approval of the University of California, Davis Institutional Animal Care and Use Committee Protocol 19288, Canadian Wildlife Service (CWS) Banding permit 10695, and CWS Research permit SC2742.

To record provisioning behavior, we monitored nest attendance patterns using radio-frequency identification (RFID) readers combined with passive integrated transponder (PIT) tags. PIT tags encased in plastic leg bands (EM4102 125 KHz, Eccel Technology Ltd, Aylesbury, UK) were attached to the unbanded tarsus of 148 birds during burrow inspections. PIT tags are passive and rely on the electromagnetic field produced by the RFID reader to transmit the unique identification number of the PIT tag. This number is then recorded by the RFID reader along with the detection time. Our RFID system was based on the design described in Bridge and Bonter (2011), but added a second antenna to decrease the possibility of missed detections and to assist with determining whether individuals were entering or exiting the burrow (details given in Appendix 1). We deployed 74 RFID readers at the start of the chick-rearing period and chicks in each of these burrows were followed using the protocol described above. To evaluate the potential impacts of the RFID readers, we weighed chicks in 34 control burrows once during the provisioning period (age of control chicks ranged from 19 to 43 days) and compared the age-specific mass of RFID-monitored and control chicks.

Statistical analyses

All statistical analyses were conducted in R 3.5.1 (R Core Team, 2014). When relevant, the assumptions of normality were assessed by visual inspection of residual plots. Throughout, means are given plus/minus the standard error. Significance was assessed based on an alpha level of 0.05. All figures were generated using the ggplot2 package (Wickham, 2016).

We compared two general features of provisioning between each sex: feeding frequency and meal size. Feeding frequency depends entirely on the duration of foraging trips;

we used the interval between nest visits, which were rounded to day-long intervals as adults only provision at night and only once per night. During the first week post-hatching, adults may brood the chick and remain in the burrow during the day. To exclude these brooding events from our analyses of provisioning behavior, we used RFID detection sequences to classify whether individuals were entering or exiting the burrow and thus brooding or foraging, respectively (see Appendix 1 for details of the classification procedure). Meal size was calculated based on the 24-hour change in chick mass (g). Total provisioning amount was also calculated for each individual as the sum of all meals delivered by that individual. We excluded nights when both parents provisioned as the individual contribution could not be determined.

To evaluate the impact of sex on parent provisioning amount, linear mixed models (LMMs) were fit using the lme4 package (Bates, Maechler, & Bolker, 2012). We first developed a global model of daily mass change as a function of chick mass, chick age, parent sex, and trip duration as fixed effects (as well as all two-way interactions) and adult identity (band number) as a random effect. All sub-models were then generated and compared using AIC to identify the top model.

Leach's storm-petrels are nocturnal at the breeding colony and predation risk by owls and gulls may vary with lunar phase leading to altered provisioning behavior if one sex is more risk averse. To evaluate whether sexes displayed distinct provisioning rhythms relative to the lunar phase, we examined nest attendance rates and arrival time at the colony for each sex during the new, waning and waxing quarters, and full moon. Nightly attendance rates for each sex were Z-transformed to account for the higher average attendance rates of males, which was then compared across sexes and lunar phase through a two-way ANOVA. We assessed arrival time (minutes since sunset) as a function of sex and lunar phase with adult identity as a random effect using a LMM. The significance of each explanatory variable was assessed with the ‘Anova’ function using type III Wald Chi-square tests from the R package *car* (Fox & Weisberg, 2011).

Chick condition for each day was calculated as the residual of body mass regressed on body size, which was calculated from the factor score of the first principal component of tarsus, head-bill (the length from the back of the skull to the tip of the bill), and wing chord (Weimerskirch & Cherel, 1998). Since chick morphometric measurements were only taken every three days, predicted values for each morphometric measurement were used to interpolate between measurements. Predicted values were found by fitting a logistic model to tarsus and head bill and a quadratic model to wing chord using the *easynls* R package (Arnhold, 2017). We then used this measure of chick condition to assess whether adults of each sex adjusted meal size relative to chick condition through a linear mixed model with adult identity as a random effect. Furthermore, we assessed how chick condition at the start of a foraging trip affected the duration of the subsequent foraging trip for each sex through a separate linear mixed model with adult identity as a random effect. As above, the significance of each explanatory variable was assessed using type III Wald Chi-square tests.

If one sex is energetically constrained from provisioning at higher rate, we would expect to observe greater within-individual variation in trip duration, as occurs in dual-foraging species that alternate between short and long trips for the purpose of chick and self-provisioning, respectively (Chaurand & Weimerskirch, 1994). Trip duration variation was calculated for all individuals with at least three foraging trips, as this is the minimum number of necessary trips in order to calculate variation. Given that short foraging trips provide less time for self-provisioning and are thus more energetically demanding, we also explored how individuals responded after making single day trips, the shortest observed trip duration. To do so, we compared the duration of trips after single day trips between males and females with individual as a random effect through a linear mixed model. Additionally, we compared the observed distribution of trip durations after single day trips to the expected distribution for males and females. To generate the expected distribution, we used the overall pool of recorded trip durations, which were then compared to the observed trip duration distribution following single day trips through Chi-squared tests for males and females separately.

1.3 RESULTS

Provisioning behavior

Our RFID reader array monitored 2,605 chick nights and recorded 221,520 detections from 148 parents (74 pairs). After classifying detection sequences, we identified 1,589 foraging trips. We also identified 63 brooding stints, which were excluded from further analysis. Females and males showed distinct foraging behavior with males making shorter duration trips (mean 2.1 days, median = 2, mode = 2, range 1 - 7) than females (mean 2.7 days, median = 3, mode = 2, range 1 - 9, Mann-Whitney U test, U = 462,540, $P < 0.001$, Figure 1.1). On average, females' trip duration was a third longer than males', and females made double the number of longer trips (> 4 days) than males. Mass, wing chord, and tarsus measurements differed by less than 1.6% between the sexes, indicating negligible size dimorphism in our colony (Table 1.1).

During chick-rearing, we collected 2,470 weights from the 74 chicks in RFID monitored burrows. The average meal size after a visit by one and two parents was 3.47 ± 4.30 g and 10.7 ± 5.26 g, respectively. The top model of daily mass change included the number of provisioning parents, chick age, chick mass, and previous trip duration ($R^2 = 0.55$, each fixed effect $P < 0.001$). The next best model (ΔAIC = 2.06) included the same terms as the top model as well as the sex of the provisioning parent, though this term was not significant ($P = 0.749$). Other candidate models were greater than 5 ΔAIC from the top model and so were not considered further (Burnham & Anderson, 2004).

Though the sex of the provisioning parent was not related to daily chick mass change, the total mass change across the provisioning period due to males (25.7 ± 0.26 g) was significantly greater than that due to females (18.4 ± 0.17 g, paired t-test $t_{76} = 3.18$, $P = 0.008$).

Explanations for sex-specific provisioning

We did not observe differences in nest attendance rates relative to moon phase (ANOVA, $F_{3,54} = 1.752$, $P = 0.167$). This was true for both sexes (ANOVA, $F_{1,54} = 0$, $P = 1.000$) and there was no interaction between moon phase and sex (two-way ANOVA, $F_{3,54} = 0.831$, $P = 0.831$). Arrival time at the nest after sunset varied by lunar phase with individuals returning later during the full moon (LMM, $\chi 2 = 44.9$, $P < 0.001$; Tukey test, $P < 0.001$ for all combinations between the full moon and all other phases). There was no general difference in arrival times between sexes (LMM, $\chi 2 = 0.06$, $P = 0.800$) and we found no evidence for an interaction between sex and lunar phase on arrival time (LMM, $\chi 2 = 2.22$, $P = 0.527$).

Both males and females were responsive to chick condition and increased meal size after encountering a chick in poor condition (LMM, $\chi2 = 78.1$, $P < 0.001$). We observed an interaction between adult sex and chick condition on the duration of the subsequent foraging trip (LMM, $\chi2 = 7.69$, $P < 0.001$, Figure 1.2) with females increasing foraging trip duration after encountering a chick in good condition, while males did not adjust foraging trip duration.

Females had greater within-individual variation in trip duration than males (ANOVA, $F_{1,123} = 13.8$, $P < 0.001$). Additionally, after making an energetically taxing, single day trip, females took longer subsequent trips than males (LMM, $\chi2 = 58.5$, $P < 0.001$). The observed versus expected distributions of trip lengths following one day trips were also significantly different for females (Chi-square, $\chi2\ (6) = 46.3$, $P < 0.001$) and males (Chi-square, $\chi2\ (4) = 34.8$, $P < 0.001$), and this was driven by females making longer trips than would be expected and males following the opposite pattern (Figure 1.3).

Impacts of RFID readers and PIT tags

No birds were observed to abandon in direct response to tagging as all study individuals were detected at least once. Moreover, compared to control pairs, age-specific (19 to 43 days) chick mass was not significantly different for RFID monitored pairs (60 g) and control pairs (56 g), which suggests that attendance rates and meal sizes were similar (t-test $t_{31} = 1.7$, $P = 0.098$).

1.4 DISCUSSION

Using data on a large sequence of consecutive foraging trips, we observed distinct sex-specific provisioning behaviors in the sexually monomorphic Leach's storm-petrel across the chick-rearing period. Males provisioned more frequently and consequently provided a greater overall amount of food to their offspring. Our findings confirm that male-biased provisioning is likely a general characteristic of this species, rather than being an effect of location or year. We examined multiple hypotheses to account for sex-specific provisioning in monomorphic seabirds and found that the energetic constraints hypothesis best explained the reduced provisioning rates of female Leach’s storm-petrels.

We did not find support for two of the four hypotheses that have been proposed as explanations of sex-specific provisioning in monomorphic birds. Different nest attendance rhythms did not explain lower provisioning rates by females. Both sexes exhibited similar arrival time and activity at the colony relative to lunar phase. As such, one sex was not consistently encountering a hungrier chick, which could lead them to provision a greater amount or perceive chick condition differently than the other sex. Additionally, sexes showed similar responses to lunar phase, with both males and females returning later during the brighter, full moon suggesting that both sexes are equally cautious about increased predation risk. There is also little support for subtle physical differences between sexes giving rise to the observed differences in provisioning rates, though this was not a mechanism we could directly test with our data. Leach's storm-petrels are largely solitary at sea with limited interactions during foraging (Ingrid L. Pollet et al., 2019), making it unlikely that interference competition results in niche segregation as is observed in other species that congregate at sea (Peck & Congdon, 2006). Moreover, as surface feeding birds, the slight asymmetries in body size are unlikely to give rise to meaningful discrepancies in foraging efficiency such as those observed in diving species where slight differences in mass can profoundly affect diving depth (Lewis et al., 2002; Peck & Congdon, 2006).

We found partial support for sex-specific responses to chick condition. Previous studies on provisioning behavior in response to chick condition in Leach's storm-petrels were conducted on individuals of unknown sex and so could not demonstrate an effect of parent sex on provisioning behavior (R. E. Ricklefs, 1992; Robert E Ricklefs, 1990; Takahashi, Niizuma, & Watanuki, 1999). We observed that while both sexes delivered larger meals to chicks in poor condition, only females increased the duration of their subsequent foraging trip after encountering chicks in good condition. This suggests that both sexes are responsive to chick condition, but that females are more apt than males to decrease parental effort when possible. Many species adjust provisioning effort in response to chick condition (Phillips & Croxall, 2003; Weimerskirch, Prince, & Zimmermann, 2000) and in some cases this behavior is sex-specific (Low, Makan, & Castro, 2012; Quillfeldt, Masello, & Hamer, 2004; Ryser, Guillod, Bottini, Arlettaz, & Jacot, 2016). One proposed explanation for sex-specific provisioning rules is that if one sex is energetically constrained it will be selected to more finely regulate levels of parental care (Kilner, 2002; Quillfeldt, Ruiz, Rivera, & Masello, 2008). As such, this finding is also consistent with the final hypothesis we considered.

Overall, our findings provide the most support for the energetic constraints hypothesis. We found that within-individual variation in trip duration was larger for females than males, suggesting that females are alternating between short and long trips to a greater degree. This pattern is similar to the dual-foraging strategy employed by several other seabird species, which allows individuals to balance self and chick care (Chaurand & Weimerskirch, 1994;

Weimerskirch et al., 1994). Short duration trips ensure continual provisioning to the chick, but entail a high cost of repeatedly commuting to foraging areas, whereas long duration trips allow individuals to spend more time foraging at the expense of reduced provisioning frequency. Additional support for females being energetically constrained is that after making single day trips, females, unlike males, significantly increased the duration of their subsequent trip, suggesting a need to recover from these short, energetically taxing trips. The observed change in foraging trip duration following single day trips cannot be explained by sex-specific provisioning rules as there was no relationship between single day trips and chick condition (i.e., chicks did not tend to be in better condition after females returned from a single day trip).

As a long-lived species, Leach's storm-petrel adults typically maximize lifetime reproductive output by prioritizing their own survival over that of their offspring (S. C. Stearns, 1977; Williams, 1966). As such, adults are not expected to over-invest in parental care at the expense of their own condition. Leach's storm-petrel eggs are exceptionally large relative to adult body size, up to 22% (Montevecchi, Kirkham, Roby, & Brink, 1983) and thus represent a substantial initial energetic investment by the female. During egg production, females also pay an energetic cost of higher basal metabolic rates (Whittow, 2002). These costs are likely not trivial; in the similarly sized European storm-petrel, after the first breeding season, overwinter survival is significantly lower for females, but not for males (Sanz-Aguilar, Mínguez, & Oro, 2012). Our findings suggest that the large initial investment in the egg places an energetic constraint on females that is apparent during the chick-rearing period, limiting female provisioning.

If breeding is more energetically demanding for females, this may result in female-biased mortality, which could have important population-level effects. On Bon Portage Island, females drop out of the breeding pool more frequently than males, which may lead to an overall male-skewed adult sex ratio (ASR) despite a balanced primary sex ratio (C.W. Tyson personal observation). Male-skewed ASRs are characteristic of many avian species, which is expected to be the result of higher mortality in the rarer sex as most avian species have an even primary sex ratio (Donald, 2007). A variety of explanations may account for sex-specific mortality rates, but, in general, reproductive effort is expected to impact female mortality (Székely, Liker, Freckleton, Fichtel, & Kappeler, 2014). Size-relative clutch mass, in particular, is strongly related to female mortality (Richard M Sibly et al., 2012). As such, despite male-biased parental effort observed during incubation (Mauck et al., 2011) and chick-rearing (this study and Mauck et al. 2011), female mortality may nevertheless be elevated due to the extreme investment in offspring production, resulting in a male-skewed ASR.

In monogamous species, uneven ASRs, especially if male-biased, are expected to increase a species' extinction risk (Donald, 2007). Marine birds, which are almost exclusively monogamous (Cockburn, 2006), are one of the most threatened groups of birds (Croxall et al., 2012). Leach's storm-petrels, though abundant throughout the north Pacific and Atlantic, are declining locally at several important breeding colonies (Ingrid Louise Pollet & Shutler, 2018; Robertson, Russell, Bryant, Fifield, & Stenhouse, 2006; Wilhelm et al., 2015) and their conservation status is considered vulnerable (Ingrid L. Pollet et al., 2019). Like other long-lived species, adult survival is a key demographic parameter in the population viability of Leach's storm-petrel (E. A. Schreiber & Burger, 2001). Our findings suggest that females may be especially sensitive to environmental changes that impact breeding effort. Further research, however, is required to assess whether there is a causal connection between female reproductive investment and increased mortality for this group.

Table 1.1 Average measurements for wing chord, tarsus, and mass of males and females banded between 2014 and 2016 within our study colony. Standard deviations for each measurement are given in parentheses. The percent difference between each measurement is calculated as one minus the smaller measurement divided by the larger measurement.

Measurement	**Male (n = 180)**	**Female (n = 211)**	**Difference (%)**
Wing chord length (mm)	162.2 (3.4)	164.6 (3.3)	1.4
Tarsus length (mm)	24.4 (0.8)	24.7 (0.8)	1.1
Mass (g)	46.4 (4.3)	47.1 (4.6)	1.6

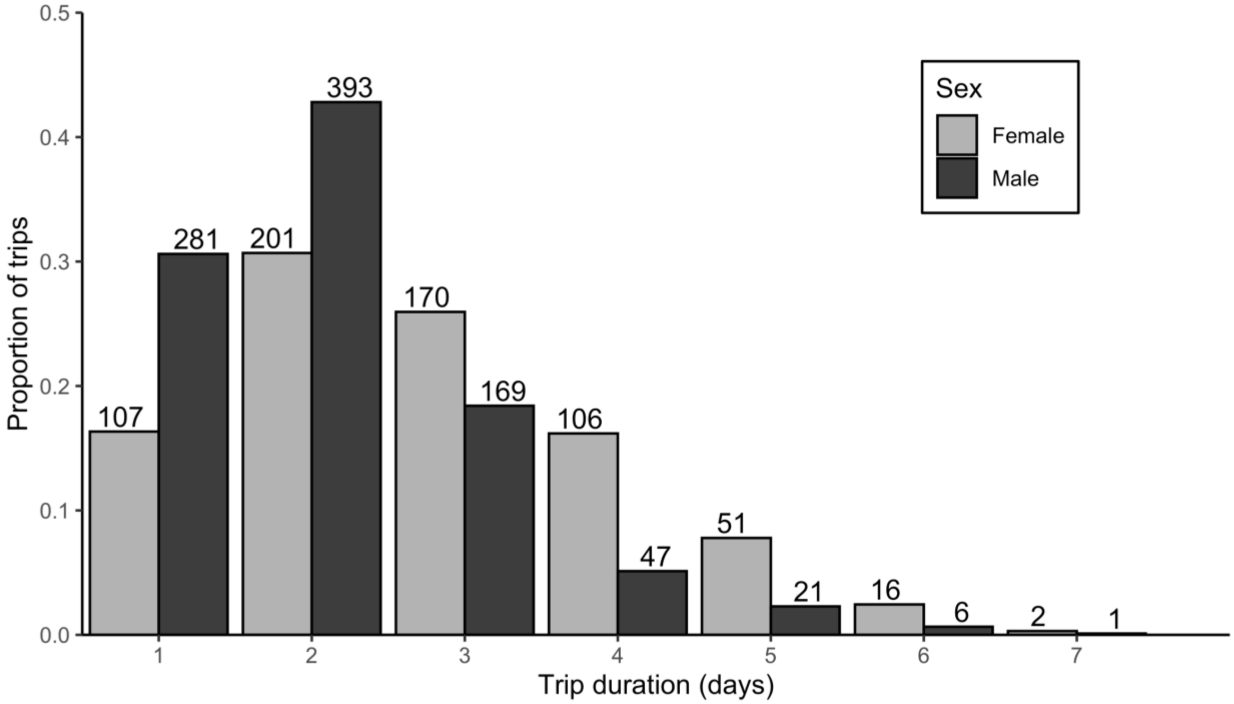


Figure 1.1 Relative frequencies of trip lengths (in days) for male and female Leach's storm-petrels on Bon Portage Island. Counts of each trip length are given above each bar. In addition to the trips shown, one male made a trip of eight days and two females made trips of nine days.

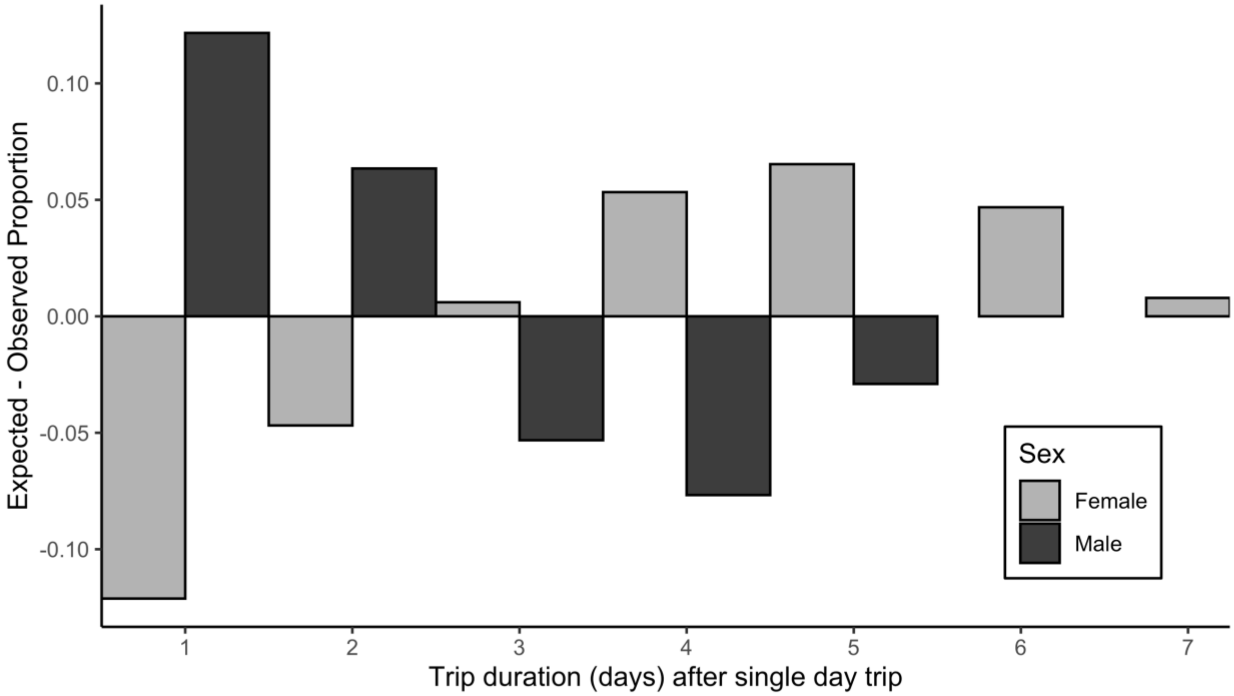


Figure 1.2 Difference between observed and expected relative proportions of each foraging trip duration following one day foraging trips. Expected values were found by randomly sampling trip durations for each sex. Observed values were based on the actual trip durations made by each sex following a one-day trip.

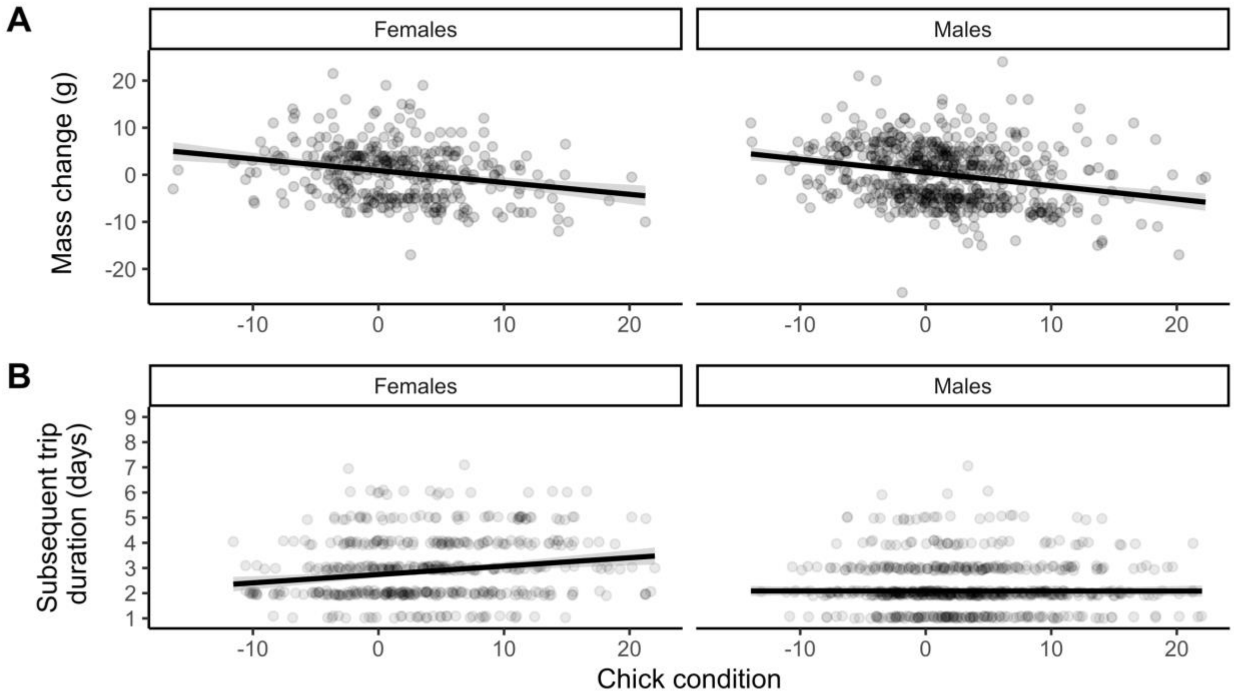


Figure 1.3 A) Chick mass change (g) as a function of chick condition for females (left) and males (right). Chick condition was determined based on the residual of the regression of body size (the first factor of a principal components analysis of tarsus, wing chord, and head bill) against mass on each day. Smaller numbers indicate a lower mass relative to body size (i.e. poor condition). B) Trip duration (days) as a function of chick condition (calculated as above) for females (left) and males (right).

Appendix 1.1

Radio-frequency identification (RFID) reader design

Radio-frequency identification (RFID) readers were used to monitor nest attendance patterns of individual birds tagged with passive integrated transponder (PIT) tags. Our RFID system consisted of three basic parts: 1) the RFID logger board, 2) a power source, and 3) two antennas for detecting PIT tags. The RFID logger board included a 256 MB SD card for data storage and a real time clock, which was programmed to the nearest second. To power each RFID logger, we used rechargeable 12V 12Ah sealed lead acid batteries (SigmasTek, Bridgeview, IL), which lasted for at least two weeks of night time recording (between 2200 ADT and 0800 ADT) with our polling settings (400 ms reading interval with 100 ms pause between each polling cycle). The RFID reader recorded a separate log of the start and pause times each evening in order to exclude periods of potentially missed detections during data processing. RFID loggers and batteries were housed in waterproof plastic food storage boxes (2.5 L Snapware rectangular container), which were placed within 0.5 m of the burrow entrance so as not to obstruct the path to the burrow (Figure A1.1). Circular antenna (90 mm internal diameter) were staked to the burrow entrance floor using paperclips. Antenna were installed such that antenna 1 was outermost (first to be encountered by an entering bird) and antenna was innermost (second to be encountered by an entering bird). In this way, the direction could be unambiguously determined if both antennas registered a detection. RFID readers were deployed at 74 occupied burrows prior to the end of incubation and were removed on August 29, 2016. The data generated from the RFID readers included a detection history with the date and time of a detected PIT tag as well as the antenna on which the PIT tag was detected. Additionally, a log of the battery status was recorded each night when the RFID reader commenced searching for tags each night.

Figure A1.1 RFID reader and battery housed in waterproof plastic food storage box with two antennas placed in the burrow entrance. The first antenna is visible within the burrow opening.

RFID data processing

To determine periods of potentially missed detections, which would lead to overestimating foraging trip duration, we generated a sequence of days spanning the dates that RFID readers were deployed for each burrow. To this sequence we merged each battery log for each burrow, as well as the daily chick mass change for each burrow. Trips that included periods where the RFID reader log indicated that the reader did not operate between 2000 ADT and 0800 ADT were excluded as a detection might have been missed during this time. Additionally, dates when no PIT tags were registered, but when chick mass increased, indicating a feed, were considered instances of missed detections, and were also excluded. If any foraging trips included periods without battery coverage or potentially missed detections, these trips were discarded as the trip length could not be reliably determined.

Behavioral state classification

While our dual antenna RFID readers theoretically allowed for direction to be unambiguously inferred based on the sequence of detections, in some cases missed detections on either antenna complicated assigning detections as ingress or egress events based on antenna detection sequence alone. In order to identify periods when birds were in the burrow or at sea, we used a random forest classification algorithm (Breiman, 2001) using features of the detection sequences from each individual on each night. These features reflected the stereotypical way that individuals enter and exit the burrow. For example, when entering the burrow, birds typically do so quickly, resulting in few detections, a short period between the first and last detection in the sequence, and a higher probability of a missed detection on at least one antenna. In contrast, when departing the burrow, birds typically wait at the entrance for a prolonged period, resulting in a large number of detections, a long period between the first and last detection, and a lower probability of missed detections on either antenna. Table A.1 describes the features of detection sequences each night that were used to classify whether an individual was in the burrow or out at-sea on the subsequent day.

After summarizing detection sequences each night for all individuals, we trained the random forest classification algorithm using a manually classified subset of ingress and egress events. In total, we manually classified 144 detection sequences (34 as burrow, 110 as at-sea). The random forest model was then used to classify the remaining detection sequences as ingress or egress events. For the final model, the out-of-bag error for egress (at-sea) and ingress (brooding) events was 0.05% and 19%, respectively. The higher error rate for brooding was driven by an under-classification of ingress events, but as brooding was infrequent (less than 70 instances out of 1,500), this did not qualitatively impact any of our findings.

Table A.1 Variables used to classify detections as a bird entering or exiting the burrow.

Variable
Count of detections on antenna number 1
Count of detections on antenna number 2
Total number of detections
First antenna with a detection
Last antenna with a detection
First antenna detected on the next night
Time between first and last detection of the evening
Total detection count in the first 5 minutes after the first detection
Time in days until the next detection
Time post sunset for the first detection
Age of the chick

Chapter 2. Coordinated dual foraging benefits chick growth, but does not relate to mate familiarity in Manx shearwaters

ABSTRACT

In long lived species that provide parental care, individuals are expected to balance investment in their offspring with self-care. In seabirds, a common strategy for meeting these conflicting demands during the chick rearing period is dual foraging, in which individuals alternate between a long trip for self-care and a sequence of short trips for chick provisioning. Recently, it has been found that breeding partners will coordinate dual foraging routines, though little else is known regarding this behavior. In this study, we used radio-frequency identification (RFID) readers to monitor the nest attendance patterns of breeding Manx shearwaters pairs (n = 104) in order to further explore coordinated dual foraging during two breeding seasons. We confirmed that pairs coordinated dual foraging routines, but the degree of coordination was highly variable between pairs. More coordinated pairs provisioned more consistently, which resulted in reduced daily variation in the mass of their chick. Chicks from more coordinated pairs also reached peak mass at a younger age, though the peak mass was ultimately not higher. Coordination did not increase with pair experience, but in one year of our study, showed a negative relationship. For a subset of pairs (n = 15) that were tracked in multiple years, however, the degree of coordination showed by pairs in each year was not more similar than between random pairs, suggesting that this behavior was not highly repeatable. Our results show that coordination is likely important for maximizing reproductive success, but that pairs are likely limited by the energetic condition of each partner.

2.1 INTRODUCTION

Sexual conflict is conspicuous in the animal world and considerable attention has been given to understanding the consequences of breeding partners maximizing their fitness in different ways (Arnqvist & Rowe, 2005; Wedell et al., 2006). This fixation on sexual conflict, however, may have led to an underestimation of the role of cooperation and coordination in socially monogamous systems. Recently, there has been a growing focus on the interactions that arise when the reproductive interests are aligned, particularly in terms of parental care (Griffith, 2019). Broad life-history traits, such as longevity, fecundity, and certainty of parentage, are expected to shape the degree of overlap between partners' lifetime reproductive output (Balshine, 2012). In short-lived species with mate replacement following partner mortality and frequent extra-pair mating, partners will share proportionally less of each other's reproductive output (Arnqvist & Rowe, 2005). In long-lived species, however, with little extra-pair mating and where mate replacement is costly, the shared proportional reproductive output of partners will be substantially higher. In such cases, there are greater incentives for cooperative or coordinated behaviors to emerge (Griffith, 2019).

An imperative to coordinate may itself also play a causal role in aligning the long-term fitness prospects of individuals. Avian species commonly have biparental care for at least a portion of the breeding period where it is essential that partners coordinate breeding behaviors (Cockburn, 2006). If such coordination increases with the experience of the pair, this will select for long-term partnerships (J. M. Black, 1996). Many studies have found evidence for this 'mate familiarity effect' in observing a positive relationship between reproductive success metrics and pair bond duration after controlling for individual traits, such as age or breeding experience, which may independently improve reproductive success (Emslie, Sydeman, & Pyle, 1992; Pyle, Sydeman, & Hester, 2001; Van De Pol, Heg, Bruinzeel, Kuijper, & Verhulst, 2006). These findings suggest that reproductive success is not merely an individual trait, but that it is affected by an interaction between the phenotypes of each partner. As such, candidate behaviors that improve reproductive success in more experienced pairs are likely to depend on how partners respond to each other, which is to say, how they coordinate. The ability for pairs to coordinate may depend on intrinsic traits of each partner, such as behavioral (Schuett, Dall, & Royle, 2011) or physiological (Hirschenhauser, Möstl, & Kotrschal, 1999) compatibility. Coordination, however, may also progressively improve with pair bond duration if, for example, partners learn to anticipate each other's behavior.

While few studies have examined specific coordinated breeding behaviors within the context of mate familiarity, coordinated behaviors in general are well-documented. A conspicuous example of a coordinated behavior in many avian species is incubation, which is often shared by males and females and requires that partners synchronize changeovers to continuously attend the eggs, reduce nest visibility, and balance periods of foraging to offset energy lost while incubating (Deeming, 2002). As such, each individual must adjust its own behavior in response to its partner. In the last decade, a variety of other breeding behaviors have also been found to be coordinated (Table 2, Griffith, 2019). In particular, a growing number of studies have found that provisioning is often coordinated between partners. In passerines, where coordinated provisioning has received the most attention, partners alternate feeding visits in a way resembling conditional cooperation where each partner withholds provisioning until after their partner provisioned (zebra finches, Mariette & Griffith, 2012; great tits, Johnstone et al., 2014; long-tailed tits, Bebbington & Hatchwell, 2016). Yet despite examples of seemingly coordinated provisioning, there is doubt as to the biological and functional significance of this behavior. Demonstrating active behavioral coordination requires showing that the observed level of alternation is greater than would be expected by chance and also that it is not the product of some indirect cause structuring the provisioning routines of each partner, such as the weather (Ihle, Pick, Winney, Nakagawa, & Burke, 2019; Santema, Schlicht, & Kempenaers, 2019). Additionally, coordinated provisioning has been proposed as a possible mechanism for ameliorating sexual conflict in species with biparental care, leading to an overall higher level of parental investment, and thus benefiting offspring (Johnstone et al., 2014; Johnstone & Savage, 2019). Yet in many of the studies that have reported coordinated provisioning, the benefits to both the chicks and adults were equivocal (Bebbington & Hatchwell, 2016; Grissot et al., 2019; Lejeune et al., 2019).

Seabirds are a group in which long-term partnerships and coordination are characteristic features. While most bird species display biparental care, far fewer maintain long-term partnerships (21% of 159 avian families; J. M Black, 1996). Among seabirds, however, perennial monogamy is observed in the majority of species (Bried & Jouventin, 2001). This pattern is likely the product of the nesting habits of seabirds and the nature of the marine environment in which they forage (Cockburn, 2006). Seabirds typically nest in dense colonies where predation and interference from conspecifics is high (E. A. Schreiber & Burger, 2001). Furthermore, during breeding, seabirds are central place foragers that often depend on distant marine resources which can only be reached during extended foraging trips (Shealer, 2001). Additionally, most seabirds have protracted breeding periods (Table 9.2, Bried & Jouventin,

2001) during which caregiving adults must also maintain their own condition. Consequently, pairs that better coordinate parental care are likely to have higher reproductive success and adult survival. This is especially true of pelagic seabirds, where individuals may make foraging trips lasting multiple weeks to reach the most profitable foraging zones (Shealer, 2001). To exploit these distant foraging areas while also providing parental care, many species within this group display a dual-foraging strategy during chick-rearing, wherein individuals will alternate between a single long-duration trip primarily for self-feeding and a sequence of short, day-long trips for offspring provisioning (Baduini & Hyrenbach, 2003). If pair members were independently switching between trip types, two scenarios would be likely to occur: the sequence of short trips or the long trip would overlap. In the former case, the chick may be overfed, leading to an inability to assimilate the meal (Waugh, Weimerskirch, Cherel, & Prince, 2000), and in the latter case, chicks would be starved, leading to decreased growth and potentially to death (Robert E. Ricklefs, 1968). Recently, it has been shown that some dual-foraging species do coordinate provisioning (Grissot et al., 2019; Tyson et al., 2017; Wojczulanis-Jakubas, Araya-Salas, & Jakubas, 2018), though aside from this observation, little else about this behavior is known.

In this study, we examine the functional significance of coordinated dual-foraging in Manx shearwater (*Puffinus puffinus*) pairs during chick-rearing. Manx shearwaters are long-lived (> 55 years, Clark et al., 2004) and display high mate fidelity (Brooke, 1990). During breeding, both partners care for a single egg throughout an incubation period lasting 50-55 days and then both parents provision the chick for an additional 70 days (Brooke, 1990), though care is slightly male biased during provisioning (Gray & Hamer, 2001). During chick rearing, Manx shearwaters display a dual-foraging strategy (Shoji et al., 2015) with partners coordinating the timing of long trips (Tyson et al., 2017). Aside from observing coordinated dual foraging within pairs, however, our understanding of this behavior is limited. In particular, the fitness benefits of coordinated dual foraging, from either the perspective of the chick or the caregiving adults, are unknown. Given that coordination enables partners to simultaneously balance their own condition with that of their chick, reduced coordination should result in a deviation from either self-care or chick-care. Additionally, it is unknown whether coordination is a consistent behavioral trait of pairs and whether coordination improves with mate familiarity. As such, in this study we aim to examine these aspects of coordinated dual foraging. In particular, we first examine how coordination affects chick provisioning and growth. Second, we look at the inter-annual consistency of coordination within pairs and whether coordination improves with pair experience.

2.2 METHODS

Study site and breeding monitoring

Fieldwork was conducted on Skomer Island, Wales, UK (51°44’N, 5°17’W), a nearshore island within the Irish Sea. Since 2009, approximately 150 marked burrows have been inspected each breeding season to identify mated pairs and to track productivity by recording laying, hatching, and fledging dates as well as chick growth for each occupied burrow. Each year, monitored burrows are inspected beginning in mid-April and breeding adults are given a metal leg band (British Trust for Ornithology), if necessary, and sexed by cloacal inspection (Gray & Hamer, 2001). Methods were approved by the British Trust for Ornithology Unconventional

Methods Technical Panel (permit number C\5311) and by the Wildlife Trust for South and West Wales under the name of Professor 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. All methods and procedures adhere to ASAB/ABS Guidelines for the Use of Animals in Research.

Nest attendance monitoring

We tracked the nest attendance patterns of breeding pairs in 2018 (n = 74) and 2019 (n = 55) using radio-frequency identification (RFID) readers combined with uniquely coded passive integrated transponder (PIT) tags (Figure 2.1). RFID readers record the time of detection and the identity of the detected bird (see Bridge et al. 2019 for details of the RFID system). RFID readers were placed at the burrow entrance of target pairs prior to hatching. Pairs were selected to include newly formed and experienced pairs. Study birds were captured at the nest during the incubation period by day. Individuals were then equipped with a PIT tag (2 x 12 mm, EM4102 glass tag, Cyntag Cynthiana, KY, USA), which was shrink wrapped to a black zip tie and then attached to the tarsus. The total tag weight was 0.3 g, which is 0.07% of the average mass of Manx shearwater adults during chick rearing and 0.08% of the minimum adult mass during chick rearing that we observed.

RFID readers were programmed to operate from sunset to sunrise (i.e., the period that Manx shearwaters return to the burrow). In addition to recording detections, RFID readers recorded a status log indicating whether the unit was on. Occasionally, RFID readers failed to turn on automatically and these nights were excluded. Additionally, if chick mass increased overnight, but no detections were recorded, these nights were excluded.

Coordination scoring

Provisioning data from both partners was used to determine coordination of the pair, which was quantified using two different metrics that represented different aspects of coordinated dual foraging. The first reflected the stereotypical form of coordinated dual foraging between two partners. Namely, it is expected that three general features of the nest attendance patterns will be observed for pairs that are dual foraging in a coordinated manner. First, the chick will be fed once per night, i.e., not starved or fed by both parents except on nights when long-trip changeovers occur. Second, on occasions when both partners return to the nest to feed, each partner will adopt different foraging strategies (short or long) on the subsequent trip. Third, partners will have equal provisioning rates. We derived a metric to quantify these features:

Metric 1: Coordination scores =

$$\frac{\left[1 - \left(\frac{|Feeds_{\text{♀}} - Feeds_{\text{♂}}|}{Feeds_{All}}\right) x\ Feeds_{All}\right] + Changeover_{Coord}}{Total\ nights}$$

where $Feeds_{\text{♀}}$ and $Feeds_{\text{♂}}$ are the number of feeds by females and males, respectively; $Feeds_{All}$ is the combined number of feeds; $Changeover_{Coord}$ is the number of nights when both partners and partners subsequently changed foraging trip duration as expected if they were coordinating (i.e., one partner increased foraging trip duration and the other partner decreased foraging trip duration); and total nights is the number of monitored nights.

Ultimately, this metric captures the general nest attendance patterns characteristic of coordination, namely that coordinated pairs will be feeding themselves half of the nights and the chick on the other half (see Figure 2.2 for examples). As such, deviations from this expectation are also indicative of lower coordination. We quantified this more general feature of coordination using the metric:

Metric 2: Balanced feeding =

$$\|(Feed_{chick} - 0.5)| + \left|(Feed_{female} - 0.5)\right| + |(Feed_{male} - 0.5)|$$

This metric is the sum of the absolute value of the difference between 0.5 and the proportion of nights when the chick was fed and when each adult was feeding themselves. Low values indicate strong coordination and high values indicate reduced coordination either through excessive chick feeding or self-feeding. While the two metrics are related in that both depend on a balance between adult and chick feeding, the second metric is insensitive to the temporal sequence of short and long trips and so a variety of different uncoordinated situations could give a similar value to cases of coordinated dual foraging. Each metric of provisioning coordination was calculated between hatching and the night on which the last detection by the first adult to cease feeding was recorded.

Provisioning routines may appear to be coordinated just by chance. In order to determine whether the observed degree of coordination was significantly greater than would be observed if individuals provisioned independently, we simulated provisioning sequences for each pair. To generate expected provisioning sequences, we randomly sampled from the distribution of foraging trip durations for each partner in each pair. This process yielded a sequence of provisioning events for the pair, based on which we calculated a coordination score as above (metric 1). This process was repeated 10,000 times for each pair (see Bebbington & Hatchwell (2016) for additional information about a similar approach as well as Ihle, Pick, Winney, Nakagawa, & Burke (2019) for a detailed justification of this approach.

A subset of pairs (n = 15) were followed in two years. To evaluate the consistency of coordination within-pairs, we compared the observed similarity in coordination scores for these pairs between years to the average similarity in coordination between random pairs. Coordination scores in each year were Z-transformed to account for potential differences between years. For the pairs with two years of data, the observed similarity in coordination scores was calculated as the absolute value of the difference in coordination scores. The expected between-pair coordination score was similarly calculated as the absolute value of the difference in coordination scores between randomly sampled pairs, repeated 10,000 times.

Fitness correlates of coordination

Coordinated dual foraging is expected to allow caregiving parents to switch between periods of chick-care and self-care with partners alternating between each behavior. As such, this coordination should result in more consistent provisioning, which can be measured by the inter-visit interval (Savage & Hinde, 2019). The inter-visit interval is the duration (here measured in days) between visits or feedings. We calculated the coefficient of variation (CV) in the duration of inter-visit intervals for each pair (Grissot et al., 2019) and fit this value as the response in a linear mixed-effect model (LMM) with coordination score as a fixed effect and year and pair as random effects. Consistent feeding should also translate into less variable chick mass (g), which we evaluated by relating the standard deviation of the daily change in chick mass to the coordination score of each pair using a LMM with year and pair as random effects. To explore whether consistent feeding benefited chick development, we compared the time to fledging age (days) and the peak mass (g) to coordination scores for each pair through a separate LMM with year and pair ID as random intercepts.

Effect of pair experience on coordination

Breeding records were used to quantify the pair-bond length for each pair. When pairs reunite, they almost exclusively remain in the same burrow as the previous year. For these pairs, pair-bond duration was measured as the total number of years in which the pair was observed sharing incubating duties. As it is uncommon for a pair to jointly relocate to a new burrow, if a previously unbanded pair was found in a monitored burrow during the study years, the pair was assumed to be inexperienced as it is likely that this would be their first year breeding together. To explore whether coordination increased with pair experience, we used a LMM with year as an additional fixed effect and pair ID and random intercepts. Coordination scores for each pair were weighted by the number of nights the pair was tracked. We also compared whether changes in the degree of coordination were related to pair experience using a linear model to compare differences in coordination scores between years to pair bond length of each pair. Coordination scores were Z-transformed to account for potential differences between years.

All data processing, statistics, and plotting was done in R (R Core Team, 2014). We used the R package 'lme4' to fit all mixed effect models (Bates et al., 2012). P values for each parameter in mixed effect models were determined using likelihood ratio tests by removing each term and comparing the reduced model to full model. Parameter estimates (β ± standard errors) are presented where relevant.

2.3 RESULTS

We observed no adverse effects of tagging on adult behavior as all tagged individuals were observed to continue normal breeding behavior. The RFID readers also did not appear to impact breeding behavior as fledging rate was high for both monitored and control pairs in both years (2018: control, 100% and RFID, 98%; 2019: control, 88% and RFID, 96%).

Using RFID readers, we monitored nest attendance for an average of 41 days (range 6 – 63) and 31 days (range 7 – 54) in 2018 and 2019, respectively. During these monitoring periods, we identified 2,095 complete foraging trips in 2018 and 1,336 foraging trips in 2019. Trip duration was highly variable, ranging from 1-14 days. Females trip duration (in days) tended to be slightly longer than for males (LMM: $\beta = 0.23 \pm 0.06$, $\chi^2(1) = 18.1$, $p < 0.001$) and trip duration was shorter overall in 2019 (LMM: $\beta = -0.12 \pm 0.05$, $\chi^2(1) = 5.5$, $p = 0.02$; Figure 2.3). Detection timelines for each pair are shown in Appendix 2.1 Figure 1.

Coordination scores (metric 1) ranged from 0.35 to 0.89 suggesting considerable variation between pairs. Observed coordination scores were significantly greater than the coordination scores from simulated sequences of provisioning events indicating that observed coordination in dual-foraging routines was not simply due to chance ($\text{t-test}_{71} = 6.9$, $p < 0.001$, Figure 2.4). The coordination metrics were negatively correlated (LM: $R^2 = 0.47$, $p < 0.001$) suggesting that greater coordination led to pairs more evenly balancing the number of nights on which parents spent feeding themselves versus the chick (Figure 2.5).

In both 2018 and 2019, increased coordination showed a positive relationship with lower variation in the inter-visit interval of each parent (LMM: β = -0.56 ± 0.12, χ2(1) = 19.9, $p < 0.001$) confirming that increased coordination resulted in more consistent chick provisioning (Figure 2.6A). Similarly, increased coordination was positively related to lower daily variation in chick mass throughout the entire chick rearing period (LMM: $\chi^2(1) = 13.47$, $p < 0.001$; Figure 2.6B). Chicks of more coordinated pairs also reached peak mass more quickly after hatching (LMM: $\chi^2(1) = 6.510$, $p < 0.01$; Figure 2.6C), though peak mass ultimately did not vary with coordination (LMM: $\chi^2(1) = 0.284$, $p = 0.59$; Figure 2.6D).

The pair bond length of monitored pairs ranged from 1 (first-time breeders) to 11 years. In both 2018 and 2019, the distribution of pairs in each experience category was similar, though we were only able to monitors two inexperienced pairs in 2019 (Figure 2.7). Coordination was significantly higher in 2019 (LMM: $\chi^2(1) = 10.63$, $p < 0.001$; Figure 2.7) and there was a significant interaction between year and pair bond length (LMM: $\chi^2(1) = 4.759$, $p < 0.05$) with coordination decreasing with pair bond length in 2019 and showing no relationship in 2018. Pair coordination scores, however, were not more similar within pairs that were tracked for two years than between randomly matched pairs (t-test: $t_{14} = -0.86$, $p = 0.40$; Figure 2.8). Additionally, we found no relationship between pair experience and changes in coordination scores between years (LM: β = -0.08 ± 0.08, t value = 0.95, $p = 0.39$).

2.4 DISCUSSION

We measured provisioning coordination in Manx shearwater pairs and associated this parental behavior with aspects of chick growth during two consecutive breeding seasons. Our findings extend the previous reports of coordinated dual foraging in several ways. First, we constructed a metric for quantifying the degree of coordination between pairs. Using this method, we showed that coordination is significantly greater than would be expected if pairs were provisioning in an independent manner. Pairs that were more coordinated provisioned the chick more consistently, which resulted in reduced daily variation in the mass of the chick. Additionally, chicks of more coordinated parents reached peak mass sooner, though peak mass was unrelated to the degree of coordination. For the subset of pairs tracked in two years, the degree of coordination was no different within pairs than between random pairs, suggesting that this behavior was not consistent between the two years of our study. Contrary to expectation, we observed that newly formed breeding pairs showed higher coordination than experienced pairs, though this relationship was only observed in one year.

Coordinated dual foraging has been previously reported in only a small number of species, but more generally, there are many reports of coordinated provisioning via alternation. To quantify alternation, studies typically compare the number of alternated provisioning visits to the total number of visits by each partner, which gives a ratio representing the proportion of visits that were alternated (Bebbington & Hatchwell, 2016). This ratio is then compared to the expected alternation score, which depends on the relative number of visits by each partner (Iserbyt, Fresneau, Kortenhoff, Eens, & Müller, 2017). While coordinated dual foraging also entails alternation by the pairs, partners are expected to alternate sequences of long trips and short trips, rather than single visits. We constructed a way to quantify this more complex form of alternation (metric 1), which can also be used to compare whether the observed rates of coordination are significantly greater than what would be expected by chance. We also quantified the proportion of nights on which the chick was provisioned and on which adults were self-feeding (metric 2). Coordinated dual foraging is expected to result in a balance between these two demands and the correlation between our two metrics suggests that the first metric was sensitive to the more general features of the second metric. Dual foraging has been widely reported in seabirds, but there are relatively few reports of pairs coordinating this behavior (Booth, Minot, Fordham, & Imber, 2000; Congdon, Krockenberger, & Smithers, 2005; Tyson et al., 2017; Wojczulanis-Jakubas et al., 2018). Though dual foraging is largely observed in seabirds (Baduini & Hyrenbach, 2003), there is also evidence of similar foraging patterns in other groups, e.g. kestrels (Hernández-Pliego, Rodríguez, & Bustamante, 2017). Our metric provides a straightforward way to identify whether dual foraging is occurring in a coordinated fashion and to measure the degree of coordination in order to relate this behavior to other traits of interest, such as traits of the pair or of the environment.

Consistent with a previous study on Manx shearwaters, we found that pairs do coordinate dual foraging though there was substantial variation between pairs in the degree of coordination (Tyson et al., 2017). Pairs that were more coordinated fed their chick more consistently, which resulted in reduced variability in chick growth rate and led to the chick reaching peak mass sooner. A previous study on coordinated dual foraging in little auks (*Alle alle*), similarly found that coordination reduced the variation in the inter-feed interval, though they did not find any additional effect on offspring growth. As such, our study helps to make a direct functional link to the benefits of coordination in dual foraging species. While peak mass was ultimately not related to coordination, by reaching this point sooner, chicks may be better buffered against late season decline in prey availability (Verhulst & Nilsson, 2008). Also, reduced provisioning is known to cause oxidative stress (Pascual, Pedrajas, Toribio, López-Barea, & Peinado, 2003; Wasselin et al., 2014) and elevated corticosterone (Kitaysky, Kitaiskaia, Wingfield, & Piatt, 2001), both of which may detrimentally affect neurological and behavioral development (Welberg & Seckl, 2008). Furthermore, though seabird chicks have evolved mechanisms to cope with stochastic feeding, such as by selectively allocating energy to the morphological structures most critical for fledging, e.g. the skull and wings (Kitaysky, 1999), this may result in smaller structural size, which can in turn affect survival (Weimerskirch, Barbraud, & Lys, 2000). Consequently, chicks from less coordinated pairs are likely to experience a range of more subtle, detrimental effects.

We found no evidence for coordination being higher in more familiar pairs and similarly changes in interannual coordination within pairs was unrelated to pair experience. Surprisingly though, we observed a decrease in coordination among more experienced pairs in 2019. This relationship, however, was driven by two observations and so should be interpreted with caution. In agreement with this finding, however, a study on black-browed albatrosses, *Thalassarche melanophris*, found that coordination was highest for inexperienced pairs and declined with pair experience (Patrick, Corbeau, Réale, & Weimerskirch, 2020). If sexual conflict increases with pair bond duration due, for instance, to reduced survival of each partner and thus lower re-pairing rates, then selection for coordination may be lower in more experienced pairs where future shared reproductive interests are less certain (Griffith, 2019). Another possible explanation is that more benign environmental conditions in 2019 made coordination easier for inexperienced pairs. We observed higher overall coordination during this year and if coordination serves to signal reproductive commitment in new pairs, then this could be more easily accomplished during environmentally favorable periods. Environmental conditions impact foraging effort, and thus provisioning, and so are likely to affect the ability of the pair to coordinate. For example, Lejeune et al. (2019) found that alternated provisioning in Blue tits (*Cyanistes caeruleus*) was reduced in harsh environmental conditions. In contrast, however, Grissot et al. (2019) found no relationship between prey availability and coordination in little auks. The possibility of interactive environmental effects indicates that detecting coordination and understanding these behaviors is challenging and may require observations spanning multiple years.

Given that the degree of coordination did not appear to be consistent between years, pairs may simply have a limited ability to control this behavior. Rather, some more stochastic process may be dictating whether pairs manage to coordinate. As a long-lived species, adults are expected to maximize lifetime reproductive success by prioritizing their own condition (S. Stearns, 1992). In some procellariform seabirds, dual-foraging strategies depend solely on adult body condition (Weimerskirch, 1998; Weimerskirch, Zimmermann, & Prince, 2001; but see: Ochi, Oka, & Watanuki, 2010). As such, if each partner independently follows a dual-foraging routine whereby the 'short-trip' individual consistently loses mass after each short trip and the 'long-trip' adult gains mass each day, then a coordinated pattern might simply emerge without any active coordination by partners. Coordination may also deteriorate if one individual has low foraging success, leading to reduced provisioning. Similarly, if either partner begins the chick-rearing period in poor condition, those individuals may be unable to maintain a sufficient sequence of energetically demanding short-trips while waiting for their partner to return (Shoji et al., 2015). Subsequent breeding effort is known to adversely affect breeding performance in

Manx shearwaters and other seabirds (Catry, Dias, Phillips, & Granadeiro, 2013; Fayet et al., 2016). As such, adverse carryover effects may drive reduced coordination and could explain why coordination is not highly consistent between years.

That pairs breeding together for the first time had high levels of coordination suggests that this behavior may not be limited by pair experience. Currently, it is not clear how Manx shearwater pairs coordinate switching foraging trip types on nights when both partners return to feed. It was previously found that switching trip types in a coordinated manner did not require partners to physically meet at the nest, but still occurred if partners returned to the colony on the same night (Tyson et al., 2017). This would suggest that partners might detect each another aurally via calling at the colony or through olfactory cues at the nest. Manx shearwaters are known to recognize calls by their partner and Procellariforms have a highly developed sense of smell. Another possibility is that coordination during chick rearing is carried over from incubation when individuals alternate between periods at the nest and foraging. If this is the case, it would suggest that successful coordination does not require that individuals learn to adjust to their partner's provisioning rhythms. This would be consistent with our findings that increased mate familiarity does not lead to higher coordination.

In this study, we primarily focused on the benefits of increased coordination to the chick. Coordinated dual foraging, however, is also expected to benefit adults. At a general level, our results do show that more coordinated pairs spend a more equal proportion of nights on self-feeding and chick-feeding. Though this is likely to translate into caregiving adults maintaining better condition throughout the chick-rearing period while also consistently feeding the chick, further work is necessary in order to quantify the extent of this benefit and the costs of lower coordination. In many species, routinely recapturing adults to monitor condition is at best impractical and at worst is likely to be disruptive, inducing stress and possibly abandonment. Automated weighing systems are one method for remotely monitoring adult mass and can be integrated with other biologging devices, such as RFID readers, to simultaneously identify individuals. Studies on coordinated parental care have tended to focus on the costs and benefits to offspring but developing a complete understanding of these behaviors will require understanding how adult condition is affected.

2.5 FIGURES

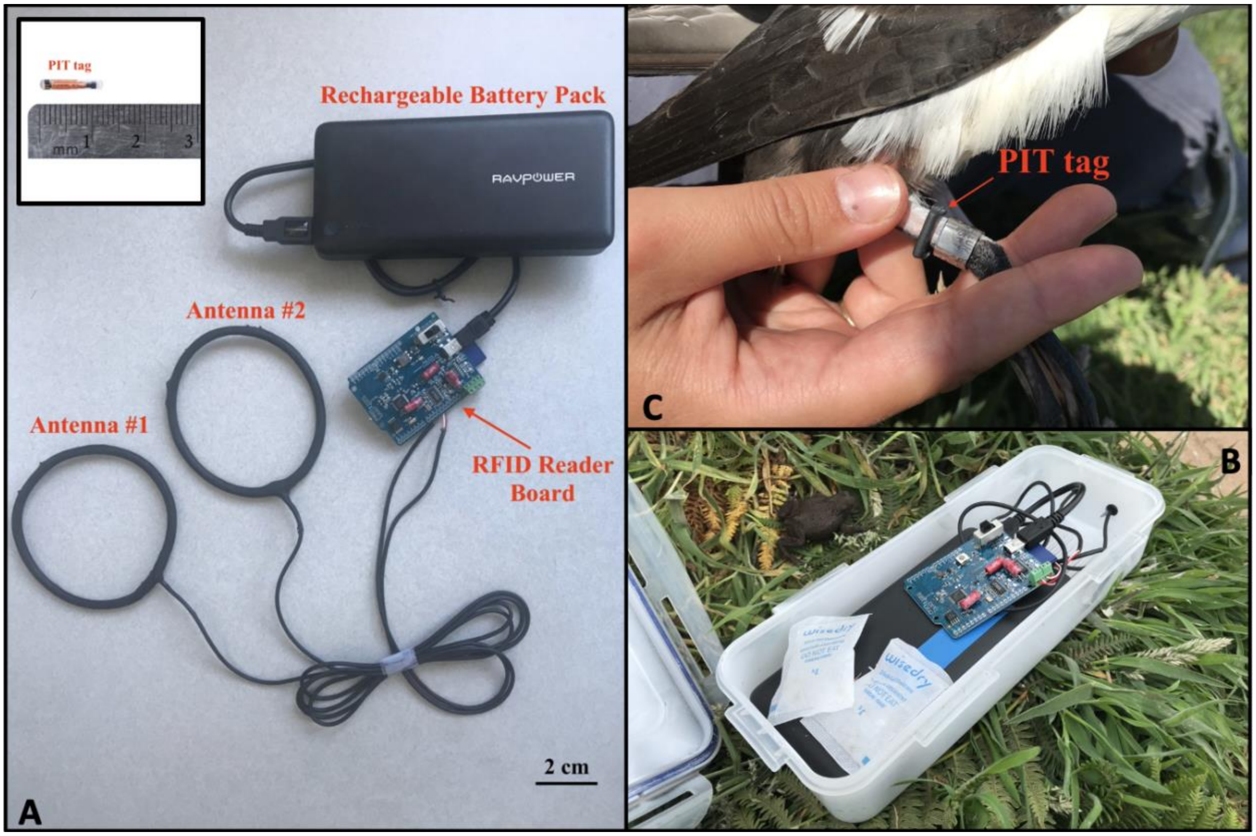


Figure 2.1 Pictures of the radio-frequency identification (RFID) readers and passive integrated transponder (PIT) tag system. A) The components of the RFID readers showing the two antennas, the RFID reader board, and the rechargeable battery pack. Inset shows an unhoused glass PIT tag. B) RFID reader house in a plastic food storage container in the field. C) PIT tag that has been attached to the banded tarsus of a Manx shearwater using a zip tie.

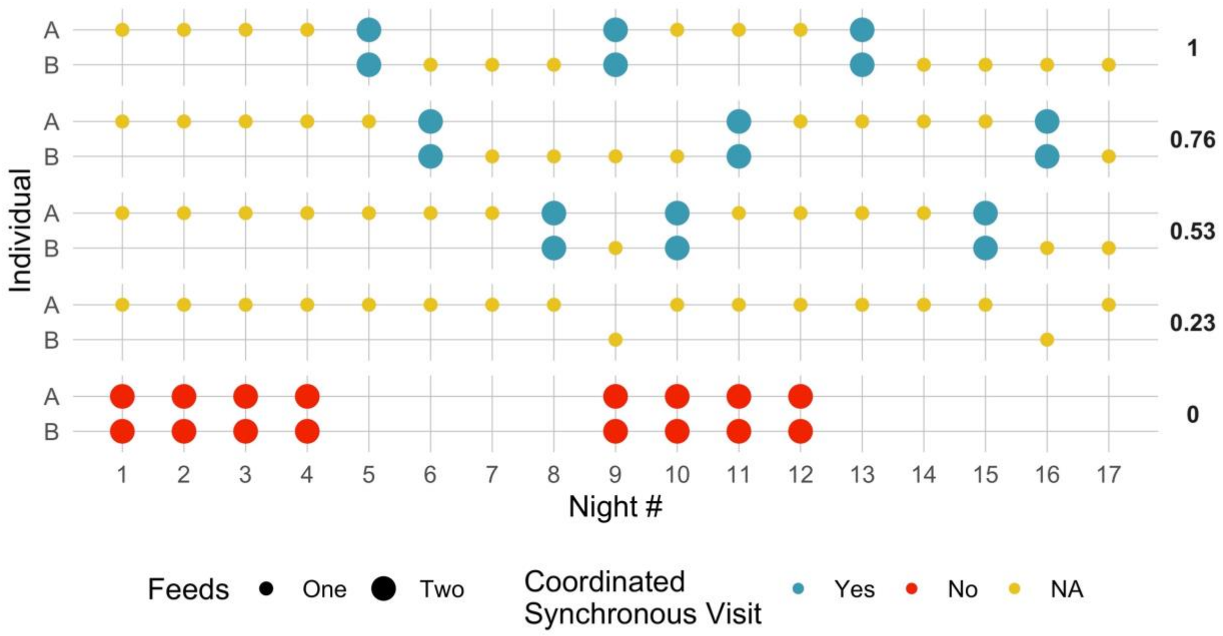


Figure 2.2 Cartoon representation of different provisioning scenarios ranging from complete coordination between two partners that are both dual foraging (top) to fully uncoordinated dual foraging (bottom). Each point represents a feeding. Point size corresponds to whether one (small) or two (large) adults returned to the nest to feed. Points are colored according to whether adults were coordinated following synchronous nest visits, which is only applicable on nights when both partners returned to feed. The corresponding coordination scores for each pair as calculated using metric 1 are given to the right of each provisioning scenario.

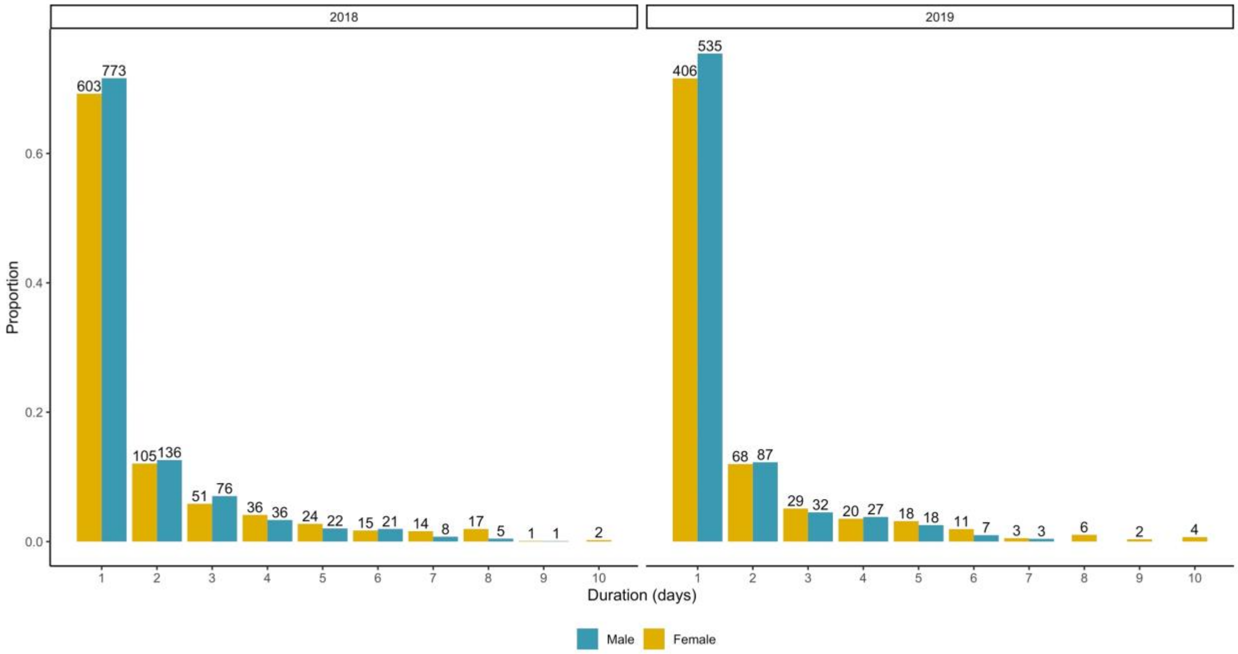


Figure 2.3 Proportion of trip durations by males and females in 2018 and 2019. Only trips from sexed birds are shown. Counts of each trip duration are given above the corresponding bar. Trip lengths greater than 10 days (n = 5), all of which were made by females in 2018, are not shown.

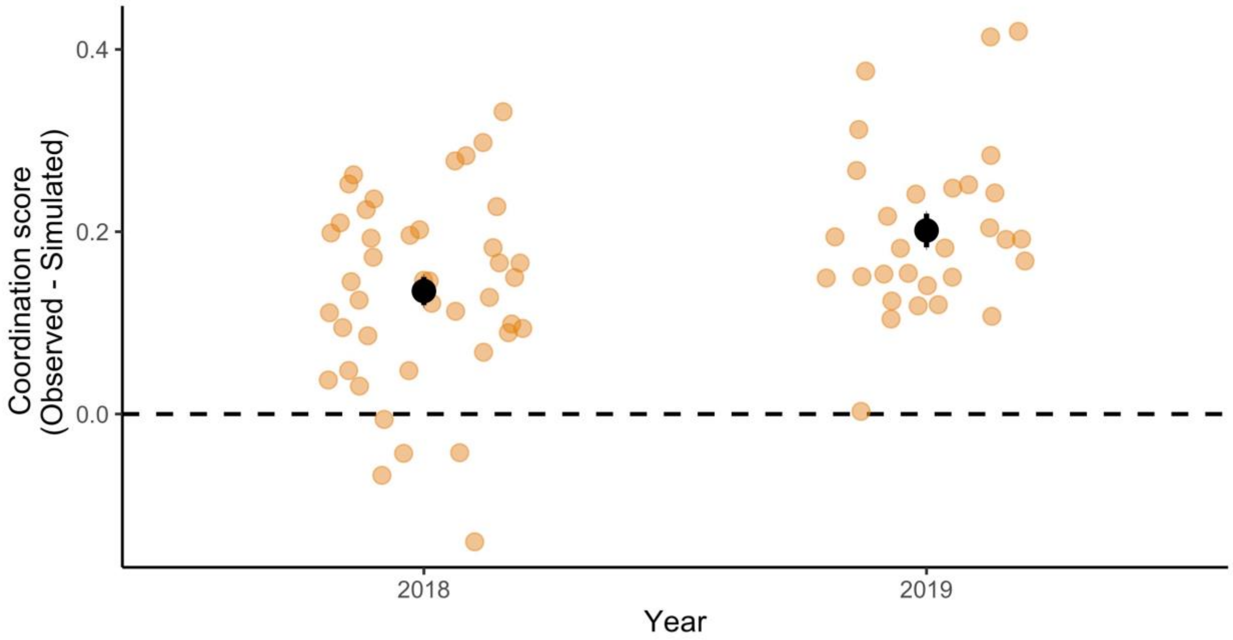


Figure 2.4 Differences in coordination scores (observed – simulated) for each pair in 2018 and 2019. Raw values are shown as orange points. Black points show the estimated marginal means (± S.E.). Values above zero suggest greater coordination than would be expected by chance.

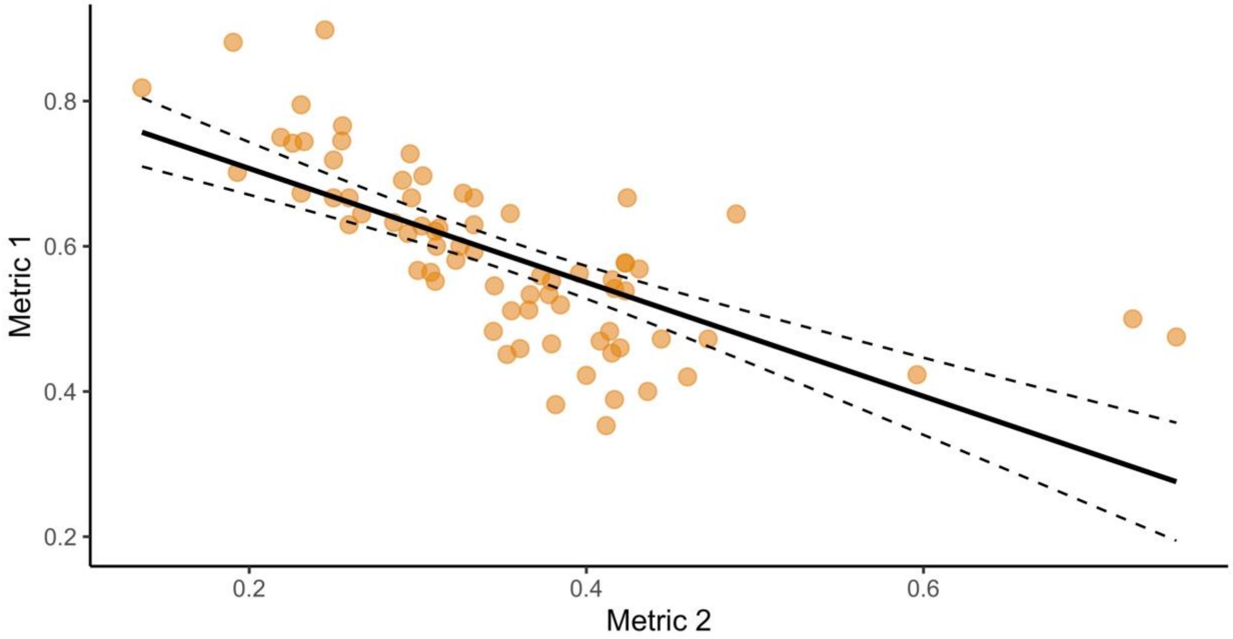


Figure 2.5 Comparison between coordination scores (metric 1) and the difference from a balanced proportion of adult feeding and chick feeding (metric 2).

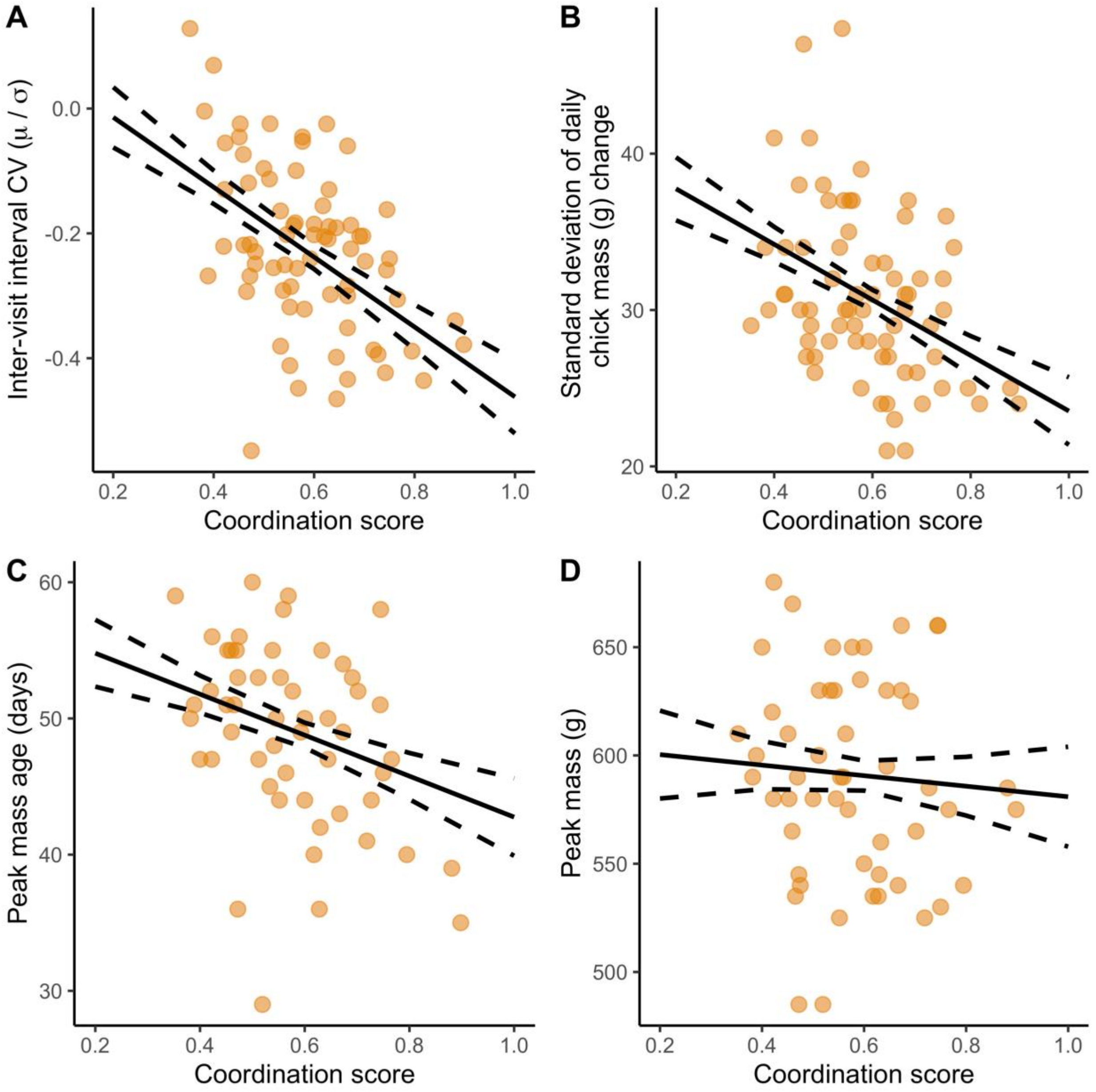


Figure 2.6 Relationship between coordination score for each pair (in 2018 and 2019) and the coefficient of variation in inter-visit interval. Pairs with higher coordination scores fed more consistently than did less coordinated pairs.

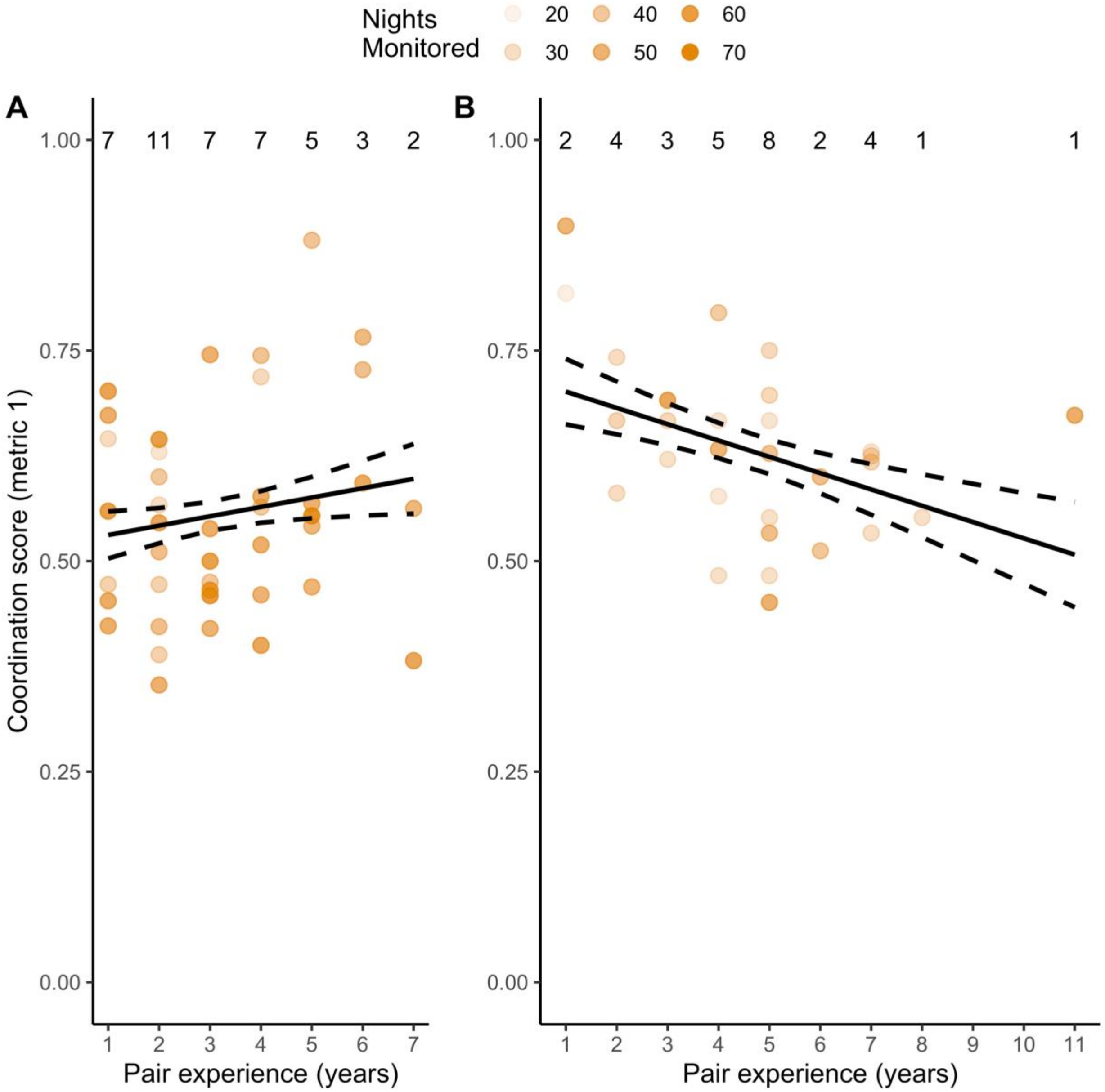


Figure 2.7 Relationship between pair experience (duration of the pair bond in years) and the observed coordination score for each pair in 2018 and 2019. Sample sizes for each group are given at the top of each panel. Coordination was significantly lower in 2018 than in 2019 and was observed to decrease with pair experience in 2019.

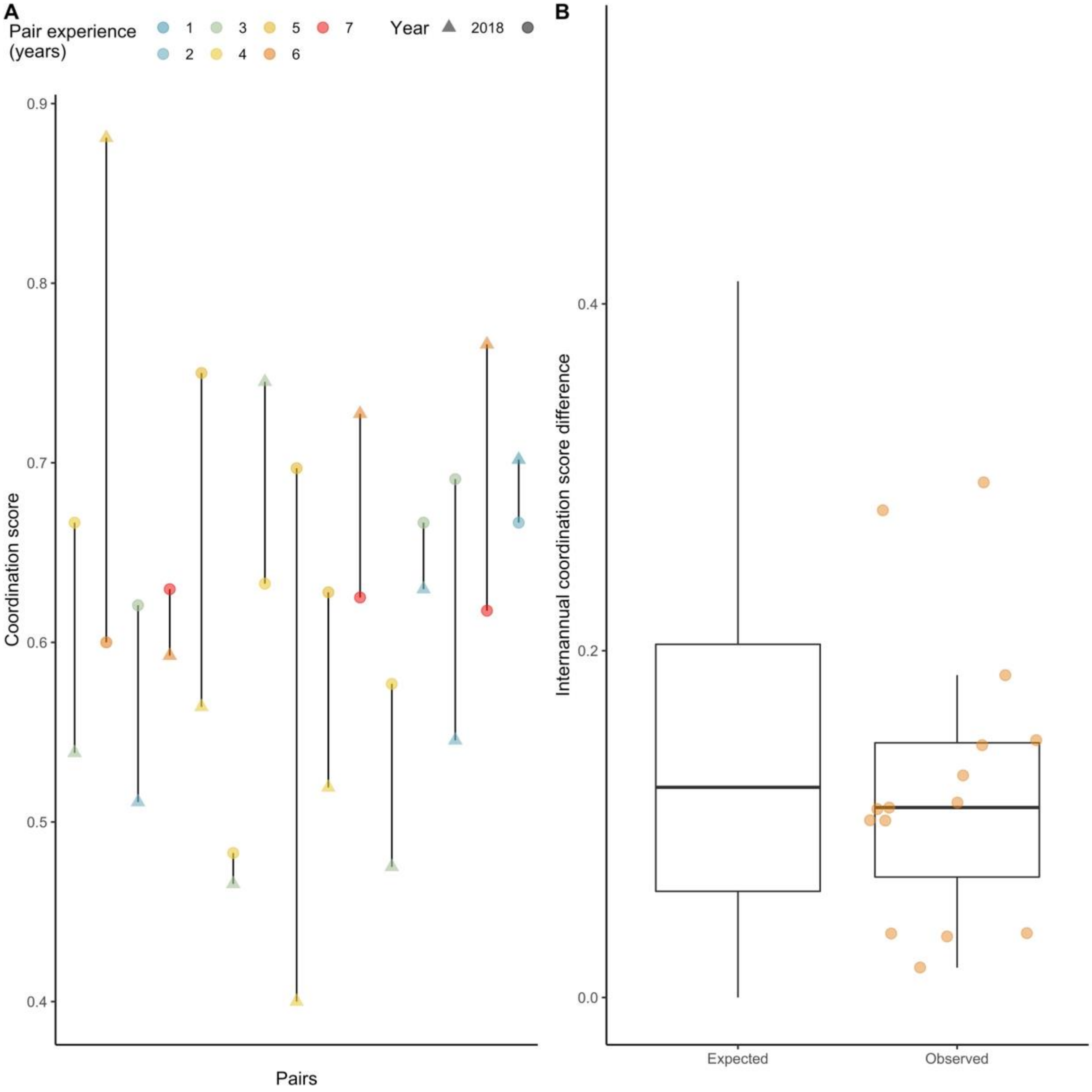
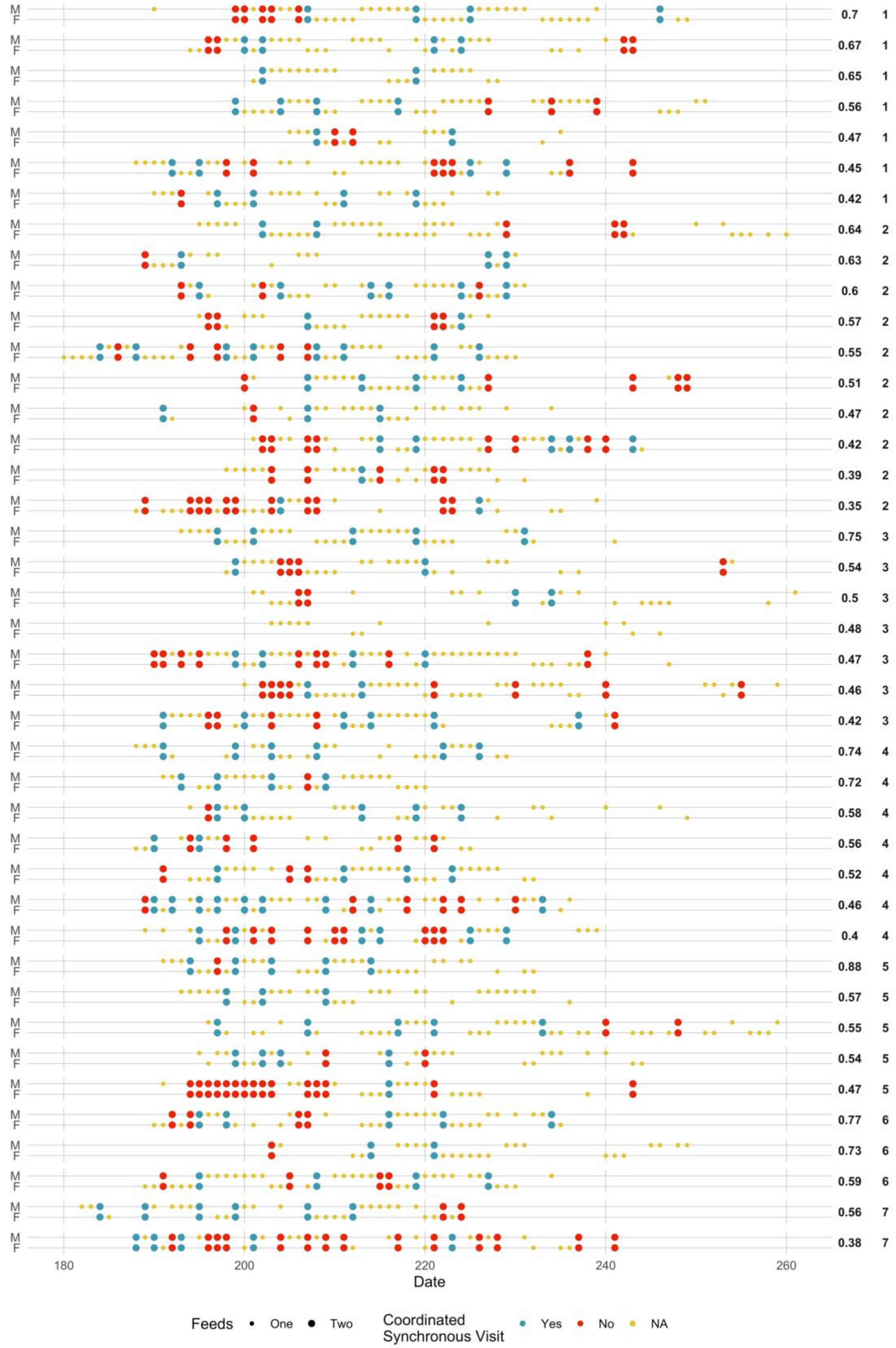
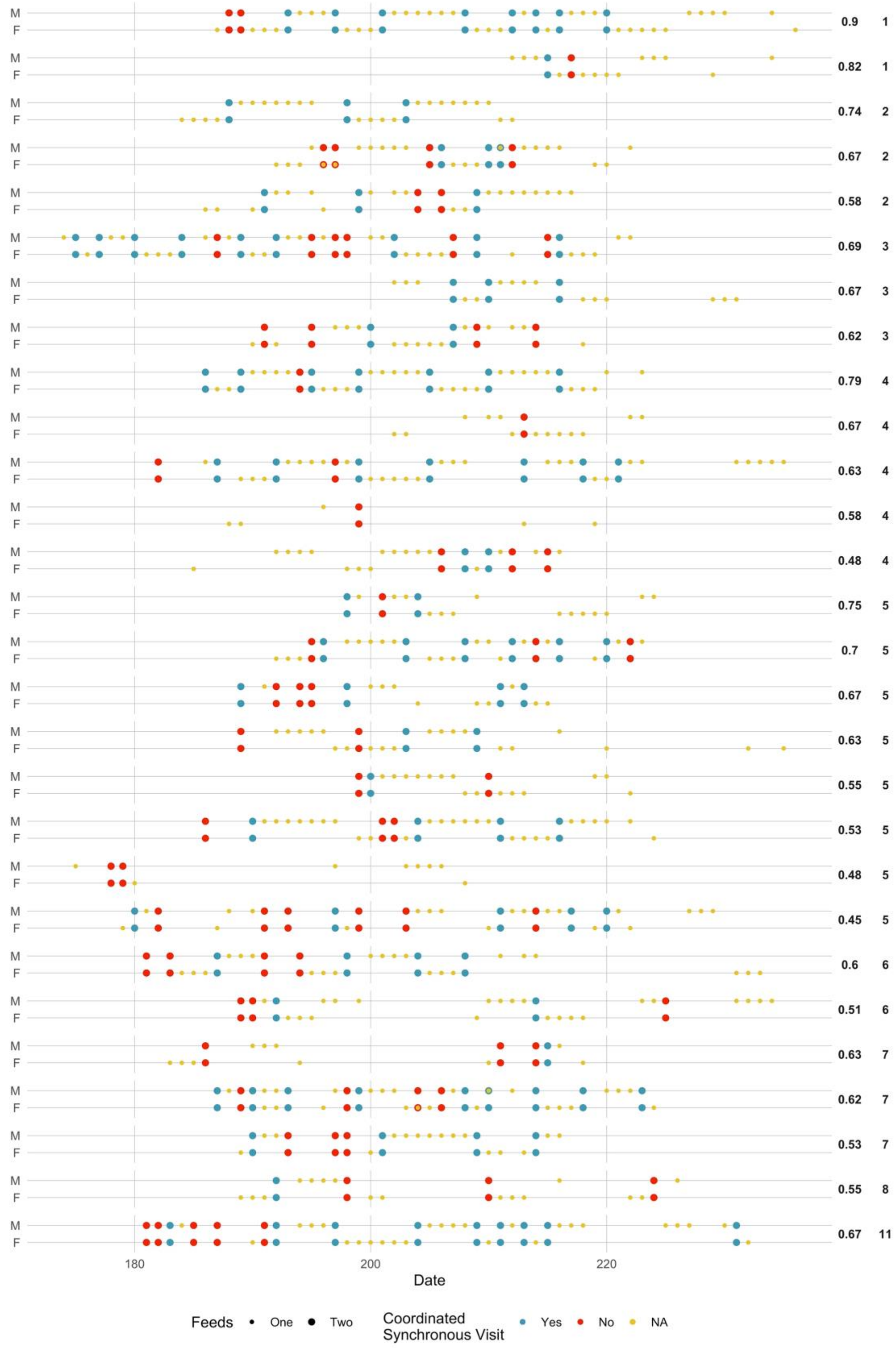


Figure 2.8 A) Coordination scores for pairs tracked in two years (n = 15). Points show the coordination score for that year (2018 = triangle, 2019 = circle) and are colored according to the experience of the pair in that year. B) Comparison of the observed differences in coordination scores within years as shown in pasnel A and the expected differences in coordination scores between a random pair in 2018 and a random pair in 2019.


M
F
0.7 1
0.67 1
0.65 1
0.56 1
0.47 1
0.45 1
0.42 1
0.64 2
0.63 2
0.6 2
0.57 2
0.55 2
0.51 2
0.47 2
0.42 2
0.39 2
0.35 2
0.75 3
0.54 3
0.5 3
0.48 3
0.47 3
0.46 3
0.42 3
0.74 4
0.72 4
0.58 4
0.56 4
0.52 4
0.46 4
0.4 4
0.88 5
0.57 5
0.55 5
0.54 5
0.47 5
0.77 6
0.73 6
0.59 6
0.56 7
0.38 7
180
200
220
240
260
Date
Feeds
• One
● Two
Coordinated Synchronous Visit
● Yes
● No
● NA


M
F
0.9 1
0.82 1
0.74 2
0.67 2
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0.69 3
0.67 3
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0.79 4
0.67 4
0.63 4
0.58 4
0.48 4
0.75 5
0.7 5
0.67 5
0.63 5
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0.53 5
0.48 5
0.45 5
0.6 6
0.51 6
0.63 7
0.62 7
0.53 7
0.55 8
0.67 11
180
200
220
Date
Feeds
One
Two
Coordinated Synchronous Visit
Yes
No
NA

Appendix 2.1 Figure 1 Detection timelines for all pairs of known experience in 2018 (top) and 2019 (bottom). As in Figure 1, each line is the detection history for one individual and each point represents a feeding on one night. Point size correspond to whether one (small) or two (large) adults returned to the nest to feed. Points are colored according to whether adults were coordinated following synchronous nest visits, which is only applicable on nights when both partners returned to feed. The corresponding coordination scores for each pair as calculated using metric 1 are given to the right of each provisioning scenario. On the far right, the experience for the pair is given.

Chapter 3. Increased behavioral flexibility during incubation drives higher hatching success for experienced Cassin's auklet pairs

ABSTRACT

Long-term partnerships are common in socially monogamous birds. In these species, pairs that remain together for multiple breeding seasons often have higher reproductive success. Yet while the maintenance of long-term partnerships may be ultimately explained by the higher reproductive success enjoyed by experienced pairs, the proximate, behavioral drivers of this 'mate familiarity effect' are largely unknown. In this study, we explored the mate familiarity effect in Cassin's auklets (*Ptychoramphus aleuticus*), a small seabird that maintains long-term partnerships. Using 34 years of breeding records from Southeast Farallon Island, we show that after controlling for age and lay date, pairs with more years of breeding experience had higher hatching success. The strength of the effect of pair experience on hatching success, however, varied with environmental conditions and was less pronounced in years with higher prey availability. To assess behavioral differences between new and experienced pairs, we measured the frequency of egg neglect during incubation as an indicator of pair coordination in three years with varying environmental conditions (2017-2019). We found that egg neglect rates were higher for pairs that failed during incubation and were also higher in a year with low prey availability. We did not, however, observe any differences in egg neglect rates between new and experienced pairs during any of our study years. Consistent with the findings from our analysis of the long-term breeding records, we found that in 2019, a year with low breeding success, experienced pairs had higher reproductive success despite not showing any differences

in egg neglect rates. This suggests that individuals in experienced pairs may be responding more flexibly to neglect by their partner by not abandoning the breeding attempt.

3.1 INTRODUCTION

In many avian species, males and females form exclusive bonds during the breeding season and, in some cases, throughout the entire year. Some species take this relationship further and maintain the same partner for multiple breeding attempts, which is known as perennial monogamy (Ens et al. 1996). Among species with perennial monogamy, however, there is substantial variation in pair bond duration and the propensity for divorce, which has prompted interest in the causes of this variation (Dubois & Cézilly, 2002; Jeschke & Kokko, 2008). Understanding the benefits of long-term partnerships is challenging, as it requires multi-year studies on the same breeding pairs and disentangling confounding effects such as individual experience and age, which may independently affect reproductive success.

Many explanations have been proposed as to why individuals maintain long-term partnerships as well as for the corollary of this behavior, divorce. Ultimately, mate retention should be expected when reproductive success is higher for more familiar pairs than for inexperienced pairs (J. M. Black, 1996). This ‘mate familiarity effect’ has been reported in a number of species, yet the proximate behavioral drivers of this relationship remain unclear. One possibility is that mate familiarity may allow individuals to avoid costs associated with mate selection, such as delayed breeding (Choudhury, 1995), and a number of studies have found that mate retention is often associated with laying earlier (Fowler, 1995). Lay date may independently determine hatching and fledging probability since pairs that lay earlier are more likely to have access to sufficient resources (Verhulst & Nilsson, 2008). As such, pair experience may indirectly benefit reproductive success by allowing pairs to better match their breeding timing to resource availability. Mate familiarity might also directly benefit reproductive success by increasing the breeding competence of the pair by allowing pairs to refine shared behaviors, such as establishing breeding territory, incubating eggs, or protecting and provisioning offspring (Griggio & Hoi, 2011; Mariette & Griffith, 2015; Tyson et al., 2017). Importantly, behavioral benefits from pair experience may also depend on the environmental context, i.e. a quality-by-environment interaction (Wilson & Nussey, 2010). For instance, experienced, high-quality pairs may breed successfully even in environmentally stressful, low resource years, due to the improved coordination of the pair, but differences between pairs may be diminished during environmentally favorable periods (Lescroël et al., 2010). As such, if mate familiarity does benefit reproductive success, it may do so indirectly or directly, but interactively with environmental conditions. Though many studies have suggested that direct, behavioral benefits from mate familiarity might explain long-term partnerships, no studies have found evidence for increased coordination among experienced pairs in any species and to our knowledge, no studies have examined how environmental context may moderate the effects of pair experience.

Cassin's auklets (*Ptychoramphus aleuticus*) display perennial monogamy and some of the strongest support for the mate familiarity effect comes from research on this species breeding on Southeast Farallon Island (SEFI). Using a long-term dataset of known-age individuals, two previous studies found that more experienced pairs laid earlier, had higher hatching and fledging rates, and fledged larger chicks (Emslie et al., 1992; Pyle et al., 2001).

While these studies provide compelling evidence that pair experience indirectly benefits reproductive success, these studies did not explore whether the relationship between experience and reproductive success was independent of lay date. Consequently, it is unclear whether the mate familiarity effect in this species is entirely driven by indirect effects from earlier lay dates or whether there are also direct effects from pairs improving their coordination of critical breeding behaviors.

Like most seabirds, Cassin's auklets have an extended breeding period and reproductive success depends on continual participation from both partners. Breeding failure in this species typically occurs during the incubation period, which lasts roughly 38 days (Manuwal, 1974). During this period, partners alternate between energetically taxing 24-hour incubation stints, where individuals lose approximately 9% of their body mass, and an equal amount of time foraging at sea to recuperate (Manuwal, 1979). If the foraging partner does not return after 24-hours, the incubating partner may continue to incubate and further lose mass or leave the nest, resulting in egg neglect. Unattended eggs face a greater risk of predation and are exposed to ambient temperatures, which slows development, extends the overall incubation period, and may be lethal (Astheimer, 1991). Consequently, improved turn-taking during incubation is likely to strongly influence overall reproductive success (Heaney & Monaghan, 1996). Given that incubation coordination depends on interactions between partners, this behavior is commonly suggested as a possible benefit of increased mate familiarity (Gabriel & Black, 2013; Sánchez-Macouzet, Rodríguez, & Drummond, 2014; Van De Pol et al., 2006). To date, however, no studies have shown this behavior to relate to the experience of breeding pairs.

In this study, we reexamined the mate familiarity effect in Cassin's auklets and assessed whether a critical breeding behavior, namely, incubation coordination, was related to differences in hatching success between pairs. We began by analyzing a 34-year dataset of breeding records from known-age pairs of Cassin's auklets to assess whether a direct effect of mate familiarity on hatching success remained after controlling for additional covariates that were not previously considered, in particular, lay date and oceanographic indicators. We then evaluated behavioral differences between pairs by monitoring incubation coordination in new and experienced pairs during three years with contrasting environmental conditions. We hypothesized that experienced pairs would better coordinate breeding behaviors and predicted that experienced pairs would show reduced rates of egg neglect. Observing behavioral differences between pairs would provide further support for a direct mate familiarity effect in this species.

3.2 METHODS

Field Methods

SEFI (37°42'N, 123°00'W) is a rocky offshore island that is part of the Farallon Island Wildlife Refuge within the California Current. Since 1972, Point Blue Conservation Science has continuously monitored Cassin's auklets breeding in wooden artificial nest boxes on the island (Pyle, 2001). Each year, boxes are checked for occupancy and birds that recruit into these boxes are banded and sexed morphometrically (Nelson, 1981). Occupied boxes are checked every 5 to 15 days to establish the lay date for the single egg, and then checked 25 days later to determine the egg's fate. Chicks that reach the fledging stage (>35 days old or fully feathered) are outfitted with a United States Geological Survey (USGS) stainless steel leg band. Birds banded as chicks that later recruit into a nest box constitute the known-age individuals in the study. Non-known-age individuals are birds that recruit into nest boxes, but are born in natural nesting sites and so are not banded as a chick. Individuals typically return to the same nest box each year. This allows for pairs to be tracked for multiple years and for the breeding experience of each pair to be determined. Records from this monitoring procedure were used to model the effect of pair-bond duration on reproductive success.

Behavioral data on pair coordination were collected during the 2017-2019 breeding seasons. In each year, we monitored continuous nest attendance for 40 pairs from early incubation (immediately following laying) through the cessation of provisioning. Relatively few known-age pairs form each year, which prevented us from tracking only pairs where both individuals were of known age. Only pairs with at least one known-age individual, however, were tracked. From the 40 pairs tracked each year, we targeted pairs based on the experience of the pair and the age of the known-age individual. Within each pair-group, we selected individuals ranging from 2 to 17 years of age (Figure 3.1). Pairs were considered inexperienced if breeding together for the first time (i.e., they had not been observed occupying the same nest box in a previous year) and experienced if they had previously bred together. We chose a cutoff of one year to classify experience given the pronounced change in reproductive success between the first-year pairs mated together and the second year (Figure 3.2).

To monitor nest attendance, we used radio-frequency identification (RFID) readers and passive integrated transponder (PIT) tags. RFID readers were powered by a 12 V 12 aH sealed lead acid (SLA) battery and had two circular antennas for detecting PIT tags (Bridge & Bonter, 2011). The RFID reader and SLA battery were enclosed in a plastic food-storage container and placed nearby the nest box. The two antennas were attached to the nest box entrance tunnel, which allowed for the direction of individuals moving through the entrance tunnel to be determined, based on the sequence of detections on the antennas (procedure described below). RFID readers were programmed to scan for tags between sunset and sunrise, i.e., the period when Cassin's auklets enter and leave the nest. Individuals (n = 80) in nest boxes with RFID readers (n= 40) were equipped with uniquely coded PIT tags (EM41012, 125 khZ). We used several different methods for attaching PIT tags. In 2017 and 2018, we used a combination of commercially made tags (IB Technology, UK) and Darvic leg bands to which a shrink-wrapped PIT tag was attached. In 2018 and 2019, we also used tags that were 3D printed in acrylonitrile butadiene styrene (ABS), in which we inserted a glass sealed PIT tag (2 x 12mm EM4102, 125 khZ, Cyntag, USA). The combined weight of all tags was less than 0.5 g or ~0.2% of the average mass (179 g) of an adult Cassin's auklet in our dataset. In the field, target birds were retrieved from their nest box and tags were affixed to the unbanded tarsus. Tags were sealed closed with a small amount of a cyanoacrylate glue, which was allowed to dry before returning the bird to the nest box.

RFID data processing

During incubation, pair members alternate foraging and incubating stints, which typically last one day. To determine whether individuals were incubating or foraging, we classified the nightly RFID detection sequences for each individual using supervised random forests with two states, incubating or foraging. We observed that when birds return from a foraging trip (and before incubating the next day), individuals rapidly enter the nest resulting in few detections. Conversely, when leaving to forage, individuals wait at the nest entrance, in some cases for hours, resulting in a large number of detections. The random forest model was first trained on a dataset of RFID detections, which were manually classified as either individuals entering the nest (to incubate) or departing the nest (to forage). The random forest model was then applied to all incubation detections. (Additional detail on processing the RFID data and the variables used in the random forest model are given in Appendix 1.)

Hatching probability

In this study, we focused on one primary measure of breeding performance relative to pair experience: hatching success. To estimate the probability of hatching success, we fit a generalized linear mixed model (GLMM, binomial with a logit link) as a function of a suite of predictor variables. Predictors included sex, individual age and pair bond length in years (first time breeding pairs had a pair bond length of one) as well as an interaction between individual age and pair experience. Quadratic terms for both age and pair bond length were included to account for possible effects of senescence. GLMMs for hatching success also included lay date and hatch date, respectively. We also included average upwelling strength (March to June), which is a measure of environmental conditions that is linked to primary production along the California coast. Upwelling strength, defined as the average water volume transported through the Ekman Layer per second along 100 meters of coastline ($m^3 \times s^{-1} \times 100\ m^{-1}$), was measured for the area surrounding SEFI (36°N, 122°W). Data were obtained from the NOAA Pacific Fisheries Environmental Laboratory (www.pfeg.noaa. gov). Interaction terms between upwelling strength and both age and pair experience were included to account for potentially unequal effects of environmental conditions on pairs with varying levels of experience. Individual and year were included as random intercepts to account for repeated measurements at these levels. All predictors were centered and scaled to facilitate comparing estimated effects. The GLMM was fit using the R package 'lme4' (Bates et al., 2012). P values for each predictor were calculated by likelihood ratio tests comparing the full model to a reduced model without the predictor of interest. Post-hoc comparisons of significant predictors were conducted using the R package 'emmeans' (Lenth, Singmann, Love, Buerkner, & Herve, 2018).

Incubation coordination

We assessed the degree of incubation coordination between breeding partners by measuring the rate of egg neglect. We considered egg neglect to occur anytime at least one parent was not within the nest during the day. In some cases, both partners may remain in the nest by day, but we did not consider these as instances of reduced coordination in order to give a more conservative estimate of coordination (see Appendix 1 for a detailed justification). Egg neglect rates for each pair were calculated as the number of days of neglect relative to the number of days monitored during incubation. The monitoring period during incubation for each pair was taken to begin on the first night that both parents were detected at the nest and to end either when the egg hatched or six days after one pair member was assumed to have abandoned the nest. Six days was used as a cutoff to determine abandonment as this was the longest observed trip during incubation where the egg still hatched.

We modeled egg neglect rates for each pair as a function of year, age, pair experience (categorical: inexperience or experienced), and whether the egg hatched (categorical: failed or hatched). We also included interactions between year and both age and pair experience. The model was fit as a GLMM (binomial logit link). Pair ID was included as a random effect as some pairs were tracked in multiple years. The observed number of days of egg neglect for each pair was weighted by the total number of days monitored to account for unequal monitoring periods between pairs. We classified pair experience into two groups as our sample size did not allow us to treat pair experience as a continuous variable (Figure 3.1).

3.3 RESULTS

Ethics statement

We observed no instances of abandonment as a result of tagging as all tagged individuals were later detected during incubation. In each of the three years, hatch rates were not significantly different between PIT tagged pairs and control pairs that laid during the same period. Similarly, fledging rates were not significantly different between tagged pairs and control pairs.

Hatching probability

In total, our dataset included 2,539 laying records of 728 known-age birds between 1985 and 2019. The average annual hatching rate over this 34-year period was 0.78 and ranged from 0.24 to 0.92. The oldest individual in our dataset was 20 and the longest observed pair bond was 12 years (Figure 3.2). Age and pair experience were weakly correlated (Pearson's r =

0.37). Across all age groups, hatching success increased from 0.72 in first time pairs to 0.86 in pairs that were remating for the second time.

Lay date, age, and the interaction between pair experience and upwelling were all significant predictors of hatching success (Table 3.1). Hatching probability decreased strongly with lay date ($\beta = -0.38 \pm 0.06$, $\chi^2 = 30.5$, $p < 0.001$). Controlling for lay date, the main effects of age and pair experience showed similar, positive relationships with hatching probability ($\beta = 0.24 \pm 0.09$, $\chi^2 = 11.6$, $p < 0.001$ and $\beta = 0.33 \pm 0.11$, $\chi^2 = 7.84$, $p = 0.005$, respectively). There was an interaction, however, between the effect of pair experience with upwelling strength ($\beta = -0.18 \pm 0.07$, $\chi^2 = 5.41$, $p = 0.02$). In years with low upwelling, there was a larger positive relationship between pair experience and hatching probability. In contrast, in years with stronger upwelling, the effect of pair experience was attenuated with pairs showing higher overall hatching rates irrespective of experience level (Figure 3.3).

Incubation coordination

From 2017 to 2019, we monitored the incubation behavior of 86 unique pairs over 2,977 bird-days from 2017 to 2019. During this period, we recorded 1,464 incubation stints and 1,513 foraging trips (Table 3.2). Both incubation stints and foraging trips predominantly lasted one day, though in 2019 the average foraging trip duration was longer (Figure 3.4). Individual consistency in foraging and incubating times was additionally reflected by the relatively low rates of egg neglect as both partners tended to only make day long trips. In total, we identified 379 instances of egg neglect. Between pairs there was considerable variation in the rate of egg neglect. Incubation was completely coordinated (i.e., there were no days of egg neglect) in 44 pairs, but egg neglect rates were as high as 0.33 (of the days monitored) in some pairs that still hatched an egg. We found no relationship, however, between inexperienced pairs and experienced pairs (inexperienced: 0.11 ± 0.01; experienced: 0.11 ± 0.02; $\chi^2 = 0.06$, $p = 0.74$; Table 3.3, Figure 3.5A). Similarly, we found that the rates of egg neglect were unrelated to the age of the known-age individual in the pair (Table 3.3). Across all years, egg neglect rates were significantly higher among pairs that failed during incubation than pairs that hatched their egg (failed: 0.15 ± 0.02; hatched: 0.06 ± 0.01, $z = 3.2$, $p = 0.001$; Table 3.3, Figure 3.5B). Additionally, between years, egg neglect rates were significantly higher in 2019 (0.19 ± 0.02) than in both 2017 (0.05 ± 0.01) and 2018 (0.08 ± 0.02; Table 3.3; Figure 3.5C).

3.4 DISCUSSION

Using 34-years of breeding records, we evaluated the effect of pair experience on hatching success in Cassin's auklets. Consistent with previous studies, we found that individual age and lay date were both positively related to hatching success. Even after accounting for these factors, however, we found that the number of years of breeding experience with the same partner had a positive, independent effect on the probability of hatching. This suggests there is a direct benefit of mate familiarity beyond the indirect benefits of familiar pairs laying earlier (Emslie et al., 1992). The strength of the benefit of pair experience, however, varied with environmental conditions. In environmentally poor years, there was a stronger effect with more experienced pairs maintaining relatively high hatching success. Given this evidence for a direct, context specific effect of pair experience, we explored whether incubation coordination differed between pairs in three years with contrasting environmental conditions. In two years of our study, 2017 and 2018, there was strong upwelling in the region surrounding SEFI and Cassin's auklet breeding success was high. In contrast, 2019 had very low upwelling and there was widespread breeding failure during the incubation period. Consistent with these interannual differences in breeding success, there was significantly more egg neglect in 2019. Additionally, across years, egg neglect was more common in pairs that ultimately failed during incubation. Contrary to our expectations, however, we did not observe increased rates of neglect among inexperienced pairs during any of the years of our study.

While many studies have reported benefits of increased mate familiarity, the extent to which pair experience directly affects reproductive success, as opposed to indirectly via lay date, has been considered less frequently. On SEFI, more experienced Cassin's auklets lay earlier and this is associated with other measures of reproductive success (Emslie et al., 1992). Mate fidelity likely shortens the mate selection period (Servedio, Price, & Lande, 2013) and as Cassin's auklets are also site faithful, this likely facilitates the ability for familiar pairs to begin breeding earlier in the season. There is an additional benefit to laying earlier as Cassin's auklets on SEFI may double brood, and the likelihood of a pair double brooding decreases with lay date (Johns et al., 2018). Consequently, there are clear indirect benefits of pair experience on annual reproductive success. We observed that after controlling for lay date, there was still a positive relationship between hatching success and pair experience (Figure 3.3). This indicates that experienced pairs are likely to be more successful than inexperienced pairs that lay at the same time of year, which suggests a direct, benefit of mate familiarity. However, as more familiar pairs are necessarily comprised of older individuals and if older individuals have higher reproductive success, then a direct effect of pair experience might be spuriously concluded from a positive relationship between experience and reproductive success. Age-specific changes in breeding success in birds are common and may be caused by a variety of proximate drivers, such as improved foraging efficiency for older individuals (Forslund & Pärt, 1995; Martin, 1995). We observed a positive effect of age on hatching probability, consistent with previous reports (Lee, Warzybok, & Bradley, 2012; Pyle et al., 2001). Another possibility, aside from the effects of age or pair experience, is that more experienced pairs are comprised of higher 'quality' individuals, which are more likely to have initially high reproductive success and show high mate fidelity as well. A previous study on this population found that the pair-bond effect was independent of the identity of individuals within the pairs (Pyle et al., 2001). Additionally, in this study, the variability in hatch rate explained by the random effect term 'individual ID' was small and was not significant (result not shown), suggesting relatively a minimal effect of quality at the level of the pair.

The strength of the effect of both pair experience and individual age on hatching success, however, was mediated by environmental conditions. In weak upwelling years, age and pair experience were more strongly related to hatching success and this relationship decreased with increasing upwelling strength (Table 3.1, Figure 3.3). SEFI is located within the California Current System where primary productivity is largely driven by wind-forced upwelling, which ultimately determines the abundance of zooplankton within this region (Checkley & Barth, 2009). Cassin's auklets breeding on SEFI primarily prey on two krill species, *Euphausia pacifica* and *Thysanoessa spinifera* (Abraham & Sydeman, 2006). Consequently, in weak upwelling years, prey is likely to be less available or less accessible, requiring individuals to increase their foraging effort. During these periods, younger individuals may be disproportionately affected, due to lower foraging competence or less knowledge of prey distributions (Forslund & Pärt, 1995). Interestingly, we also observed that more experienced pairs were similarly less affected by poor environmental conditions, but that the effect of experience on hatching success was attenuated in high resource years. To our knowledge this is the first reported instance of the effect of mate familiarity on reproductive success being mediated by environmental conditions.

Though improved incubation coordination is commonly suggested to be a possible benefit of increased mate familiarity, we did not observe any differences in the rate of egg neglect between new and experienced pairs. In the two years of our study with favorable environmental conditions, egg neglect rates were very low, which are consistent with previous studies on egg neglect in this species (Astheimer, 1991; Ronconi & Hipfner, 2009). While Cassin's auklet eggs can tolerate short periods of neglect (typically less than 2 consecutive days) during the first third of incubation without substantial adverse effects, neglect later during incubation slows development, extends the incubation period, and may result in death (Astheimer, 1991). As such, there is likely to be strong selection for pairs to coordinate and so differences between pairs may simply be minimal under normal environmental conditions. During a weak upwelling year of our study (2019) with low hatching rates, egg neglect rates were significantly higher, but were similar between experienced and inexperienced pairs. Given the significant energetic costs of incubation, individuals may have limited ability to compensate for a partner. This is supported by the very infrequent occurrence of incubation stints longer than 1 day (Figure 4). As such, neglect may be unavoidable during resource poor years.

Given that we observed significantly higher hatching success for experienced pairs, but no differences in egg neglect rates, this suggests that improved coordination of incubation routines is likely not responsible for the direct effect of mate familiarity in this species. Hatching failure in Cassin's auklets typically occurs when one partner abandons the breeding attempt. As hatching success was significantly greater for experienced pairs across years, this suggests that more experienced pairs may have a higher threshold to abandon during incubation despite frequent egg neglect by both partners. Nest abandonment in birds is largely governed by hormonal levels, directing individuals towards either parental care or more survival-related behaviors (Sinervo & Svensson, 2016). In particular, the relative levels of corticosterone, a glucocorticoid hormone, and the pituitary hormone prolactin strongly affects an individual's propensity to abandon the breeding attempt (Spée et al., 2011). While incubating, individuals fast for a given interval and then must replenish energy reserves while foraging for a similar amount of time, which may not be possible during resource scarce years. Fasting individuals show elevated corticosterone and beyond a threshold this is believed to induce emergency life-history states, such as self-feeding and a reduction of parental care (Groscolas, Lacroix, & Robin, 2008; Wingfield et al., 1998). Prolactin, conversely, stimulates parental care behaviors and so modulates the impact of corticosterone (Angelier & Chastel, 2009; Buntin, 1996). Studies on the baseline levels of both of these hormones have found associations with individual experience and that pair-bond duration increases hormonal similarity, which is associated with reduced divorce rates (Adkins-Regan, 2008; Ouyang, van Oers, Quetting, & Hau, 2014; Smiley & Adkins-Regan, 2016). Consequently, while temporary egg neglect may still be observed in all pairs, if this behavior is driven by an individual's inability to recover sufficient resources while foraging, the hormonal stimulus to abandon the breeding attempt under stressful environmental conditions may be attenuated in more experienced pairs due to higher baseline prolactin levels.

This study, while unable to identify a behavioral basis for the mate familiarity effect in Cassin's auklets, nevertheless suggests that there is a direct benefit of pair-bond duration on reproductive success in this species. This finding adds to a growing appreciation that social selection may act on the interactions between pair members (Griffith, 2019). Additionally, our finding that pair experience is most critical for reproductive success in low resource years is especially salient given the increased environmental stochasticity facing many organisms. In socially monogamous species, pairs are less likely to reunite following breeding failure (Dubois & Cézilly, 2002). If increasingly variable environments induce divorce, lower mate familiarity may have carryover effects in subsequent breeding events, which could have population level implications, especially if pair bonds are routinely disrupted. Future research on this topic should focus on pair experience as a demographic trait in population projection models. It should also focus on quantifying the extent to which increased environmental stochasticity may disrupt long-term partnerships.

3.5 FIGURES

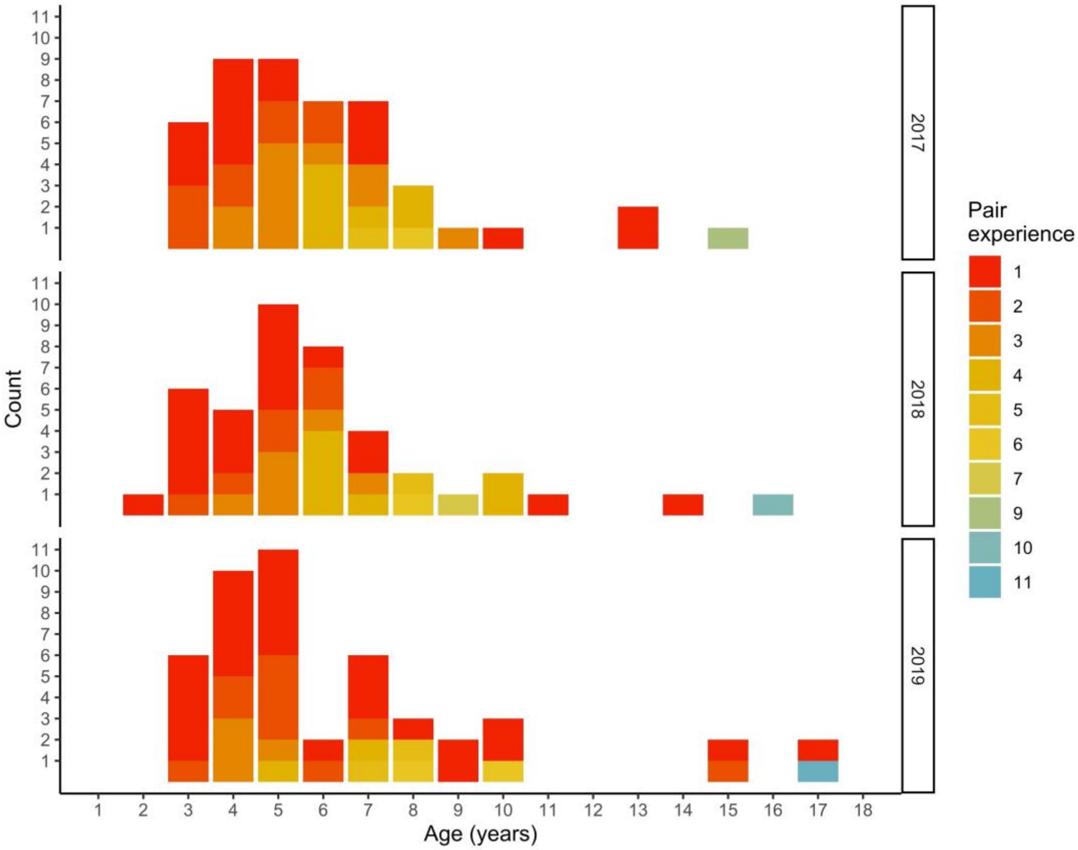
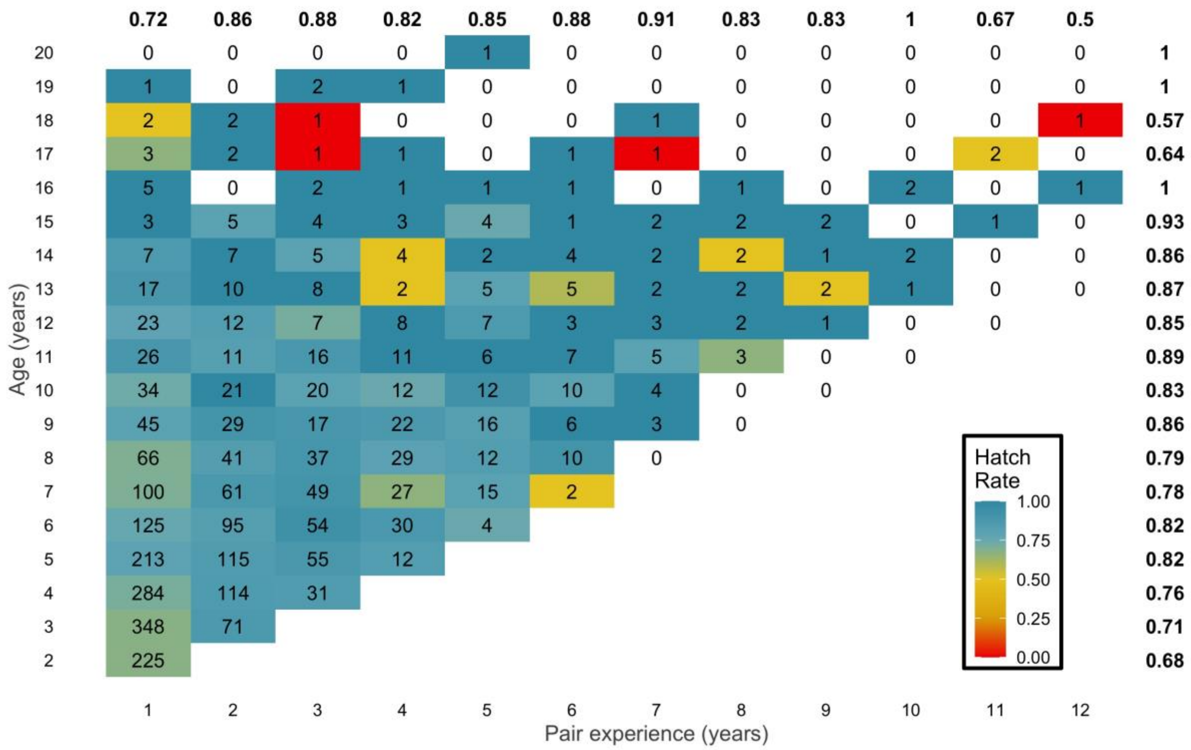


Figure 3.1 – Summary of individuals tracked with radio frequency identification (RFID) readers in each year. In each pair, at least one individual was known age and the experience of the pair was also known. Pairs were targeted to include a range of combinations in terms of pair experience and age.



Age (years)	1	2	3	4	5	6	7	8	9	10	11	12	
	0.72	**0.86**	**0.88**	**0.82**	**0.85**	**0.88**	**0.91**	**0.83**	**0.83**	**1**	**0.67**	**0.5**	
20	0	0	0	0	1	0	0	0	0	0	0	0	**1**
19	1	0	2	1	0	0	0	0	0	0	0	0	**1**
18	2	2	1	0	0	0	1	0	0	0	0	1	**0.57**
17	3	2	1	1	0	1	1	0	0	0	2	0	**0.64**
16	5	0	2	1	1	1	0	1	0	2	0	1	**1**
15	3	5	4	3	4	1	2	2	2	0	1	0	**0.93**
14	7	7	5	4	2	4	2	2	1	2	0	0	**0.86**
13	17	10	8	2	5	5	2	2	2	1	0	0	**0.87**
12	23	12	7	8	7	3	3	2	1	0	0		**0.85**
11	26	11	16	11	6	7	5	3	0	0			**0.89**
10	34	21	20	12	12	10	4	0	0				**0.83**
9	45	29	17	22	16	6	3	0					**0.86**
8	66	41	37	29	12	10	0						**0.79**
7	100	61	49	27	15	2							**0.78**
6	125	95	54	30	4								**0.82**
5	213	115	55	12									**0.82**
4	284	114	31										**0.76**
3	348	71											**0.71**
2	225												**0.68**

Figure 3.2 – Sample sizes for each age and pair experience group in the dataset of known-age Cassin's auklets. Each cell is colored by the average hatch rate for that age and pair experience group. Hatch rate averages weighted by the sample size in each group are shown for the entire age and pair experience class at the top of each row and column, respectively.

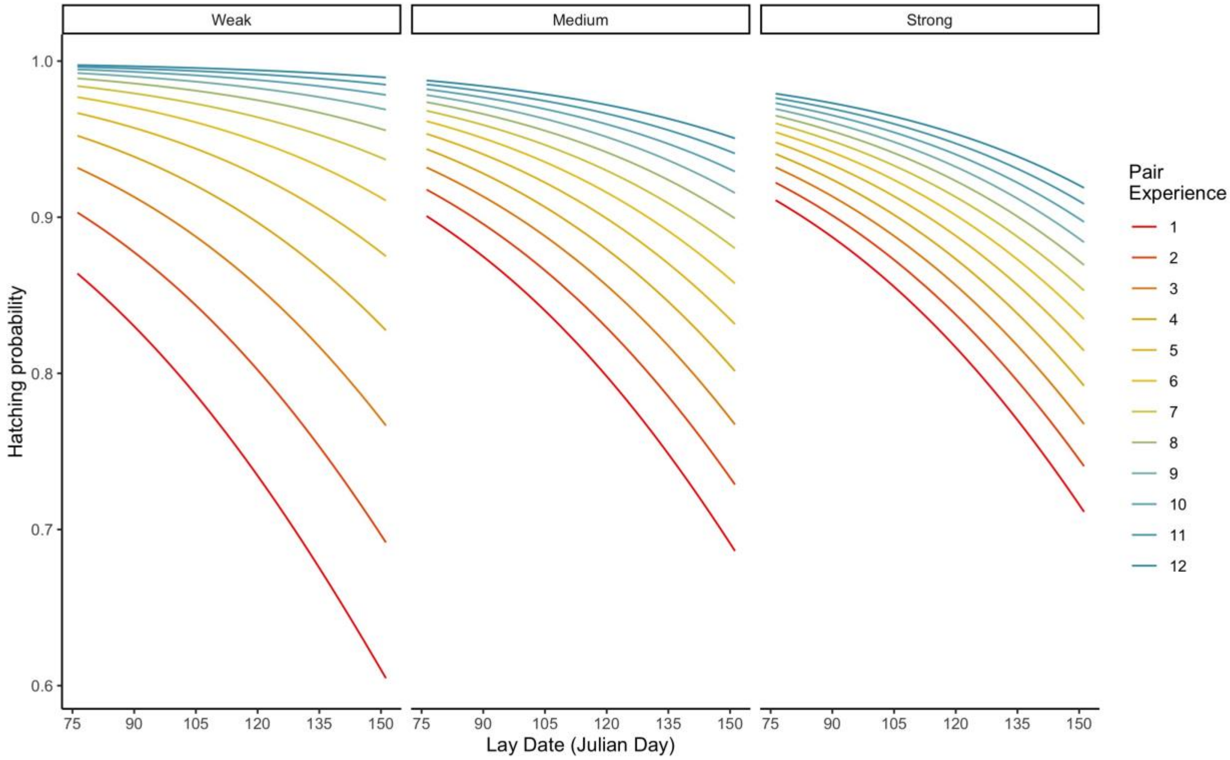


Figure 3.3 – GLMM predicted responses of hatching probability in Cassin's auklets as a function of pair experience and lay date for three upwelling scenarios. For the purpose of visualization, weak upwelling was defined as 118, medium as 175, and strong as 200 (m^3 x s^{-1} x 100 m^{-1} of coastline) for the monthly average (March to June) values near SEFI from 1985-2019.

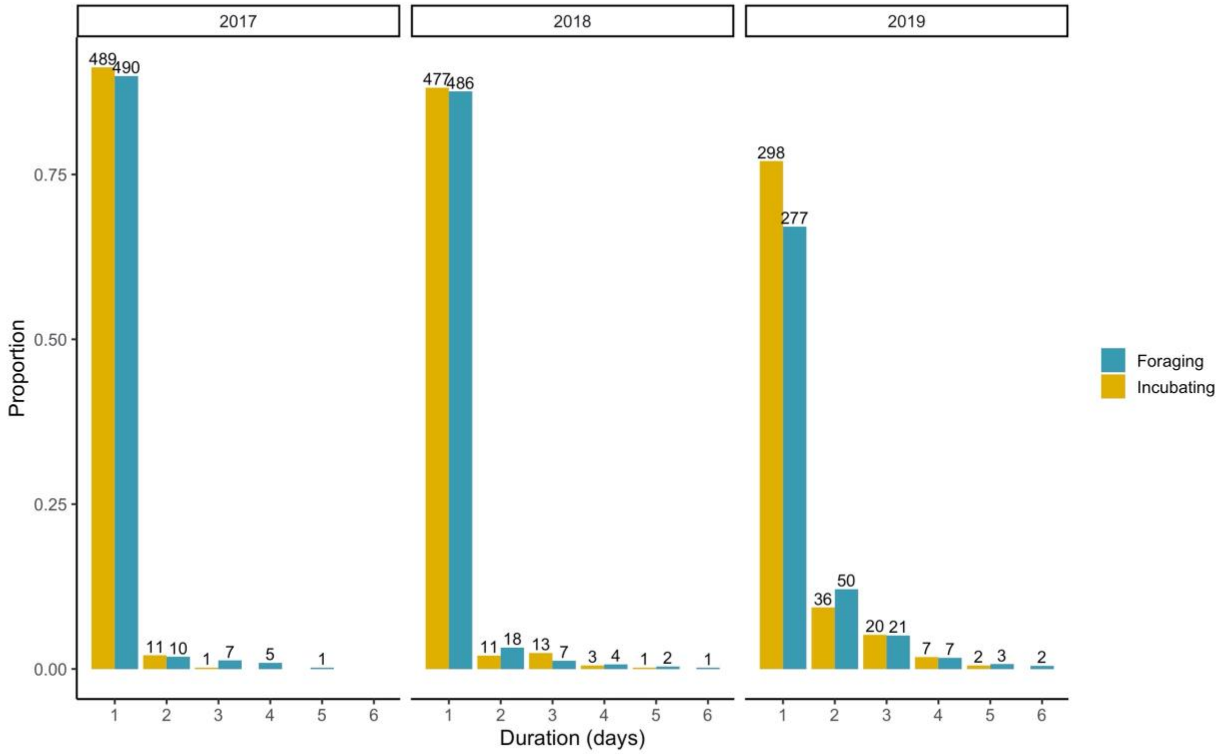


Figure 3.4 – The relative number of foraging and incubating stint lengths in each year. Total numbers for each stint length by type are given above the corresponding bar.

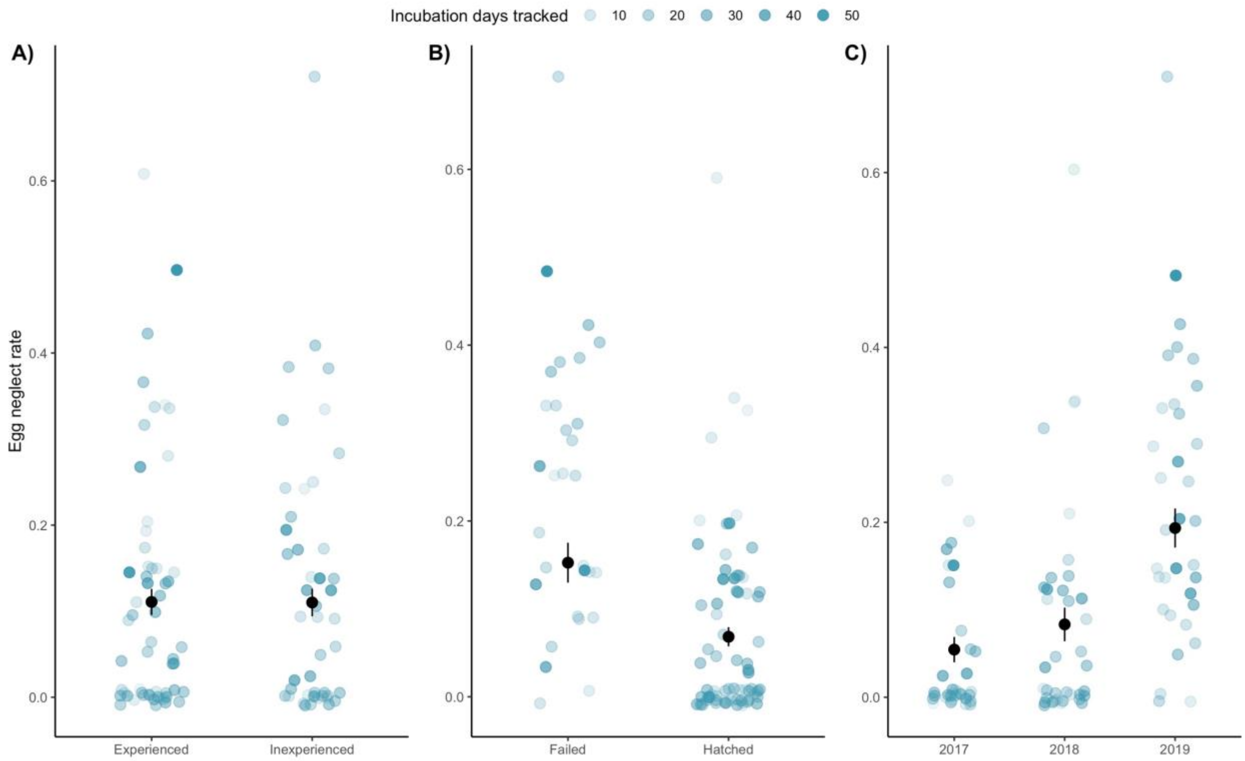


Figure 3.5 – GLMM predicted responses of egg neglect rates in Cassin's auklets between experienced and inexperienced pairs (A), pairs that failed during incubation and pairs that hatched an egg (B), and between the three study years, 2017, 2018, and 2019 (C). Black points give the estimated marginal mean (± S.E.) from the full model (Table 3) and blue points (jittered) show the raw data.

3.6 TABLES

Table 3.1 Untransformed general linear mixed effect model predictor estimates for hatching success. All predictors were centered and scaled to unit variance. Reference levels for factors are stated. Significance of each effect was estimated using chi-squared tests. P-value estimates below 0.05 are bolded. Marginal R^2 gives the proportion of the total variance described by the fixed effects within the model. Conditional R2 gives the proportion of the total variance described by both fixed and random effects within the model.

Effect	**Estimate (±SE)**	**χ^2 (df = 1)**	**p-value**
Hatching success (marginal R^2 = 0.10, conditional R^2 = 0.28)			
Intercept	2.38 (0.54)		
Lay	**-0.39 (0.07)**	**30.5**	**<0.001**
Sex (Male)	*Reference*	1.97	0.16
Sex (Female)	-0.16 (0.11)	1.97	0.16
Age	**0.24 (0.09)**	**11.6**	**<0.001**
Pair Experience	**0.33 (0.11)**	**7.84**	**0.005**
Upwelling Index	0.09 (0.19)	0.42	0.51
Age^2	-0.02 (0.05)	0.15	0.69
Pair $Experience^2$	-0.009 (0.05)	0.03	0.85
Age * Pair Experience	-0.15 (0.09)	2.21	0.13
Pair Experience * Upwelling Index	**-0.18 (0.07)**	**5.41**	**0.02**
Age * Upwelling Index	**-0.14 (0.08)**	**2.98**	**0.08**
Year variance (±SD)	0.72 (±0.84)		
Individual ID variance (±SD)	0.08 (±0.28)		

Table 3.2 Summary table for each year. Average upwelling (m^3 x s^{-1} x 100 m^{-1} of coastline) was calculated between March and June each year. The number of pairs tracked all pairs with sufficient data to calculate egg neglect rates.

Year	Average upwelling	# Pairs	Incubation stints	Foraging trips	Mean neglect rate
2017	214	34	1,035	1,050	0.06 (0 - 0.8)
2018	220	37	1,084	1,088	0.08 (0 - 0.6)
2019	149	35	901	914	0.22 (0 - 0.71)

Table 3.3 Untransformed general linear mixed effect model (logistic with logit link) predictor estimates for egg neglect rates. Reference levels for factors are stated. P-value estimates below

0.05 are bolded. Marginal R^2 gives the proportion of the total variance described by the fixed effects within the model. Conditional R2 gives the proportion of the total variance described by both fixed and random effects within the model.

Effect	Estimate (±SE)	χ^2 (df = 1)	p-value
Egg neglect rate (marginal R^2 = 0.21, conditional R^2 = 0.27)			
Intercept	-2.76 (0.82)		
Year:2017	***Reference***	**24.7**	**<0.001**
Year:2018	**0.58 (0.91)**	**24.7**	**<0.001**
Year:2019	**1.84 (0.83)**	**24.7**	**<0.001**
Age	0.03 (0.11)	3.5	0.06
Pair (Experienced)	*Reference*	0.1	0.74
Pair (Inexperienced)	0.97 (0.66)	0.1	0.74
Incubation Outcome (Failed)	***Reference***	**13.1**	**<0.001**
Incubation Outcome (Hatched)	**-0.93 (0.25)**	**13.1**	**<0.001**
Year:2017 * Age	*Reference*	0.75	0.68
Year:2018 * Age	0.01 (0.12)	0.75	0.68
Year:2019 * Age	-0.06 (0.11)	0.75	0.68
Year:2018 * Pair (Inexperienced)	-0.38 (0.64)	0.53	0.76
Year:2019 * Pair (Inexperienced)	-0.04 (0.57)	0.53	0.76
Age * Pair (Inexperienced)	-0.14 (0.07)	3.28	0.07
Individual variance (±SD)	0.26 (±0.51)		

APPENDIX 3.1

Radio-frequency identification (RFID) detections recorded each night were used to determine whether individuals were entering the nest to incubate or leaving the nest to forage. To do so, we used supervised random forest models, which were trained on a manually classified dataset (Breiman, 2001). Behaviors were manually classified by visually inspecting the detection sequence each night. We manually classified 1,742 detection sequences out of the 5,922 in our dataset. We then calculated a number of descriptive features of each detection sequence that could be used to determine whether birds were entering or leaving the nest (Table A1). These features were chosen to reflect the differences between how individuals behaved when entering the nest after returning from foraging or before leaving to forage (Figure A1).

We used 80% of the manually classified data to train the model and the remaining 20% to validate the model. The validated model was then applied to the remaining unclassified detection sequences. The out-of-bag estimate of error rate was 2.01% and the error rates for classifying incubating and foraging was 1.7% and 2.2%, respectively. The most useful detection sequence features for discriminating between incubating and foraging were the total number of detections each night, the number of detections within the first of minutes of the first detection, and the number of detections within the last of minutes of the last detection (Figure A1).

After classifying detection sequences, we interpolated probable missed detections between detections that were separated by two days, but where both detection sequences were labelled as the individual leaving the burrow to forage. In these situations, the bird would have entered the nest too rapidly to be detected, but would have been detected leaving after incubating for one day. We identified 80 missed detections in 2017, 67 in 2018, and 16 in 2019. We opted to interpolate these missed detections in order to make estimates of neglect more conservative.

Table A3.1 Description of features that were used to describe detection sequences. These features were then used as predictors of whether individuals were entering or leaving the nest in the random forest model.

Features of RFID detection sequences
Total number of detections on either antenna during
Number of detections on antenna one (the antenna at the nest tunnel entrance)
Number of detections on antenna two (the antenna nearest the nest box)
Number of the antenna to first have a detection
Number of the antenna to last have a detection
The rate of detections (total number of detections in the time between the first and last detection)
Number of detections within five minutes of the first detection
Number of detections within five minutes of the last detection
Time between the first and last detection
Whether the bird was the first bird detected
Whether the bird was the last bird detected
Number of detections on the next night detected
Number of detections on the previous night detected
Time of the first detection (minutes since sunset)
Time of the last detection (minutes since sunset)
Number of times detected on either antenna 1, then on antenna 2 and vice versa

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