Coordinated provisioning in a dual foraging pelagic seabird

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In long-lived species, care-giving parents are expected to balance their own condition with that of their offspring. Many species of seabirds display a unique behavioural adaptation for managing these conflicting demands known as dual foraging, in which long trips, largely for self-maintenance, are alternated with short trips, which are primarily for offspring care. While dual foraging is a widely studied behaviour, it entails a complication that is seldom discussed: if parents independently employ a dual foraging strategy, chicks might be abandoned for extended periods when the long trips of both partners coincide. Whether partners coordinate their dual foraging strategies, however, is largely unknown. To investigate this possibility, we used radio frequency identification readers coupled with passive integrated transponder tags to record extended sequences of foraging trips for breeding Manx shearwaters *Puffinus puffinus*. Our results show a pattern of foraging trips that indicates a high level of coordination between parents, which facilitates consistent provisioning. Additionally, we show that the propensity for pairs to coordinate declines across the chick rearing period. Given the potential costs of not coordinating, we expect this behaviour to be widely spread among dual foraging species.

Keywords: Coordinated provisioning, dual foraging, parental investment, Manx shearwater, *Puffinus puffinus*

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To maximize life-time fitness, iteroparous animals are expected to balance investment in the current reproductive period against future breeding opportunities (Williams, 1966). For long-lived species, this trade-off suggests that parents are unlikely to invest unduly in offspring at the expense of their own condition (Curio, 1988). Consequently, individuals should prioritize self-provisioning and only provide parental care when energetically capable (Sæther et al., 1993).

During chick care, many seabird species display a unique behavioural adaptation to reconcile these conflicting energetic demands known as “dual foraging” wherein long trips are interspersed with one or more short trips (Chaurand & Weimerskirch, 1994). During long trips, parents avoid the high travel costs of repeated commuting and may travel further to utilize more productive foraging grounds, but at the cost of reduced provisioning of the offspring. During short trips, however, the average daily provisioning load to the chick is larger (reviewed in Baduini & Hyrenbach, 2003). This strategy is likely an adaptation to the lengthy period of parental care undertaken by many seabird species, especially those with pelagic foraging habits, and the constraints of central place foraging. Numerous studies have documented dual foraging across a variety of taxa, including Procellariiformes (Weimerskirch et al., 1997; Granadeiro et al., 1998; Weimerskirch & Cherel, 1998), Sphenisciformes (Saraux et al., 2011) and Alcids (Welcker et al., 2009). While there is some suggestion that dual foraging might be more prevalent in offshore foraging species, this is not uniquely so as inshore foraging species have also been observed to display dual foraging, e.g. little penguins (*Eudyptula minor*) (Saraux et al., 2011).

While dual foraging is a widely studied behaviour, it entails a complication that is seldom discussed. Namely, if parents independently employ a dual foraging strategy, chicks might be abandoned for extended periods when long trips coincide. As prolonged bouts of starvation are likely to increase mortality, especially in young chicks, there should be selection for within-pair coordination in species with variable foraging trip lengths. While there is some evidence that the timing of “long trips” is not independent between partners in some species (Booth et al., 2000; Congdon et al., 2005), the degree of such coordination and the mechanisms underlying it are poorly understood.

The Manx shearwater *Puffinus puffinus* is a monomorphic, burrow-nesting seabird that is known to display dual foraging (Shoji et al., 2015; Fayet et al., 2015) and exhibits only minor sex-specific differences in foraging duration and meal size (Gray & Hamer, 2001; Guilford et al., 2008). The similarity in parental effort between sexes makes it likely that partners can compensate for each other. Moreover, like most Procellariiformes, Manx shearwaters have protracted incubation and chick-rearing periods, together lasting approximately 120 days (Brooke, 1990; Harris, 1966), which makes the breeding period energetically demanding, and the potential need for coordinated provisioning particularly acute. Given these features, the Manx shearwater is a plausible candidate in which to observe coordination of dual foraging routines between partners.

We used an automated nest monitoring system to examine the possibility of coordinated provisioning by monitoring foraging trip durations in Manx shearwater pairs during their chick-rearing period. These data allowed us to examine how individual foraging behaviour was adjusted in response to the partner. If pairs coordinate dual foraging routines in order to provision offspring consistently, we expected that while one pair member (partner A) was undertaking a long trip, the partner (partner B) would make repeated short trips. Upon returning from a long trip, partner A would initiate a series of short trips and partner B would switch to a long trip (shown pictorially in Figure 1). While several mechanisms might allow for individuals to coordinate such behaviour, we hypothesized that reuniting at the burrow might trigger a switch between foraging strategies. Smaller chicks lack the reserves to withstand prolonged periods of fasting, which makes regular provisioning during the first few weeks post-hatching especially critical for chick survival (Phillips & Hamer, 1999). Thus, we also predicted that coordination might be most advantageous during this earlier period and would decline as chick mass increased.

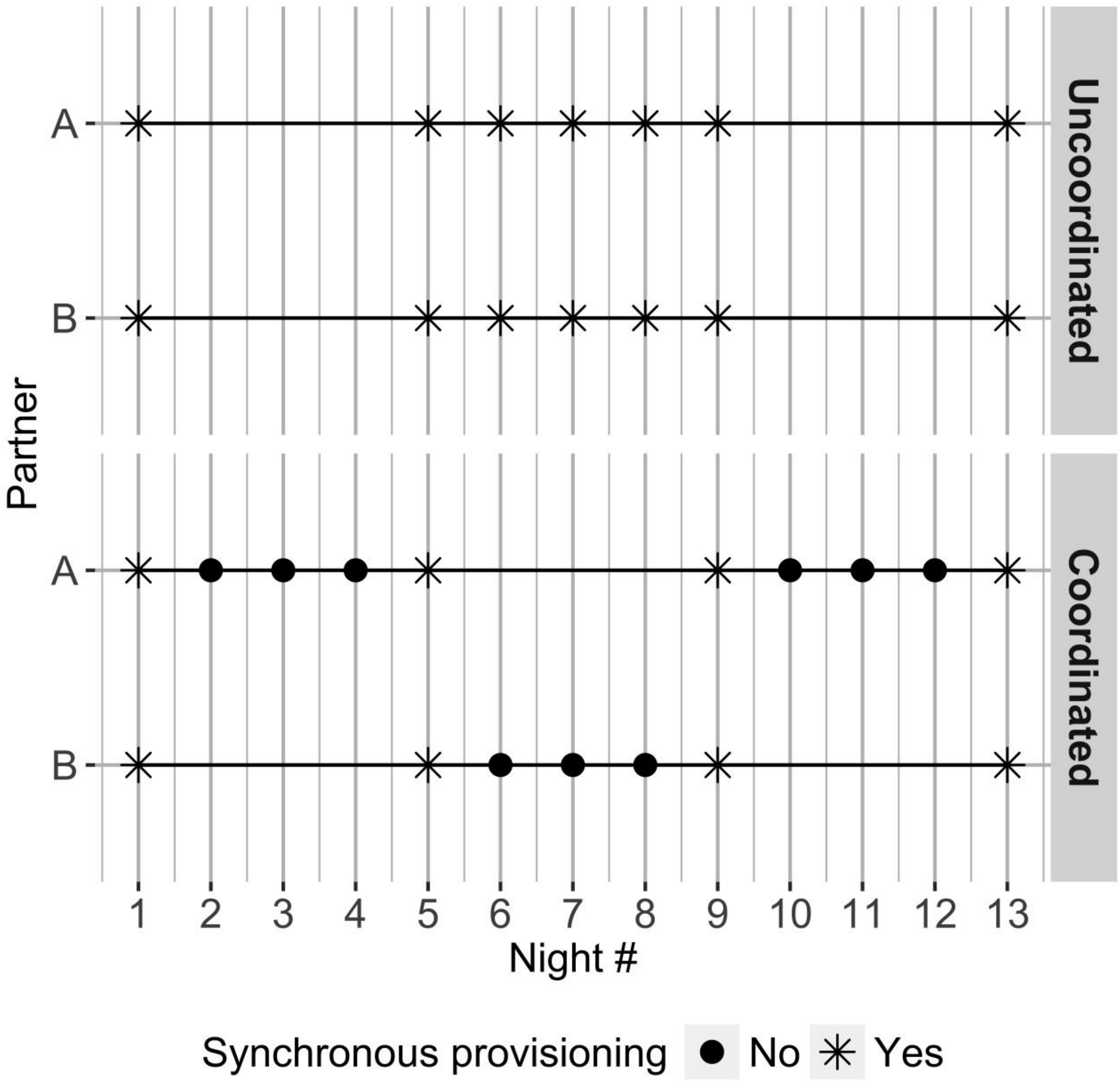

Figure 1 Illustration of expected nest attendance patterns if partners have uncoordinated or coordinated dual foraging routines. In the former case, both partners' foraging strategies are completely in phase. This maximizes the interval between feedings for the chick. In the case of coordinated dual foraging routines, each strategy is out of phase, which results in consistent provisioning. On night 1, partner B initiates a long trip and partner A initiates a sequence of short trips. When partner B next returns on night 5, partner A initiates a long trip and partner B switches to a series of short trips. This minimizes the interval between feedings. Under this scenario, pair

members switch foraging strategies after synchronously returning to the colony with their partner.

Materials and Methods

Ethical Note

All work adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, and was conducted after approval by the Countryside Council for Wales, the Skomer and Skokholm Islands Advisory Committee, the British Trust for Ornithology (BTO permit C/5311) and the University of Oxford Local Ethical Review Process (Zoo/LERC/190505). This study was part of the long-term monitoring program carried out by Oxford University since 2006 (see Dean et al. 2012 and Shoji et al. 2015 for details). The combined weight of bio-logging tags was no more than 2.2 g, roughly 0.5% of 450 g mean body mass, which is well below the recommended limit of 3% for flying birds (Phillips et al., 2003). Though handling and bio-logging tags may negatively affect birds, we observed that fledging success was not significantly lower between pairs monitored with RFID readers (0.84, n = 39) and other pairs (0.61, n = 38) within our study colony (2-sample binomial test: X^2_1= 3.9424, p-value = 0.977). Furthermore, in a detailed analysis of the impacts of our research on Manx shearwaters at our study site, we found that for a sample of 1,321 breeding attempts between 2009 and 2014 which led to an egg being laid, fledging success was 0.695 in our experimental nests versus 0.587 in control nests. This suggests that for a large sample our work has no detectable adverse effects on breeding success.

Study Site and Birds

Fieldwork was conducted on Skomer Island (54.44°N, 05.17°W), Wales, UK during the 2011 breeding period (March - August). Burrow nests were visited daily to determine hatching dates and to establish breeding pairs. When possible, adult females were sexed by cloacal inspection just after laying (Gray & Hamer, 2001). Chicks were weighed every one to three days using a Pesola spring scale. The chick-rearing period was considered to end once the chick had fledged (approximately 70 days after hatch) (Brooke, 1990).

To study foraging coordination between chick-rearing shearwater pairs, we used radio-frequency identification (RFID) readers coupled with passive integrated transponder (PIT) tags (see Naumowicz et al. (2010) for technical details of the sensor network). Our RFID readers broadly consisted of a loop antenna, the computer and a 12V battery power supply. The antenna was placed around the opening of the burrow. When a PIT tag passes within approximately 5 cm of the antenna, the tag is energized and transmits a unique identification number, which the RFID reader stores, along with the time of the detection.

We deployed RFID readers on 39 burrows nests in March at the start of the breeding season. Both pair members in each burrow were fitted with a PIT tag that was programmed with a unique identification number. PIT tags were shrink-wrapped to a cable tie, which was loosely affixed to the tarsus above the metal BTO identification ring. PIT tags including housing material weighed approximately 0.3 g. Five birds with PIT tags, each from a different pair, were also equipped with British Antarctic Survey geolocator-immersion loggers (models: Mk13, 14, 15, 18L, and 19), which weighed 1.5 - 1.9 g. Loggers were mounted to a Darvic plastic leg ring using two cable ties. All birds were taken from study burrows through an access hatch by hand and weighed at device deployment. Total handling time during the attachment procedure did not exceed ten minutes.

Data Analysis

All data processing steps and statistical analyses were conducted in R 3.2.3 (R Core Team, 2015). Means are presented throughout as ±1 standard errors. We used RFID readers to record foraging trip patterns within pairs. RFID readers record the PIT tag number and detection time, but not the direction of movement through the burrow. When a bird was detected by the reader, the direction of movement (entry to, or exit from the nest) was inferred as follows: during chick rearing (July to September), breeding shearwaters only visit the burrow for chick provisioning and do so exclusively at night. After feeding, chick rearing shearwaters immediately return to sea. This makes it likely that the first detection after sunset is an arrival at the burrow and the last detection before sunrise is a departure from the burrow. Based on this classification scheme, the time between each departure and arrival was considered the duration of the foraging trip. Similarly, during the interval between each arrival and departure the bird was assumed to be in the burrow. To validate these assumptions, saltwater immersion records from geolocator loggers from a subset of PIT tagged birds were interrogated. During any interval between RFID detections in which saltwater immersion was recorded, the bird was taken to be at sea and similarly, in any detection interval without saltwater immersion, the bird was taken to be at the nest. We used this method rather than manually checking the burrows to reduce potential impacts of visiting nests repeatedly. Our RFID readers also generated a log of the battery voltage. Below 10 volts, the RFID readers would not reliably detect PIT tags. Therefore, foraging trips during which the RFID reader fell below 10 volts for more than one hour were discarded in order to avoid potentially combining multiple trips.

Of the 39 RFID readers initially deployed, 24 operated continuously throughout the chick rearing period - the other 15 readers experienced prolonged periods of battery failure. Our foraging trip classification procedure identified 972 foraging trips. After discarding trips with more than one hour of lost battery power, 824 complete foraging trips remained for the 24 pairs. All five geolocators were successfully retrieved. Due to logger failure, however, saltwater immersion data could only be downloaded from four devices. The four individuals with functioning immersion loggers made a total of 37 foraging trips. All of these ostensible trips included periods of saltwater immersion and similarly, none of the intervening ostensible burrow visits contained periods of saltwater immersion, suggesting that our foraging classification scheme was valid.

For our analysis of foraging coordination we removed pairs with fewer than five synchronously initiated trips to promote a balanced comparison across pairs. Pairs primarily had insufficient recorded synchronous trips due to a shortened monitoring period. After this step, 17 pairs remained. These made 637 complete foraging trips. Coordination was analysed by examining whether individuals altered trip duration following synchronous visits to the burrow or to the colony. To examine this, we calculated the absolute value of the difference in duration between consecutive trips. Large differences in foraging duration between consecutive trips would indicate a shift in foraging behavior, whereas small differences would indicate consistent foraging behavior. We then compared this difference between nights when only one pair member returned to the burrow and when both pair members returned to the burrow. On nights when both pair members returned to the burrow, we considered two scenarios: partners' visits to the burrow either overlapped (synchronous visit to the burrow) or did not overlap (synchronous at the colony). Additionally, we evaluated the influence of sex. The relationship between synchronicity and sex (as independent variables) and the difference in duration between consecutive foraging trips (as the dependent variable) was investigated through linear mixed models with a maximum-likelihood fitting method using the lme4 package in R (Bates et al., 2014). Each model included individual nested within burrow as a random effect and an autoregressive within-group correlation structure representing the dependence between consecutive trip duration. The normality and homoscedasticity of predictor variables was verified by visual inspection. Models were ranked and selected based on AIC and ∆AIC relative to the model with the lowest AIC value (Burnham & Anderson, 2002).

If foraging is coordinated in order to minimize the interval between chick feedings, then partners should adjust foraging trip duration in opposite directions after reuniting at the burrow. For example, if one pair member switches from a short trip to a long trip, then the other partner should switch in the opposite direction from a long trip to a short trip. By switching foraging duration in the same direction, pairs might either increase or decrease provisioning rates, but would necessarily deviate from the pattern seen in the "Coordinated" panel of Figure 1. We examined how frequently pairs switched foraging strategies in opposite directions after synchronous returns relative to cases where pairs increased or decreased foraging duration in the same direction (i.e. both pairs shifted from a short trip to a long trip or vice versa as is shown in the "Uncoordinated" panel of Figure 1). In some cases, individuals did not alter foraging duration by a day or more between consecutive trips. These cases were not included as our study focuses on the mechanism underpinning switches in foraging strategy between partners, and so cases where birds did not switch strategy were not of interest. We used generalized linear mixed effect models with a binomial error distribution and a logit link function to evaluate the probability of parents switching foraging duration in opposite directions or the same direction as a function of 1) chick age and 2) the log of chick mass. Burrow was included as a random effect and the same model selection procedure as before was applied.

Results

Visual inspection of the histogram of trip duration suggested a roughly tri-modal distribution with the majority of trips lasting one day (Figure S1). A second, less frequent mode is observed for trips lasting 3-4 days and a third mode with low frequency appears for trips lasting 13 days. The mean trip duration was 50 hours (range of 12 to 309 hours). The difference in mean trip duration for each member of the pair was not significantly different from zero, suggesting that trip duration was similar between sexes ($t_{16} = -0.276$, $P = 0.786$). Of the 637 retained chick-rearing trips used to analyse coordinated provisioning, 223 trips were initiated following synchronous visits at the colony (but not at the burrow), and 195 trips were synchronous at the burrow (Figure S2). On synchronous returns to the burrow, males and females were equally likely to arrive at the burrow first. The amount of time that individuals remained in the burrow was highly variable, ranging from 10 minutes to six hours. Trip duration between consecutive trips shifted most strongly after synchronous returns to the colony and were not equal between sexes (Model 5, Table 1). Following synchronous visits to the colony, trip duration shifted by a mean of 30 (± 4) hours more than on nights when a trip was initiated in isolation (Figure 3A). Additionally, this shift was not equal between sexes. On average, males adjusted foraging duration between trips by 13 (± 6) hours less than females (Figure 3B). This difference between sexes was observed regardless of whether the trip was initiated synchronously with the partner or in isolation.

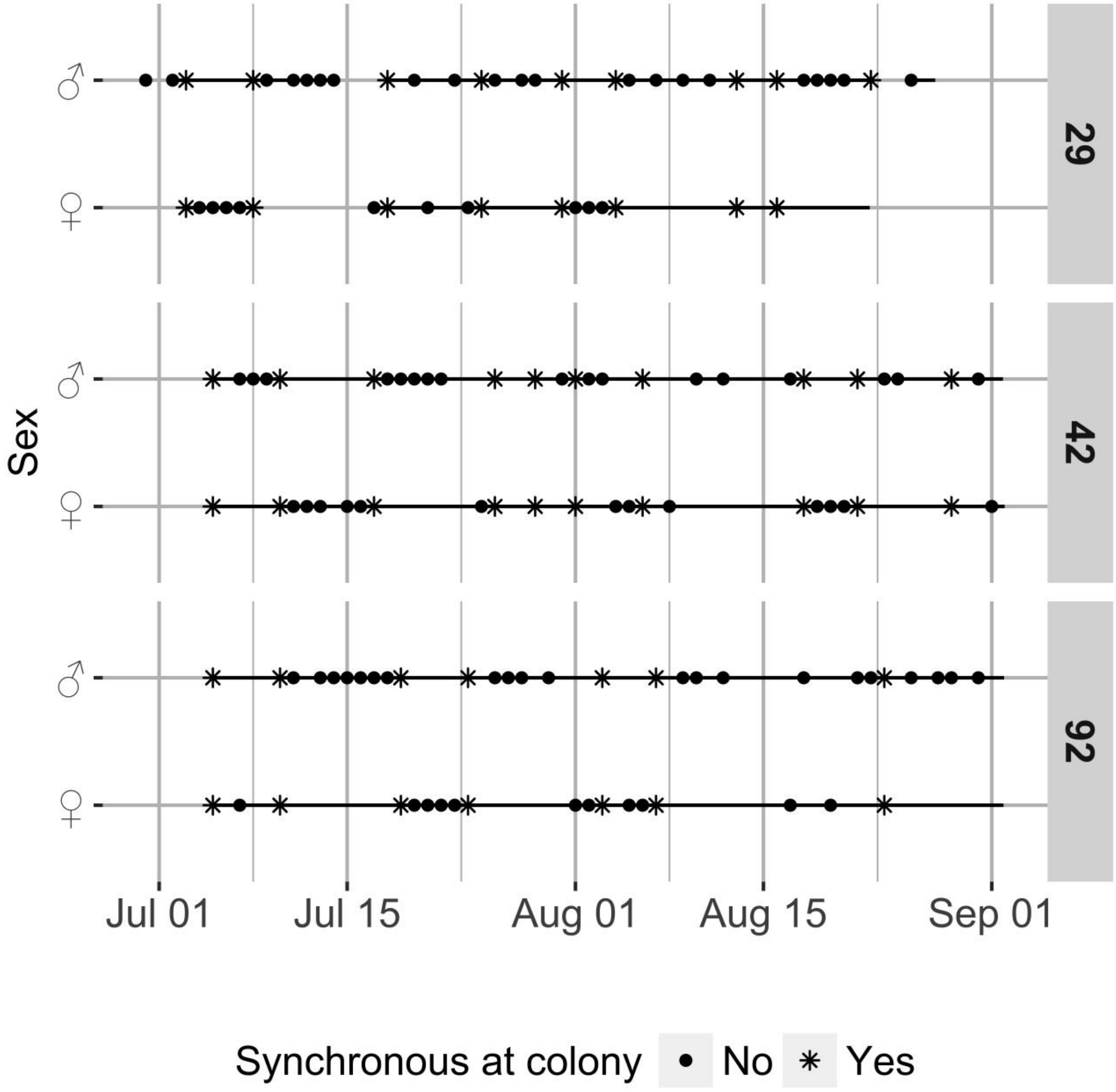

Figure 2 Three exemplar detection time lines of pairs showing coordinated provisioning (all pairs are shown in Supplementary Figure 2). Individuals (IDs shown at the left) are grouped by pair (nest IDs shown in the grey squares at the right). All detections at the colony during chick rearing, save the last, are plotted. Asterisks represent nights when both partners were detected at the colony, while circles represent nights when only one partner was detected. Black lines connecting detections denote foraging trips with less than one hour of lost battery functioning.

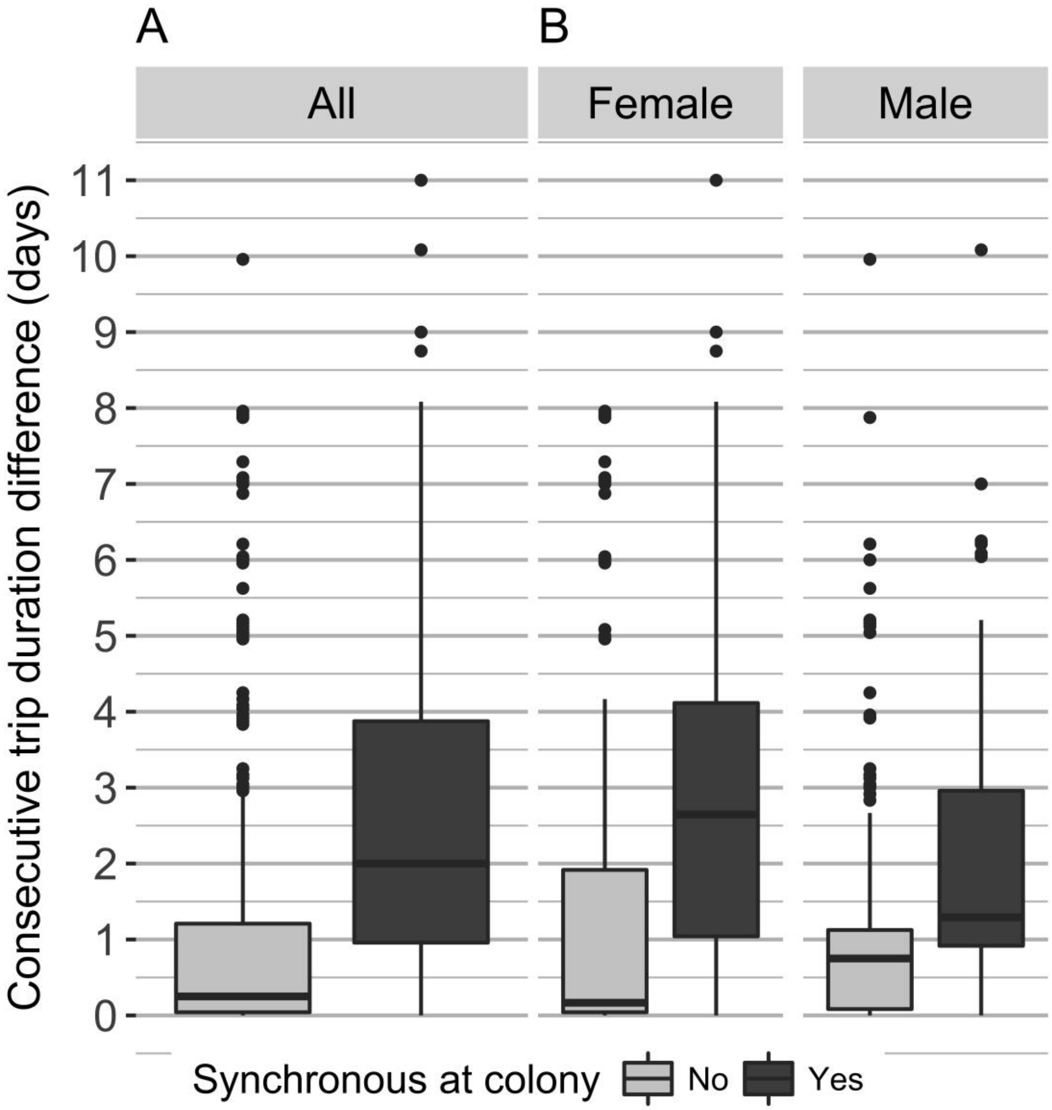

Figure 3 Duration difference (in days) between consecutive foraging trips that were synchronously or asynchronously initiated for all pairs combined (A) and for each sex (B). Trips that were begun on nights when the partner had not returned to the colony were more similar to the previous trip than on nights when the partner also returned to the colony.

We further examined the probability that pairs switched foraging duration in opposite directions following synchronously initiated trips as a function of chick mass and age. We found that the probability of pairs switching foraging duration in opposite directions was most strongly associated with chick mass (Model 3, Table 2). For newly hatched chicks, the likelihood of pairs switching foraging strategies in opposite directions after synchronously returning to the colony was nearly 0.86, but declined to 0.48 as chicks approached fledging mass (Figure 4).

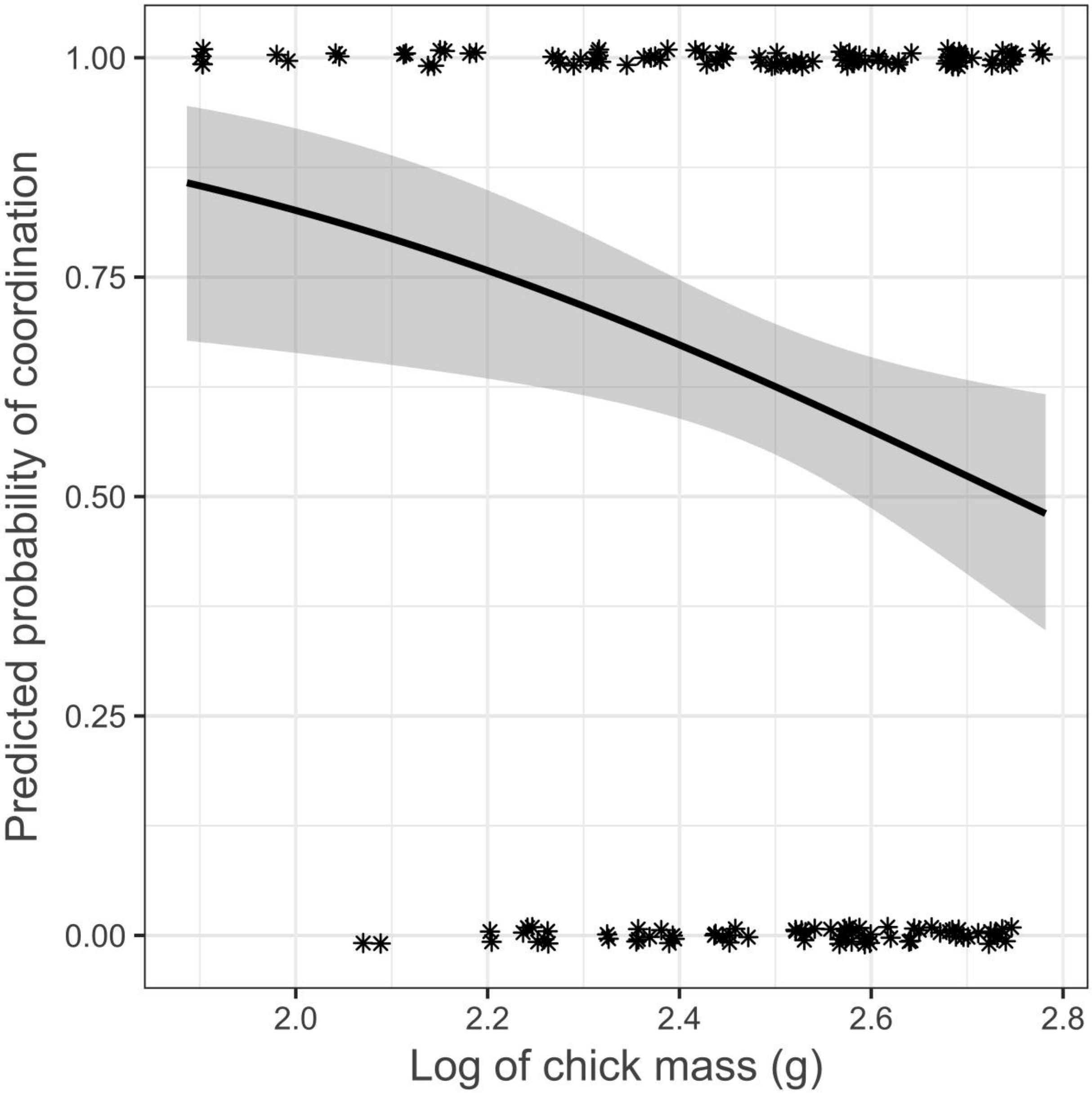

Figure 4 The probability of pairs coordinating as a function of the log of chick mass (grey area reflects the 95% CI). When chick mass was low, pairs were most likely to switch foraging strategies in opposite directions following synchronous returns to the colony. As chick mass increased, pairs were less likely to coordinate, which resulted in less regular provisioning.

Discussion

Life history theory predicts that to maximize long term reproductive success iteroparous animals should balance investment in current offspring with their own condition. Seabird species from several orders are known to alternate between short trips for the purpose of chick provisioning and long trips for self-care. Without coordination between partners, however, this variable foraging strategy would be likely to result in periods of chick starvation when long trips coincide. Protracted bouts of chick neglect are uncommon (Shoji et al., 2015), but it is unclear how this is achieved. Using an automated burrow monitoring system validated using a sample of birds with saltwater immersion loggers, we recorded provisioning trips across the chick rearing period. Using this sequential record of foraging trips for each pair, we show that Manx shearwaters displaying a variable foraging strategy, wherein individuals alternate between long trips and short trips, do indeed coordinate foraging patterns with their partner.

Following synchronous returns to the colony, partners tended to shift foraging strategies; either switching from a short trip to a long trip or vice versa. On nights when partners both returned to the colony, the duration of the subsequent foraging trip was shortened or extended by an average of 30 hours more than if the trip was begun following a visit to the colony alone. This shift amounts to a roughly 50% increase over the mean trip duration or the difference between a “short” and a “long” trip. From the other perspective, on nights when individuals returned alone, the duration of the subsequent foraging trip was largely unaltered, indicating that the same foraging strategy was employed.

Several mechanisms might plausibly enable partners to coordinate foraging patterns such as endogenous rhythms, e.g. hormonal cycles that govern foraging behaviour (Ricklefs et al. 1985; Weimerskirch, 1998); contact at the burrow, colony or at-sea (Congdon et al., 2005); or indirect cues through chick begging calls or odour (Gray & Hamer, 2001; Riou & Hamer, 2010). We found synchronous colony visits to be a better predictor of foraging shifts than synchronous burrow visits. This suggests that physically reuniting at the burrow is unnecessary for coordinating foraging movements. It is possible that pairs recognize their partner's vocalizations at the colony or meet while rafting offshore prior to coming to land (Brooke, 1990; Booth et al., 2000). While colonially breeding seabirds are known for their ability to locate their partner among numerous conspecifics (reviewed in Falls, 1982), neither of these mechanisms appears likely in this case. Upon returning to the colony, chick-rearing Manx shearwaters quickly go to their burrow and immediately return to sea after provisioning the chick, leaving little time to encounter their partner. It is also unlikely that partners would be able to reunite while rafting offshore as these congregations only form in the last few hours of daylight (Brooke, 1990) and typically consist of thousands of individuals. While our data cannot exclude these mechanisms, some indirect signal mediated through either chick begging or burrow odour would be more feasible as it would not rely on chance contact with the partner. Chick begging intensity may contain information about body condition in shearwaters (Quillfeldt et al., 2004; Granadeiro et al., 2000; Quillfeldt & Masello, 2004) that could act as a signal to the second parent returning to the nest. As this information would only be available to the second partner to return, however, one would expect to see a more pronounced shift in foraging duration for the second partner than the first. While we did not have sufficient data to explore this possibility adequately, this did seem to be the case. Future research will be required to address the specific mechanism that allows partners to coordinate parental duties as we observed.

Though overall foraging duration and the number of foraging trips was similar between sexes, on average females altered the duration of consecutive foraging trips by 13 hours more than males. This finding is consistent with other studies of Manx shearwater provisioning effort (Dean, 2012; Shoji et al., 2015) that found no sex-specific differences in foraging duration. Female Manx shearwaters, however, are known to be more sensitive to chick begging and adjust provisioning effort accordingly (Quillfeldt et al., 2004; Hamer et al., 2006). Conversely, males generally provision at consistent levels irrespective of begging intensity. This difference would account for our finding that females adjusted foraging duration between consecutive trips more than males.

Cooperation should be favoured when offspring survival is heavily dependent on contributions from both parents (Clutton-Brock, 1991). We observed that coordination was highest when chick mass was low. During early chick rearing, individuals were most likely to adjust foraging duration in opposite directions, which resulted in consistent provisioning. While the probability of coordination was inversely related to both chick age and mass, we found that the latter was a better predictor. We did not observe any seasonal changes in foraging duration, which could similarly give rise to this pattern. For young procellariiform seabird chicks without accumulated lipid reserves, there is an elevated risk of mortality (Boersma et al. 1979; Catry et al., 2006). As such, for a lean, vulnerable chick, coordination is likely to be especially valuable, which is consistent with our findings (Figure 4). This means that breeding pairs can potentially better accommodate environmental changes which may lead to a chick losing body condition despite having grown in terms of developmental stage.

Reproductive success is positively correlated with pair experience in many avian taxa (Van De Pol et al., 2006; Naves et al., 2007; Sanchez-Macouzet et al., 2014). A variety of mechanisms may account for this relationship such as increased coordination and improved foraging efficiency (reviewed in Ens et al., 1996; see Fayet et al., 2015 for this species). In seabirds, considerable research has focused on mechanisms specifically related to increased coordination that may be advantageous, such as synchronous arrival at the breeding colony (Mills, 1973) and incubation changeovers (Davis, 1988). Our work suggests that coordination in foraging routines may be an important, but overlooked, mechanism underlying reproductive success. Although we were not able here to measure directly the effect of parental coordination on reproductive success, it is known that consistent feedings, especially early during chick rearing, can reduce chick mortality (Boersma et al. 1979; Catry et al., 2006) and optimize chick growth (Schaffner 1990). An alternative explanation is that caregiving parents may directly benefit by coordinating, for instance by determining which partner is in greater need of a long, self-maintenance foraging trip, which could allow pairs to optimise their relationship accordingly. Given the potential costs of not coordinating and the possible benefits of coordinating, we expect that this behaviour is likely to be observed in a wide range of other taxa that engage in a dual foraging strategy. There are considerable prospects for future research that explores how both intrinsic factors such as pair experience or individual quality and extrinsic factors such as resource availability influence the degree of coordination.

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Tables

Table 1 Parameter estimates and standard errors (shown in parenthesis) for five alternative linear mixed effect models describing the difference in trip duration (in hours) of consecutive trips. Apart from the four predictor variables (in different combinations), each model contains individual, nested within burrow, as a random effect. Models are ordered by ∆AIC. Full model descriptions are given in the Methods.

Model / Parameter	**5**	**4**	**3**	**2**	**1**
Intercept	40.51 (4.80)***	33.69 (3.58)***	42.23 (4.95)***	35.25 (3.67)***	44.16 (3.41)***
Synchronous at colony (Yes)	29.59 (4.23)***	29.92 (4.22)***			
Sex (M)	−12.65 (6.05)*		−12.99 (6.36)*		
Synchronous at burrow (Yes)			29.17 (4.40)***	29.58 (4.40)***	
AIC	**6359.34**	**6361.36**	**6364.21**	**6366.06**	**6407.67**
ΔAIC	**0.00**	**2.02**	**4.87**	**6.72**	**48.33**

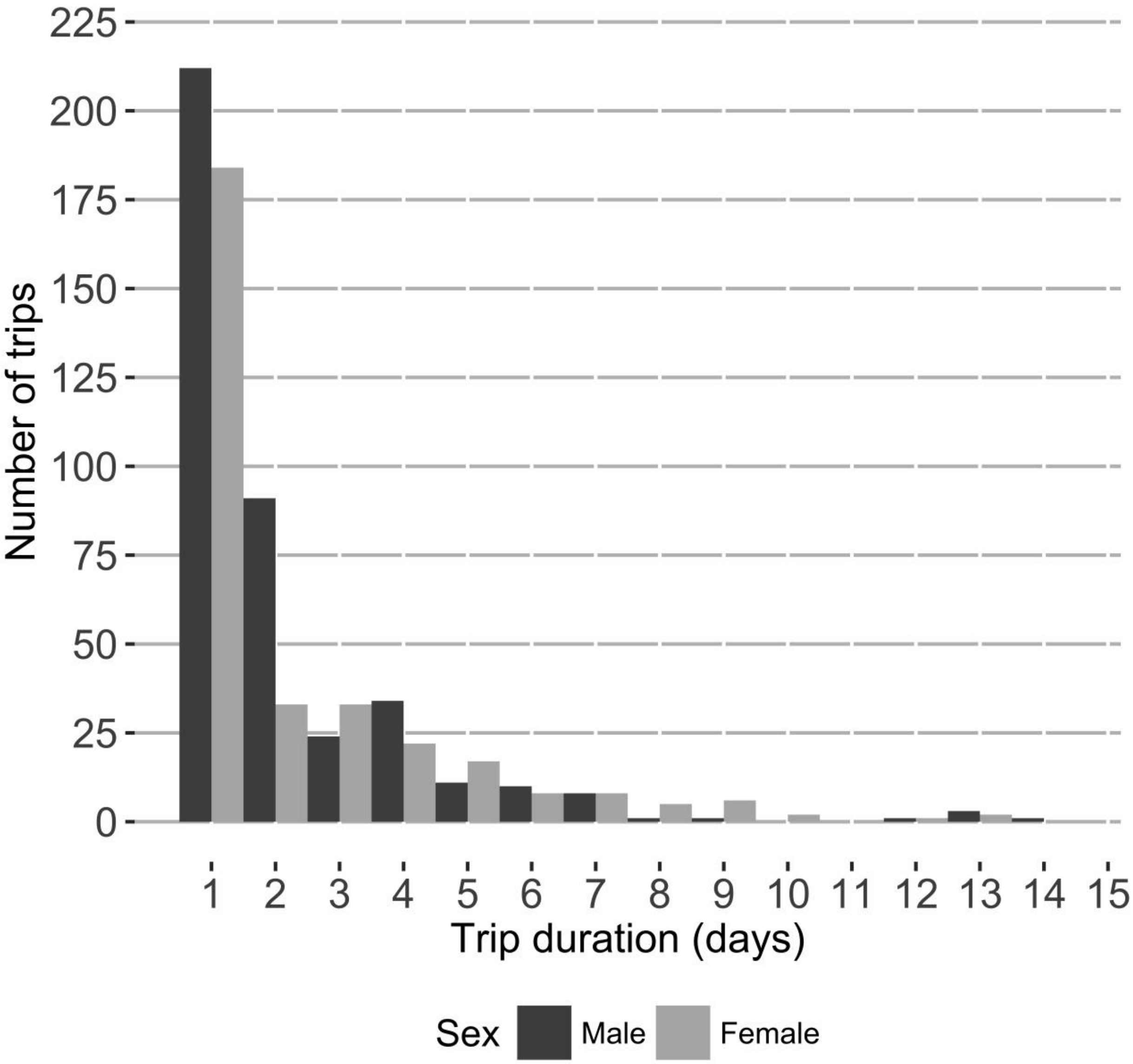
*** p < 0.001, ** p < 0.01, * p < 0.05

Table 2 Parameter estimates and standard errors (shown in parenthesis) for three alternative generalized linear mixed effect models (using a binomial error distribution and a logit link function), describing the probability of switching trip duration following synchronous returns to the colony. The natural logarithm of chick mass and chick age were used as predictor variables (the variables were not combined as they are highly correlated), in addition to a random effect of burrow. Models are ordered by ΔAIC. Full model descriptions are given in the Methods.

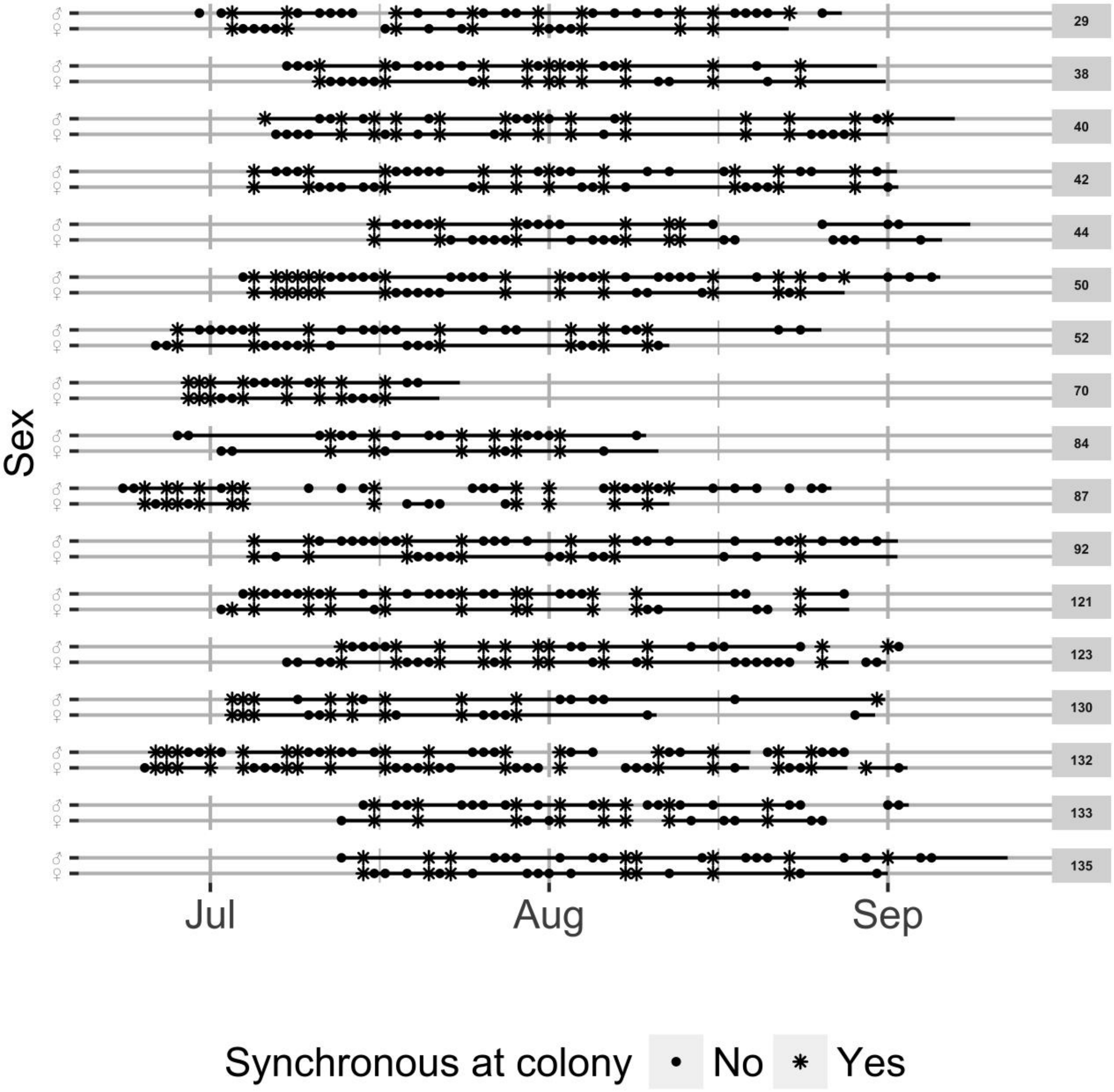
Model / Parameter	**3**	**1**	**2**
Intercept	5.80 (2.35) *	0.52 (0.35)	0.78 (0.52)
Log(Mass)	−2.11 (0.93)*		
Age			−0.01 (0.01)
AIC	**213.84**	**222.7**	**223.82**
ΔAIC	**0.00**	**8.43**	**9.98**

*** p < 0.001, ** p < 0.01, * p < 0.05

Supplemental figures



Supplemental figure 1 Frequency distribution of trip duration in days for each sex. Only trips that were made by known-sex birds are shown (n = 718).



Supplemental figure 2 Detection time lines for all analyzed pairs, i.e. those with more than 5 synchronous trips. All detections, save the last, are plotted. Asterisks represent nights when both partners were detected at the colony, while circles represent nights when only one partner was detected. Black lines connecting detections denote foraging trips with less than one hour of lost battery functioning.