



UvA-DARE (Digital Academic Repository)

Coordinated provisioning in a dual-foraging pelagic seabird

Tyson, C.; Kirk, H.; Fayet, A.; Van Loon, E.E.; Shoji, A.; Dean, B.; Perrins, C.; Freeman, R.; Guilford, T.

DOI

[10.1016/j.anbehav.2017.07.022](https://doi.org/10.1016/j.anbehav.2017.07.022)

Publication date

2017

Document Version

Final published version

Published in

Animal behaviour

License

Article 25fa Dutch Copyright Act

[Link to publication](#)

Citation for published version (APA):

Tyson, C., Kirk, H., Fayet, A., Van Loon, E. E., Shoji, A., Dean, B., Perrins, C., Freeman, R., & Guilford, T. (2017). Coordinated provisioning in a dual-foraging pelagic seabird. *Animal behaviour*, 132, 73-79. <https://doi.org/10.1016/j.anbehav.2017.07.022>

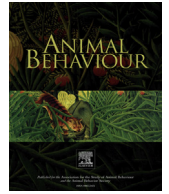
General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

UvA-DARE is a service provided by the library of the University of Amsterdam (<https://dare.uva.nl>)



Coordinated provisioning in a dual-foraging pelagic seabird



C. Tyson ^{a,*}, H. Kirk ^b, A. Fayet ^b, E. E. Van Loon ^a, A. Shoji ^b, B. Dean ^b, C. Perrins ^b,
R. Freeman ^c, T. Guilford ^b

^a Computational Geo-Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands

^b Department of Zoology, University of Oxford, Oxford, U.K.

^c Institute of Zoology, Zoological Society of London, London, U.K.

ARTICLE INFO

Article history:

Received 23 March 2017

Initial acceptance 24 April 2017

Final acceptance 9 June 2017

Available online 1 September 2017

MS. number: A17-00262R

Keywords:

coordinated provisioning

dual foraging

Manx shearwater

parental investment

Puffinus puffinus

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 radiofrequency 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.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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, Andersen, & Pedersen, 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 (Granadeiro, Nunes, Silva, & Furness, 1998; Weimerskirch & Cherel, 1998; Weimerskirch, Cherel, Cuenot-Chaillet, & Ridoux, 1997), Sphenisciformes (Sarau, Robinson-Laverick, Le Maho, Rogert-Coudert, & Chiaradia, 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*: Sarau et al., 2011).

While dual foraging is a widely studied behaviour, it entails a complication that is seldom discussed. Namely, if parents independently adopt 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, Minot, Fordham, & Imber, 2000; Congdon, Krockenberger, & Smithers, 2005), the degree of such coordination and the mechanisms underlying it are poorly understood.

* Correspondence: C. Tyson, Graduate Group in Ecology, University of California, Davis, Davis, CA 95616, U.S.A.

E-mail address: cwtyson@ucdavis.edu (C. Tyson).

The Manx shearwater, *Puffinus puffinus*, is a monomorphic, burrow-nesting seabird that is known to display dual foraging (Fayet et al., 2015; Shoji, Aris-Brosou, Culina, et al., 2015; Shoji, Aris-Brosou, 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 Fig. 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.

METHODS

Ethical Note

All work adhered 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 programme carried out by Oxford University since 2006 (see Dean et al., 2012; Shoji, Aris-Brosou, Culina, et al., 2015; Shoji, Aris-Brosou, Fayet, et al., 2015, for details). The combined weight of biologging tags was no more than 2.2 g, roughly 0.5% of mean body mass (450 g), which is well below the recommended limit of 3% for flying birds (Phillips et al., 2003). Although handling and biologging tags may negatively affect birds, we observed that fledging success was not significantly lower between pairs monitored with radio-frequency identification (RFID) readers (0.84, $N = 39$) and other pairs (0.61, $N = 38$) within our study colony (two-sample binomial test: $\chi^2_1 = 3.9424$, $P = 0.977$). 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 1321 breeding attempts between 2009 and 2014 that 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 had no detectable adverse effects on breeding success.

Study Site and Birds

Fieldwork was conducted on Skomer Island (54.44°N, 05.17°W), Wales, U.K. 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 1–3 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 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 12 V 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 burrow 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 British Trust for Ornithology (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 (Avinet, Portland, ME, U.S.A.) 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 10 min.

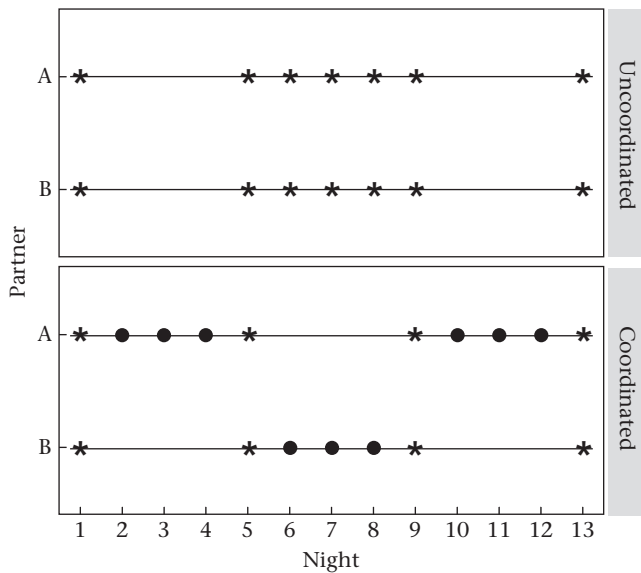


Figure 1. Expected nest attendance patterns of Manx shearwater breeding partners (A, B) when dual-foraging routines are uncoordinated or coordinated. Asterisks represent nights when both partners were detected at the nest; solid circles represent nights when only one partner was detected at the nest. In the case of uncoordinated dual-foraging routines, 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. For example, 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.

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 SE. 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–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, we reviewed saltwater immersion records from geolocator loggers from a subset of PIT-tagged birds. 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 V, the RFID readers would not reliably detect PIT tags. Therefore, foraging trips during which the RFID reader fell below 10 V for more than 1 h were discarded 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 1 h 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 potential foraging trips included periods of saltwater immersion and similarly, none of the intervening potential 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 pairs 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 behaviour, whereas small differences would indicate consistent foraging behaviour. 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 durations. The normality and homoscedasticity of predictor variables was verified by visual inspection. Models were ranked and selected based on Akaike's information criterion (AIC) and Δ 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 a 'coordinated pattern' (Fig. 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; see 'uncoordinated pattern' in Fig. 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 focused 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 in 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 was applied as before.

RESULTS

Visual inspection of the histogram of trip duration suggested a roughly trimodal distribution with the majority of trips lasting 1 day (see Appendix, Fig. A1). A second, less frequent mode was observed for trips lasting 3–4 days and a third mode with low frequency appeared for trips lasting 13 days. The mean trip duration was 50 h (range 12–309 h). 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 to the colony (but not at the burrow) and 195 trips were synchronous at the burrow (Appendix, Fig. A2). 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 min to 6 h. Trip duration between consecutive trips shifted most strongly after synchronous returns to the colony (Fig. 2) 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 h more than on nights when a trip was initiated in isolation (Fig. 3a). In addition, this shift was not equal between sexes. On average, males adjusted foraging duration between trips by 13 ± 6 h less than females (Fig. 3b). This difference between sexes was observed regardless of whether the trip was initiated synchronously with the partner or in isolation.

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

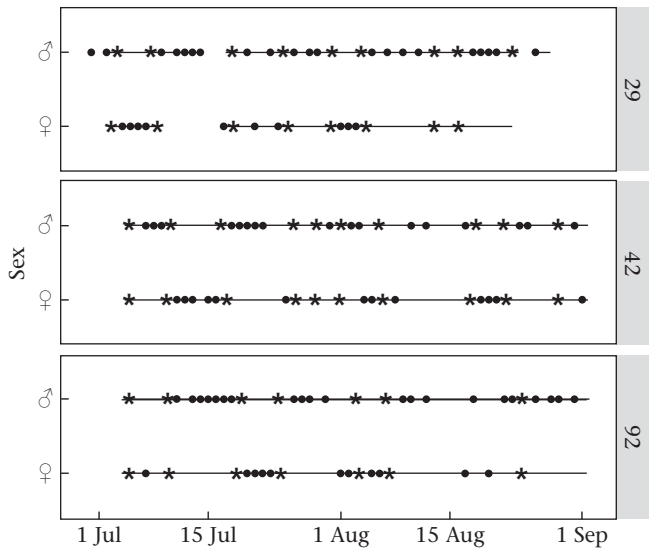


Figure 2. Exemplar detection timelines for three breeding pairs of Manx shearwaters (nest IDs 29, 42, 92) with coordinated provisioning (detection timelines for all analysed pairs are shown in Fig. A2). All detections at the colony during chick rearing, save the last, are plotted. Asterisks represent nights when both partners were detected at the colony; solid circles represent nights when only one partner was detected at the colony. Black lines connecting detections denote foraging trips with less than 1 h of battery function loss.

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 (Fig. 4).

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, Aris-Brosou, Culina, et al., 2015; Shoji, Aris-Brosou, Fayet, 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

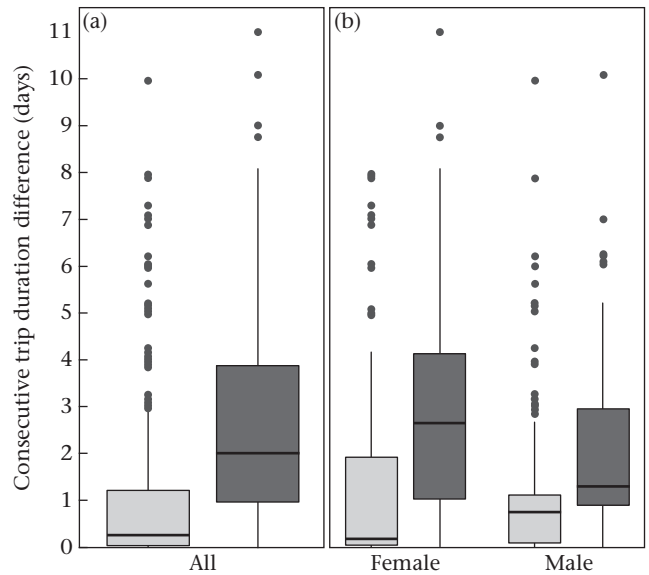


Figure 3. Duration difference (in days) between consecutive foraging trips that were synchronously (dark grey boxes) or asynchronously (light grey boxes) initiated at the colony (a) for all pairs combined and (b) for each sex. Trips that were begun on nights when the partner had not returned to the colony were more similar to the previous trip than on nights when the partner also returned to the colony. Box plots show 25% and 75% quartiles (boxes), medians (lines in the boxes), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles).

provisioning trips across the chick-rearing period. Using this sequential record of foraging trips for each pair, we show that Manx shearwaters display a variable foraging strategy, wherein individuals alternate between long trips and short trips, and 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 h 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 used.

Several mechanisms might plausibly enable partners to coordinate foraging patterns such as endogenous rhythms (e.g. hormonal cycles that govern foraging behaviour; Ricklefs, Day, Huntington, & Williams, 1985; Weimerskirch, 1998), contact at the burrow, the colony or at-sea (Congdon et al., 2005), or indirect

Table 1
Parameter estimates and standard errors (shown in parentheses) for five alternative linear mixed effect models describing the difference in trip duration (in hours) of consecutive trips

Parameter	Model				
	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)			−12.99 (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

Apart from the four predictor variables (in different combinations), each model contains individual nested within burrow as a random effect. Models are ordered by ΔAIC. Full model descriptions are given in the Methods.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2

Parameter estimates and standard errors (shown in parentheses) 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

Parameter	Model		
	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

The natural logarithm of chick mass and chick age were used as predictor variables (the variables were not combined as they were highly correlated), in addition to a random effect of burrow. Models are ordered by ΔAIC. Full model descriptions are given in the Methods.

* $P < 0.05$.

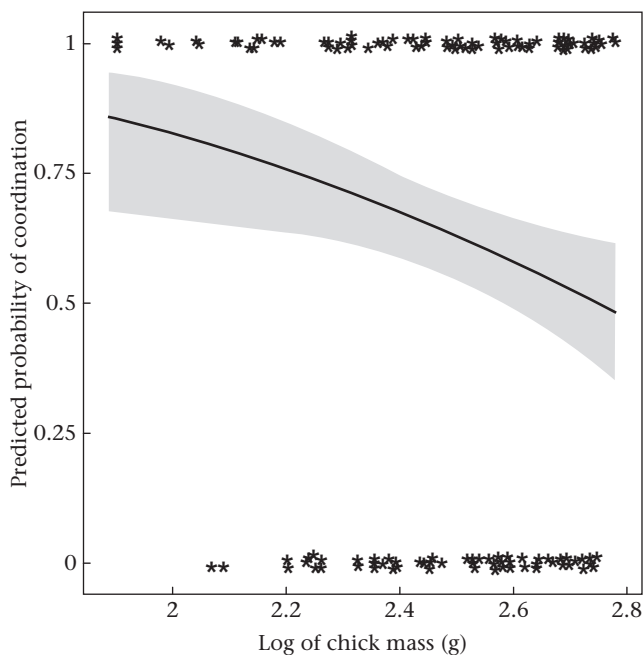


Figure 4. The probability of pairs coordinating as a function of the log of chick mass (grey area reflects the 95% confidence interval). When chick mass was low, pairs were most likely to switch foraging strategies in opposite directions following synchronous returns to the colony. As chick mass increased,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

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 (Booth et al., 2000; Brooke, 1990). 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 (Granadeiro, Bolton, Silva, Nunes, & Furness, 2000; Quillfeldt & Masello, 2004; Quillfeldt, Masello, & Hamer, 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 for the first partner. 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.

Although 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 h more than males. This finding is consistent with other studies of Manx shearwater provisioning effort (Dean, 2012; Shoji, Aris-Brosou, Culina, et al., 2015; Shoji, Aris-Brosou, Fayet, 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 (Hamer, Quillfeldt, Masello, & Fletcher, 2006; Quillfeldt et al., 2004). 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 & Wheelwright, 1979; Catry, Phillips, Forcada, & Croxall, 2006). As such, for a lean, vulnerable chick, coordination is likely to be especially valuable, which is consistent with our findings (Fig. 4). This means that breeding pairs can potentially better accommodate environmental changes that 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 (Naves, Cam, & Monnat, 2007; Sánchez-Macouzet, Rodríguez, & Drummond, 2014; Van De Pol, Heg, Bruinzeel, Kuijper, & Verhulst, 2006). A variety of mechanisms may account for this relationship such as increased coordination and improved foraging efficiency (reviewed in Ens, Choudhury, & Black, 1996; see Fayet et al., 2015, for Manx shearwaters). 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 change-overs (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 to measure the effect of parental coordination on reproductive success directly, consistent feedings, especially early during chick rearing, can reduce chick mortality (Boersma & Wheelwright, 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 optimize 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.

Acknowledgments

We thank the Wildlife Trust for South and West Wales, the wardens and assistants on Skomer Island and Dave Boyle for research assistance. We also thank I. J. Martinez and O. Padget for thoughtful feedback on an earlier version of the manuscript. Funding for this research was provided by a Volkert van der Wiligen Grant through the Amsterdam University Fund to C.T. Funding for the sensor network on which this work is based was provided by Microsoft Research Cambridge.

References

- Baduini, C. L., & Hyrenbach, K. D. (2003). Biogeography of procellariiform foraging strategies: Does ocean productivity influence provisioning? *Marine Ornithology*, 31, 101–112.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., et al. (2014). *lme4: Linear mixed-effects models using Eigen and S4 (R package version, 1(7))*. Vienna, Austria: R Foundation for Statistical Computing.
- Boersma, P. D., & Wheelwright, N. T. (1979). Egg neglect in the Procellariiformes: Reproductive adaptations in the fork-tailed storm-petrel. *Condor*, 81(2), 157–165.
- Booth, A. M., Minot, E. O., Fordham, R. A., & Imber, M. J. (2000). Co-ordinated food provisioning in the little shearwater *Puffinus assimilis haurakiensis*: A previously undescribed foraging strategy in the Procellariidae. *Ibis*, 142(1), 144–146.
- Brooke, M. (1990). *The Manx shearwater*. London, U.K.: T & AD Poyser.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer Science & Business Media.
- Catry, P., Phillips, R. A., Forcada, J., & Croxall, J. P. (2006). Factors affecting the solution of a parental dilemma in albatrosses: At what age should chicks be left unattended? *Animal Behaviour*, 72, 383–391.
- Chaurand, T., & Weimerskirch, H. (1994). The regular alternation of short and long foraging trips in the blue petrel *Halobaena caerulea*: A previously undescribed strategy of food provisioning in a pelagic seabird. *Journal of Animal Ecology*, 63(2), 275–282.
- Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.
- Congdon, B. C., Krockenberger, A. K., & Smithers, B. V. (2005). Dual-foraging and coordinated provisioning in a tropical procellariiform, the wedge-tailed shearwater. *Marine Ecology Progress Series*, 301, 293–301.
- Curio, E. (1988). Relative realized life span and delayed cost of parental care. *American Naturalist*, 131(6), 825–836.
- Davis, L. S. (1988). Coordination of incubation routines and mate choice in Adélie penguins (*Pygoscelis adeliae*). *Auk*, 105(3), 428–432.
- Dean, B. (2012). *The at-sea behaviour of the Manx shearwater* (Ph.D. thesis). Oxford, U.K.: University of Oxford.
- Dean, B., Freeman, R., Kirk, H., Leonard, K., Phillips, R. A., Perrins, C. M., et al. (2012). Behavioural mapping of a pelagic seabird: Combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *Journal of the Royal Society Interface*, 10, 20120570.
- Ens, B., Choudhury, S., & Black, J. (1996). Mate fidelity and divorce in monogamous birds. In J. Black (Ed.), *Partnerships in birds: the study of monogamy* (pp. 344–401). Oxford, U.K.: Oxford University Press.
- Falls, J. (1982). Individual recognition by sounds in birds. In E. Miller, & D. Kroodsma (Eds.), *Acoustic communication in birds* (pp. 237–278). New York, NY: Academic Press.
- Fayet, A. L., Freeman, R., Shoji, A., Padget, O., Perrins, C. M., & Guilford, T. (2015). Lower foraging efficiency in immatures drives spatial segregation with breeding adults in a long-lived pelagic seabird. *Animal Behaviour*, 110, 79–89.
- Granadeiro, J. P., Bolton, M., Silva, M. C., Nunes, M., & Furness, R. W. (2000). Responses of breeding Cory's shearwater *Calonectris diomedea* to experimental manipulation of chick condition. *Behavioral Ecology*, 11(3), 274–281.
- Granadeiro, J. P., Nunes, M., Silva, M. C., & Furness, R. W. (1998). Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chick-rearing period. *Animal Behaviour*, 56, 1169–1176.
- Gray, C. M., & Hamer, K. C. (2001). Food-provisioning behaviour of male and female Manx shearwaters, *Puffinus puffinus*. *Animal Behaviour*, 62, 117–121.
- Guilford, T., Meade, J., Freeman, R., Biro, D., Evans, T., Bonadonna, F., et al. (2008). GPS tracking of the foraging movements of Manx shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis*, 150(3), 462–473.
- Hamer, K. C., Quillfeldt, P., Masello, J. F., & Fletcher, K. L. (2006). Sex differences in provisioning rules: Responses of Manx shearwaters to supplementary chick feeding. *Behavioral Ecology*, 17(1), 132–137.
- Harris, M. (1966). Breeding biology of the Manx shearwater *Puffinus puffinus*. *Ibis*, 108(1), 17–33.
- Mills, J. A. (1973). The influence of age and pair-bond on the breeding biology of the red-billed gull *Larus novaehollandiae scopulinus*. *Journal of Animal Ecology*, 42(1), 147–162.
- Naumowicz, T., Freeman, R., Kirk, H., Dean, B., Calsyn, M., Liers, A., et al. (2010). Wireless sensor network for habitat monitoring on Skomer Island. In *Proceedings of the Fifth IEEE International Workshop on Practical Issues in Building Sensor Network Applications*, Denver, Colorado, 14 October (pp. 889–905). Washington, D.C.: IEEE Computer Society. <http://dx.doi.org/10.1109/LCN.2010.5735827>.
- Naves, L. C., Cam, E., & Monnat, J. Y. (2007). Pair duration, breeding success and divorce in a long-lived seabird: Benefits of mate familiarity? *Animal Behaviour*, 73, 433–444.
- Phillips, R., & Hamer, K. (1999). Lipid reserves, fasting capability and the evolution of nestling obesity in procellariiform seabirds. *Proceedings of the Royal Society B: Biological Sciences*, 266(1426), 1329–1334.
- Quillfeldt, P., & Masello, J. F. (2004). Context-dependent honest begging in Cory's shearwaters (*Calonectris diomedea*): Influence of food availability. *Acta Ethologica*, 7(2), 73–80.
- Quillfeldt, P., Masello, J. F., & Hamer, K. C. (2004). Sex differences in provisioning rules and honest signalling of need in Manx shearwaters (*Puffinus puffinus*). *Animal Behaviour*, 68, 613–620.
- R Core Team. (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Ricklefs, R., Day, C., Huntington, C., & Williams, J. (1985). Variability in feeding rate and meal size of leach's storm-petrel at Kent Island, New Brunswick. *Journal of Animal Ecology*, 54(3), 883–898.
- Riou, S., & Hamer, K. C. (2010). Lipid metabolism, begging behaviour and nestling obesity in a pelagic seabird. *Functional Ecology*, 24(2), 340–346.
- Sæther, B.-E., Andersen, R., & Pedersen, H. C. (1993). Regulation of parental effort in a long-lived seabird: An experimental manipulation of the cost of reproduction in the Antarctic petrel, *Thalassoica antarctica*. *Behavioral Ecology and Sociobiology*, 33(3), 147–150.
- Sánchez-Macouzet, O., Rodríguez, C., & Drummond, H. (2014). Better stay together: Pair bond duration increases individual fitness independent of age-related variation. *Proceedings of the Royal Society B: Biological Sciences*, 281(1786), 20132843.
- Saroux, C., Robinson-Laverick, S. M., Le Maho, Y., Ropert-Coudert, Y., & Chiaradia, A. (2011). Plasticity in foraging strategies of inshore birds: How little penguins maintain body reserves while feeding offspring. *Ecology*, 92(10), 1909–1916.
- Schaffner, F. C. (1990). Food provisioning by white-tailed tropicbirds: Effects on the developmental pattern of chicks. *Ecology*, 71(1), 375–390.
- Shoji, A., Aris-Brosou, S., Culina, A., Fayet, A., Kirk, H., Padget, O., et al. (2015). Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. *Biology Letters*, 11(10), 20150671.
- Shoji, A., Aris-Brosou, S., Fayet, A., Padget, O., Perrins, C. M., & Guilford, T. (2015). Dual foraging and pair coordination during chick provisioning by Manx shearwaters: Empirical evidence supported by a simple model. *Journal of Experimental Biology*, 218(13), 2116–2123.
- Van De Pol, M., Heg, D., Bruinzeel, L. W., Kuijper, B., & Verhulst, S. (2006). Experimental evidence for a causal effect of pair-bond duration on reproductive performance in oystercatchers (*Haematopus ostralegus*). *Behavioral Ecology*, 17(6), 982–991.
- Weimerskirch, H. (1998). How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. *Journal of Animal Ecology*, 67(1), 99–109.
- Weimerskirch, H., & Cherel, Y. (1998). Feeding ecology of short-tailed shearwaters: Breeding in Tasmania and foraging in the Antarctic? *Marine Ecology Progress Series*, 167, 261–274.
- Weimerskirch, H., Cherel, Y., Cuenot-Chaillet, F., & Ridoux, V. (1997). Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology*, 78(7), 2051–2063.
- Welcker, J., Harding, A., Karnovsky, N. J., Steen, H., Ström, H., & Gabrielsen, G. W. (2009). Flexibility in the bimodal foraging strategy of a high Arctic alcid, the little auk *Alle alle*. *Journal of Avian Biology*, 40(4), 388–399.
- Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist*, 100(916), 687–690.

APPENDIX

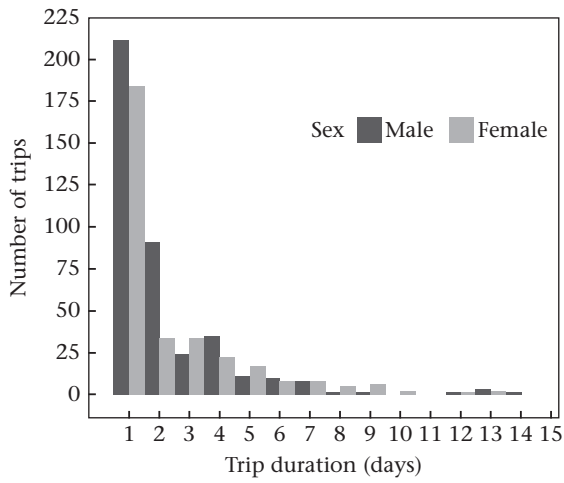


Figure A1. Frequency distribution of trip duration in days for each sex. Only trips that were made by known-sex birds are shown ($N = 718$).

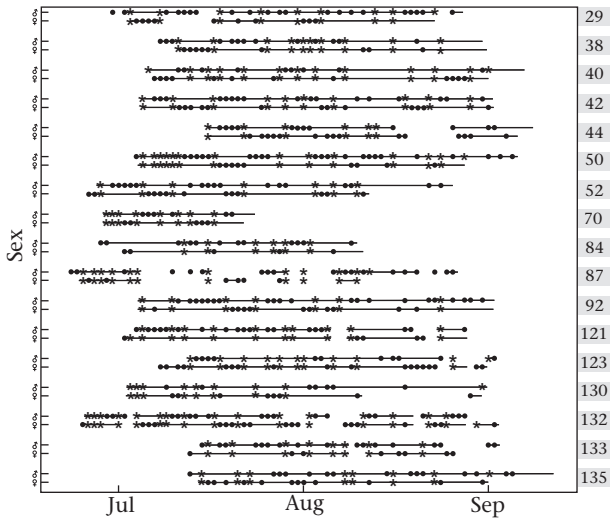


Figure A2. Detection timelines for all analysed pairs (i.e. those with more than five synchronous trips). All detections, save the last, are plotted. Asterisks represent nights when both partners were detected at the colony, while circles represent nights when only one partner was detected. Black lines connecting detections denote foraging trips with <1 h of battery function loss.