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Article

Exploring the mechanisms of coordinated chick provisioning in the Manx shearwater *Puffinus puffinus*

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Many species that provide care for their offspring in tandem with a partner coordinate their activities to maximise the efficiency of their investment. However, it is not well known exactly how this coordination is achieved. Manx shearwaters *Puffinus puffinus* are Procellariiform seabirds that exhibit a dual foraging strategy during chick provisioning in which long foraging trips to maintain condition are alternated with short, frequent trips to feed the offspring. This strategy is employed in a coordinated manner between the parents, with one making short trips while the other takes a single long trip. Previous work revealed that a complementary switch in foraging trip type is initiated by the parents following a synchronous visit to the nest. We used a combination of observational data and experimental manipulation to examine the mechanisms that may underlie this behaviour. Specifically, we investigated the evidence that physical reunion is necessary to induce a switch in trip type, whether parents change their behaviour to maximise the probability of partner encounter, and whether indirect cues gained from the chick could inform a switch in behaviour. In our experimental approach, we manipulated the information adults had available to them by supplementarily feeding chicks to alter their begging behaviour. We found no support for the role of physical reunion or indirect cues in the coordination of care in this species. We discuss the possibility that the patterns of alternated provisioning observed during chick rearing in Manx shearwaters may emerge through entrainment during the well-coordinated incubation period preceding chick provisioning.

Keywords: behavioural ecology, breeding behaviour, coordinated provisioning, dual foraging, parental care, seabirds

Introduction

As the resources available to individuals are limited both by their distribution in the environment and by the time and energy required to obtain them (Stearns 1992), iteroparous parents should partition their investment in offspring and self-maintenance in such a way that balances costs to their future reproductive success or survival against the expected benefit from the current breeding attempt (Trivers 1972). This has been historically viewed to generate conflict between parents when both provide

care to offspring, as each stands to gain from the benefits of increased reproductive output while only paying the cost of its own contribution (Chase 1980). However, for species in which the reproductive output of the two partners is highly aligned, which is the case for long-lived, sexually monogamous species, the shared fitness interests of the two parents may select for more cooperative behaviour during breeding (Griffith 2019).

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

Like many Procellariiform seabirds (Weimerskirch et al. 1994, Booth et al. 2000, Congdon et al. 2005), the Manx shearwater *Puffinus puffinus* exhibits a dual foraging strategy in which parents alternate short, approximately one-day provisioning trips with longer, condition-replenishing trips for three to four days (Shoji et al. 2015, Tyson et al. 2017). The timing of these trips is coordinated between the parents, and it has been previously observed (Tyson et al. 2017) that the switch in foraging trip type, from short to long trips or vice versa, follows a coincident visit of the two parents to the colony. It remains unclear, however, what the precise mechanisms guiding this coordination are.

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

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

We used a combined observational and experimental approach to explore whether 1) direct communication between the parents or 2) indirect signalling, mediated by chick begging, might inform switches in foraging trip type from provisioning to self-maintenance, and vice versa. Using an automated RFID-based individual detection system, Tyson et al. (2017) explored the coordination of provisioning behaviour in Manx shearwaters. While the authors' findings did not support the role of physical reunion in this behaviour, we aimed to replicate the observational findings of that study using two further years of data and an updated experimental set-up, which should improve the accuracy of detections. We further explored whether parents adjust their behaviour to maximise the chances of encountering their partner, which would provide evidence for active maintenance of coordination in this species. Finally, we designed an experiment to investigate the putative role of chick begging in the coordination of provisioning behaviour. We artificially fed chicks prior to the arrival of either parent to simulate a previous provisioning visit from the perspective of the first parent to arrive to the nest. Through this, we aimed to assess whether parents responded to satiated chicks by changing their foraging behaviour.

Material and methods

Sampling methods

This study was conducted on Skomer Island (54.44°N, 05.17°W), Wales, U.K., during the chick-rearing periods

(June–August) of 2018 and 2019. During the breeding season, adult Manx shearwaters nest in underground burrows, which they enter and leave only at night. Inside the nest chamber, shearwaters can be accessed by hand either through the burrow entrance or through a purpose-built inspection hatch. As part of the annual long-term monitoring of the colony used in this study, nests were checked daily to establish the identity of breeding pairs. Shortly after laying, adult females were sexed by cloacal inspection (Boersma and Davies 1987), and males by inference. In the last few weeks of incubation, target nests were monitored daily to determine the hatching date, taken as the first daythe chick was found entirely outside of the eggshell. During these daily checks, adults were fitted with passive integrated transponder (PIT) tags (2 × 12 mm EM4102 glass tag, Cyntag Cynthiana, KY, USA), programmed with a unique identification number. These were shrink-wrapped onto a 1 mm cable tie, which was looped around the tarsus, above the metal British Trust for Ornithology ring, and tightened sufficiently that they could not pass over the ring or intertarsal joint but could otherwise move freely. A total of 46 nests in 2018 and 55 nests in 2019 were used in the study; of these, 25 nests were monitored in both years.

Radio frequency identification (RFID) readers were deployed at the entrance to burrows to record precisely the arrival and departure times of adults into and out of the nest. These comprised two-loop antennae, a computer and a RAVPOWER 26 800 mAh portable battery. One antenna was placed at the entrance of the burrow, and the other approximately 20 cm inside the tunnel to determine directionality in the detections. When a PIT tag passes within 5 cm of the antennae, the tag transmits its unique identification number, which is stored on the RFID computer with the date and time of detection. We aimed to take recordings from RFID readers for the first 30 days of the hatched chicks' life.

Data processing and analysis

All analyses and data processing were carried out in R ver. 3.5.1 (<www.r-project.org>). Means are presented throughout with 95% confidence intervals (CI) unless otherwise specified. Model fit was assessed through visual inspection of diagnostic residual plots. To control for multiple measurements from the same nests and in different years, all our models included a random intercept of individual ID or individual ID nested within nest ID as appropriate, nested within a year.

Detections from RFID readers were used to determine the times and durations of nest visits and foraging trips. Directionality of the parents into or out of the nest was inferred based on which antenna was triggered first: if the first detection was on the antenna at the entrance and the second on the internal antenna, the parent was moving into the burrow, and vice versa. Based on this classification, foraging trip duration was taken as the time between the departure and arrival time of each bird while the time between arrival and departure indicated time spent in the burrow. RFID readers were programmed to report their status every hour. If the RFID reader was reported as off for > 1 h during the night, the two trips adjacent to the off period were discarded. Instances where the parent remained in the burrow during the day to brood-guard the chick were excluded from the analyses. From our RFID data, we extracted 2787 provisioning visits.

We split provisioning and self-maintenance foraging trips (hereby 'short' and 'long' trips, respectively) based on methods outlined by Welcker et al. (2009). We assumed that the duration of foraging trips could be represented by a bimodal distribution in which two separate lognormal distributions of duration in hours represent short and long trips, respectively. By iteratively changing the cut-off point between the two distributions, we looked for the point at which the variance in both distributions was minimised. This occurred at approximately 50 h in our dataset and was used as the threshold to divide the two trip types (Fig. 1).

Evidence for active coordination

The first evidence that Manx shearwaters actively coordinate their provisioning visits was reported by Tyson et al. (2017), who found that parents were more likely to switch from one trip type (short or long) to the other when they visited the nest on the same night as their partner, regardless of whether they physically coincided at the nest. To test this hypothesis in our dataset, we used the R package lme4 (Bates et al. 2015) to construct a generalised linear mixed effects model (GLMM) with a Gamma distribution that compared the absolute value of change in trip duration between consecutive trips (in hours) between nights when only one parent returned to the nest vs nights where both returned (Table 1, Model 1). Large changes

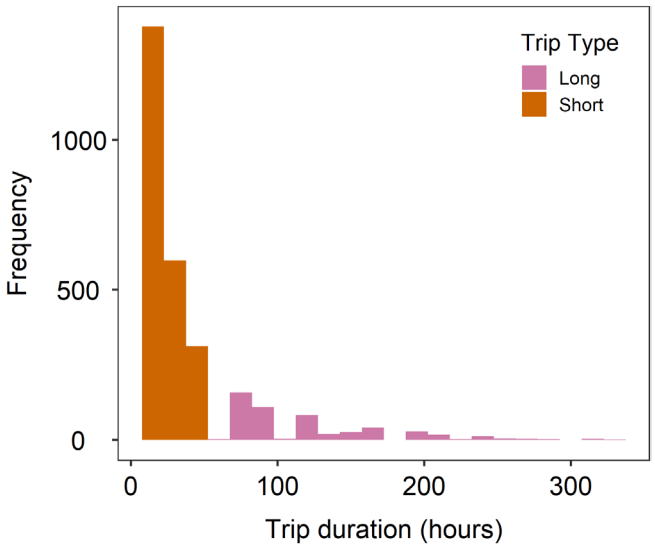

Figure 1. Histogram to show trip duration (in hours) across the dataset. Bars have been coloured according to trip type assignment, where purple bars = 'long' trips and orange bars = 'short' trips. Gaps in the histogram are an artefact of the fact Manx shearwaters can only arrive at and depart from their nests at night.

Table 1. Model structures used in the analysis. Model names are referenced in the text.

Type of model	Model	Parameters		
		Response	Fixed	Random
Gamma GLMM	1	Change in trip duration (h)	Colony synchrony + sex	Nest:ID
	2	Change in trip duration (h)	Nest synchrony + sex	Nest:ID
Beta GLMM	3	$\frac{\text{Nest visit duration}(\text{min})}{\text{Time until sunrise}(\text{min})}$	Order of arrival + sex	Year:Nest:ID
Gamma GLMM	4	Trip duration (h)	Time since encounter + sex	ID
	5	Nest visit duration	Time since encounter + sex	ID
LMM	6	Change in trip duration (h)	Fed_group + sex	Year:ID
Binomial GLMM	7	Order of arrival	Previous trip duration + sex	Year:Nest:ID

Colony synchrony = whether or not parents visited the colony on the same night; Sex = male or female; Year = year of data collection, 2018 or 2019; Nest = nest identity; ID = individual identity; Nest synchrony = whether or not parents overlapped in the nest on a given night; Order of arrival = first or second parent to visit the colony; Time since encounter = number of days since parents last met at the nest; Fed_group = Supplementarily fed or control; Previous trip duration = duration of preceding foraging trip in hours.

in trip duration would indicate a switch in trip type, whereas small changes would indicate parents continuing on the same trip type. For those nights where both parents returned (n = 1096 trips for 69 nests), we further examined whether the observed change in foraging trip duration differed depending on whether the parents physically overlapped in the nest or not (Table 1, Model 2). As an extension to this observational approach, we experimentally removed the opportunity for parents to physically meet at the nest. The methods and results of this experiment, for which we obtained a very small sample size and therefore very low statistical power, are reported in the Supporting information.

We further examined whether there were any patterns in the behaviour of parents that might suggest they attempt to maximise the probability of physical reunion with their partner, and therefore a role for this in the coordination of provisioning behaviour. We expected that if parents actively attempt to physically coincide with their partners at their nest, the first parent to arrive to feed the chick should spend longer at the nest. We examined whether the duration of the nest visit differed for the first and second parent to arrive at the nest for nights on which both parents visited (n = 1096). To account for the fact that parents that visit the colony earlier have more night time hours available to them that they could spend waiting, we divided nest visit duration by the minutes remaining until sunrise. Because this generated a proportional response variable, we modelled differences in nest visit duration with a beta distribution using the R package glmmADMB (Bolker et al. 2012), including the fixed predictor of order of arrival (Table 1, Model 3). We excluded visits for which visit duration was unknown due to reader error or where data for one parent were missing, leaving 956 visits across 67 nests retained for analysis.

If provisioning parents actively maintain coordination in their behaviour, rather than this passively emerging as a consequence of their individual decisions, we might expect behaviour to change as this coordination shows signs of breaking down. For example, as the time since the parents last encountered one another increases, the provisioning (short trip) parent might alter its behaviour to maximise the chances of meeting its partner on a given night. To investigate this possibility, we examined changes in trip duration and nest visit duration for short trip parents (n = 1232 for 68 nests) as a function of the number of days since the last partner encounter. If provisioning parents try to maximise the chances of a reunion, we would expect a decrease in trip duration and/or an increase in visit duration as the time since they last met the partner increases. We used GLMMs with a Gamma distribution to model foraging trip duration and visit duration as a function of time since partner encounter (Table 1, Models 4 and 5). As sex is known to influence provisioning behaviour in Manx shearwaters (Quillfeldt et al. 2004, Hamer et al. 2006, Tyson et al. 2017), we included the fixed effect of 'sex' in all our models.

Evidence for indirect signalling

If parents actively coordinate their provisioning behaviour without physically coinciding at the nest, other cues must inform their behaviour. We investigated the possibility that parents use chick hunger levels, probably via begging, to determine whether their partner has made a recent visit to the nest. Parents that encounter satiated chicks, which beg less (Quillfeldt et al. 2004), could infer that their partner has recently provisioned and switch trip type accordingly. We designed a supplementary feeding experiment to test this hypothesis. A sample of chicks was artificially fed before either parent had arrived at the nest so that the first parent to visit the nest would be led to believe its partner had already provisioned the chick.

Chicks were removed from the nest for feeding one hour prior to dusk (between approximately 21:00 and 22:00 UTC) to maximise the probability that parents encountered a fully satiated chick while eliminating the possibility of their returning to an empty nest, as adults do not begin to return to the colony until after dusk. Chicks were fed with whole sardines (*Clupea* spp.) in sunflower oil (60% fish by mass), which were blended with additional sunflower oil (10% by mass) and water (30% by mass), following methods by Dean (2012) and Padget (2017). The estimated energy content was

12.9 kJ g^{-1} (Dean 2012). The resulting food mixture was warmed to 30–35°C just before feeding, using a water bath. Meals were administered through intubation of the proventriculus using flexible crop tubes and delivered slowly using a plastic syringe. Immediately prior to and following feeding, each chick was weighed on a digital scale precise to 0.5 g. Total feed size was calculated as the difference between these two measures and averaged 43.6 ± 8.8 g (mean + SD). This was approximately equivalent to the normal daily food delivery for chicks (53 g per night, Hamer et al. 1998). Feeds took approximately five minutes to deliver.

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

We predicted that short-trip parents would switch to long trips after encountering an artificially fed chick (Fig. 2). To

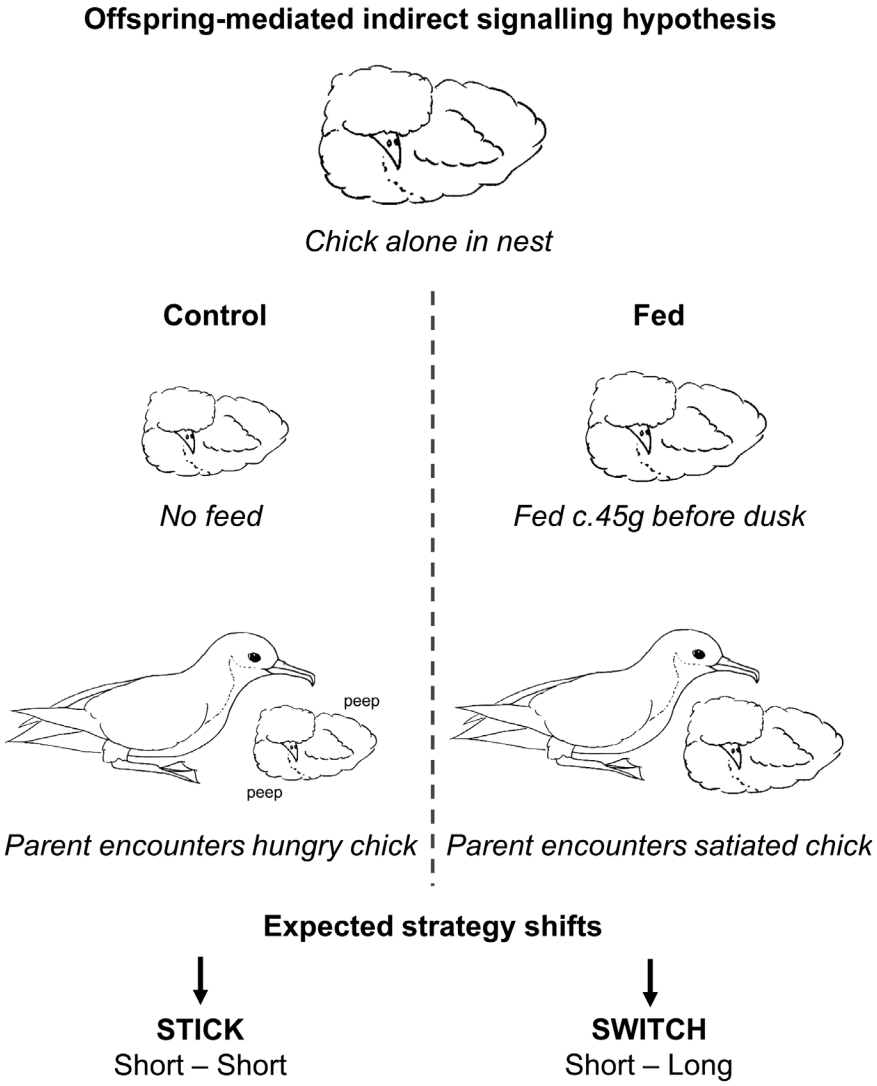

Figure 2. Schematic to illustrate the feeding protocol. Under normal or 'control' conditions, the parent visits an unfed chick, which subsequently begs to receive food. The parent continues on its short, frequent provisioning trips strategy. In the fed group, chicks are fed just before the parent arrives. The parent therefore encounters a fed, satiated chick that presumably begs less. It is therefore led to believe that its partner has visited the nest, and so switches to long, self-maintenance trips.

this end, we fitted a linear mixed effects model (LMM) to examine whether the difference between consecutive foraging trips (in hours) differed according to whether the chick had been artificially fed or not (Table 1, Model 6). A difference in trip duration of > 50 h, our threshold for dividing short and long trips (Data processing and analysis), would indicate a switch in trip type. To determine whether our sample size was sufficient to find a result, if one existed, we conducted a post hoc power analysis to determine the probability of discovering our predicted effect, if present, given this sample size.

As females are known to be more responsive to chick begging behaviour than males (Quillfeldt et al. 2004, Hamer et al. 2006) and so might be expected to show a different response to the experimental manipulation, we included the interactive effect of sex and experimental group (fed or not) in our models. To account for potential individual and temporal variation that may explain variation in trip duration when analysing the effect of our feeding experiment, we fitted our models using two different datasets: one that contained data on focal parents on experimental as well as all unmanipulated ('control') nights recorded for those parents ($n = 234$ trips for 22 nests) and another containing data on focal parents on experimental nights as well as unmanipulated ('control') nests on the same night ($n = 277$ visits for 65 nests).

Finally, as only short-trip parents can benefit from the indirect cues provided by chick begging behaviour, if parents use this information to decide to switch trip type, we would expect a consistent pattern in which parent arrives at the nest first. Specifically, following a long trip, individuals may be expected to arrive at the nest at an earlier hour than after a short trip, so that they can maximise the chance that they are seen or that their partner finds the chick to have been fed. Shearwaters are known to time their arrival to the colony based on their perceived distance from it (Padget et al. 2019), and so this might be a viable way to achieve coordination. To examine whether this was the case, we constructed a generalised mixed effects model (GLMM) with a binomial error structure to test whether previous trip duration (in hours) predicted which parent was first to arrive at the nest for those nights where both parents visited the colony ($n = 992$ trips for 67 nests; Table 1, Model 7). We predicted that parents on long trips would be more likely to be the first to arrive at the nest.

Ethical note

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

Results

Across the entire study, we collected data from approximately the first four weeks of chick provisioning, with the mean monitoring period starting when the chick was 3.55 days old and lasting until it was 32.61 days old. During this time, we collected a mean of 27.59 ± 17.37 provisioning visits per nest. In total, we identified 641 foraging trips from 46 nests in 2018 and 2146 trips from 55 nests in 2019. Mean trip duration for birds on short trip types was 25.92 ± 9.17 h for females and 25.22 ± 8.96 h for males and for long trip types was 127.46 ± 59.69 h for females and 112.16 ± 48.32 h for males. Females making short trips to provision the chick completed 3.59 ± 2.08 trips before switching to a long, self-maintenance trip; males completed 4.30 ± 3.01 trips. Both sexes usually engaged in just one long trip before resuming provisioning; the mean number of consecutive long trips was 1.20 ± 0.52 for females and 1.21 ± 0.49 for males, meaning that occasionally parents were observed to take long trips twice in a row, having provisioned the chick in between. Parents varied considerably in the amount of time they spent in the nest when provisioning their offspring. The maximum time spent in the nest was 409.10 min (6.82 h) for females and 402.02 min (6.70 h) for males, and the mean was 144.91 ± 74.93 min for females and 166.12 ± 77.02 min for males.

Evidence for active coordination

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

Parents that visited the nest on the same night as their partners showed a greater change in foraging trip duration than parents who made solo visits (synchronous change: 48.6 h; asynchronous change: 17.7 h; Fig. 3, 4; Model 1; Table 2), suggesting that these parents switched their trip type after a synchronous visit to the colony. Males changed their consecutive trip duration to a lesser extent than females (female change: 33.6 h, male change: 25.5 h; Table 2). Considering those birds that were synchronous with their partner to the colony, there was no significant change in trip duration depending on whether they physically overlapped at the nest itself (Model 2; Table 2).

When parents visited the colony on the same night but did not coincide at the nest itself ($n = 354$ visits for 59 nests), the time gap between their visits ranged from 2.05 to 288.32 min, with a mean of 65.08 ± 59.27 min. We examined whether parents spent longer in the nest when they were the first to arrive at the nest. We found that the first parent to arrive at the colony spent longer in the nest, even accounting for the difference in the remaining night time available to both parents (Model 3; first: 0.11 [0.097, 0.13]; second: 0.079 [0.066, 0.094]; $z = 4.075$, $p < 0.0001$). This result held even when analysing differences in raw visit duration (Supporting information). There was no difference in the proportion of the night males vs females spent at the nest (female: 0.088 [0.072, 0.10], male: 0.10 [0.088, 0.12]; $z = 1.74$, $p = 0.082$).

Short trip parents reduced their foraging trip durations by 0.39 [0.10, 0.69]% for each day since they had last encountered their partner (Model 4; $t = -2.64$, $df = 1$, $p = 0.0082$). This effect was very small however:

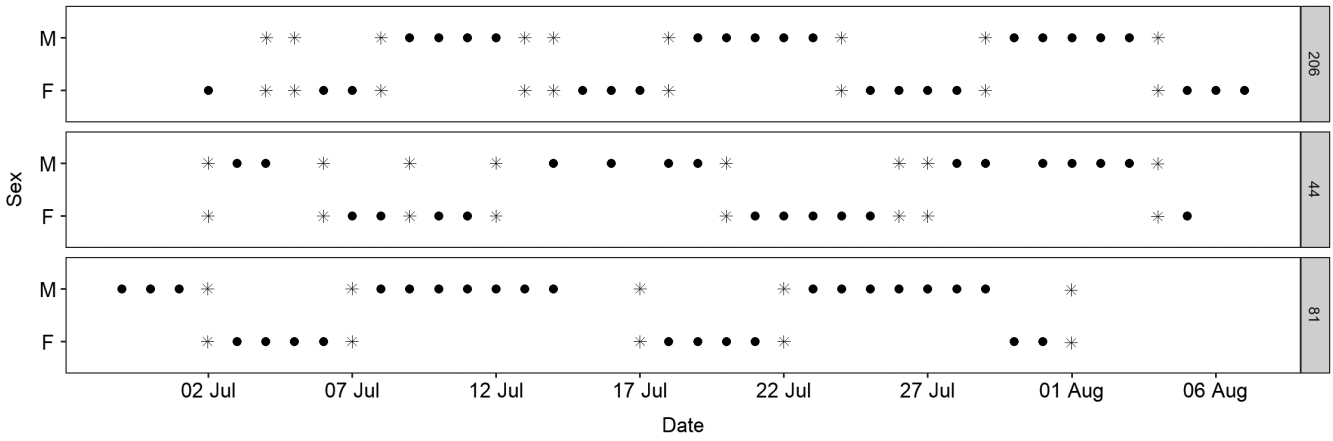

Figure 3. Example of RFID detections for three nests; nest IDs listed in grey boxes on the right of panels (206, 44, 81). Filled circles indicate nights where only one parent visited the colony, stars indicate nights where both parents visited the colony.

while an individual that had encountered its partner 1 day ago would be predicted to undertake a trip of 24.85 h, one that encountered its partner 4 days ago would undertake a trip of 24.27 h. There was no difference in nest visit duration with increasing time since the last partner encounter (Model 5; $t = -0.56$, $df = 1$, $p = 0.58$). Males and females did not differ in their foraging trip durations (male: 25.19 [24.07, 26.37] h; female: 24.58 [23.41, 25.81] h; $t = 0.72$, $p = 0.47$); however, males were found to make longer visits to the nest (male: 161.61 [149.39, 174.82] minutes, female: 134.38 [121.88, 148.15] minutes; $t = 2.87$, $p = 0.0041$).

Evidence for indirect signalling

Parents that visited chicks that had been artificially fed were not found to change foraging trip duration more than parents visiting control chicks, both when comparing focal parents on experimental vs unmanipulated nights and when comparing focal parents on experimental nights to unmanipulated nests on the same night (Fig. 5; Model 4; Table 3). This suggests that they continued to make short trips to the nest, rather than switching to long trips. There was no interactive effect of sex and experimental group (Model 4, Table 3). We had the power to detect a real effect (at least a 50 h increase in trip

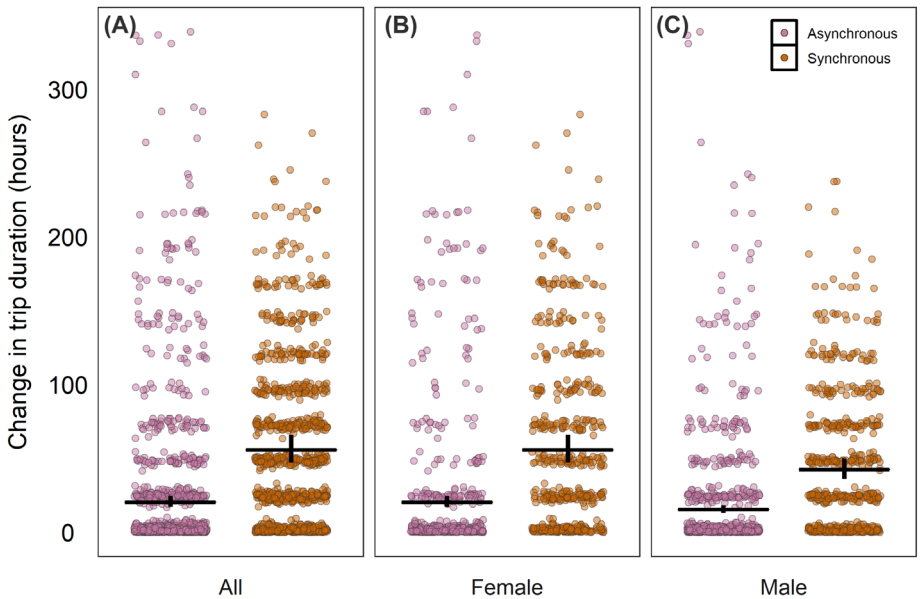

Figure 4. Absolute value of change in foraging trip duration (in hours) between consecutive foraging trips for parents that arrived at the colony on the same night as their partner (asynchronous, lilac points) or alone (synchronous, orange points) at the colony for all individuals combined (A), females only (B), and males only (C). Individuals that visited the colony on the same night as their partner showed a greater change in trip duration than those that did not overlap. Horizontal lines indicate mean, and vertical lines indicate 95% CI. Data are jittered in the x-axis for readability. The banding in trip changes is an artefact of the fact that shearwaters only visit their nests at night.

Table 2. Exponentiated coefficients and test statistics from Gamma GLMM of the absolute value of change in foraging trip duration (hours) according to whether birds were synchronous at the colony or nest, and sex. p-values were calculated from likelihood ratio tests comparing the full model to a model without the effect of interest.

Variable	Synchronous at colony			Synchronous at nest		
	Coefficient + 95% CI	t	p	Coefficient + 95% CI	t	p
Intercept	20.30 [16.90, 24.37]			60.08 [50.09, 72.07]		
Synchrony (YES)	2.74 [2.38, 3.17]	13.73	< 0.0001	0.95 [0.79, 1.16]	−0.44	0.65
Sex (M)	0.76 [0.61, 0.94]	−2.51	0.012	0.75 [0.63, 0.88]	−3.4	0.00066

duration) of 0.99, suggesting our lack of a result is unlikely to be a false negative.

Based on observational analysis of RFID data, long-trip parents are always expected to switch foraging trip type on their return to the nest, and so only short-trip parents would be expected to benefit from the information gained from indirect signalling. As such, we predicted that long-trip parents would provision at the nest first, as the resulting satiated chick could indicate to the short-trip parent that its partner had returned to the colony. Contrary to these predictions, we found that parents that had been on short trips were more likely to arrive at the nest first (Fig. 6; Model 7; $\chi^2 = 4.91$, df = 1, p = 0.027). The probability that a parent would be the first to arrive at the nest decreased by 0.44 [0.045, 0.84]% for each additional hour that the bird spent on its foraging trip. Males were more likely to arrive at the nest before females (males: 58.6 [49.1, 67.5]%; females: 43.4 [34.1, 53.2]%; $\chi^2 = 4.52$, p = 0.033).

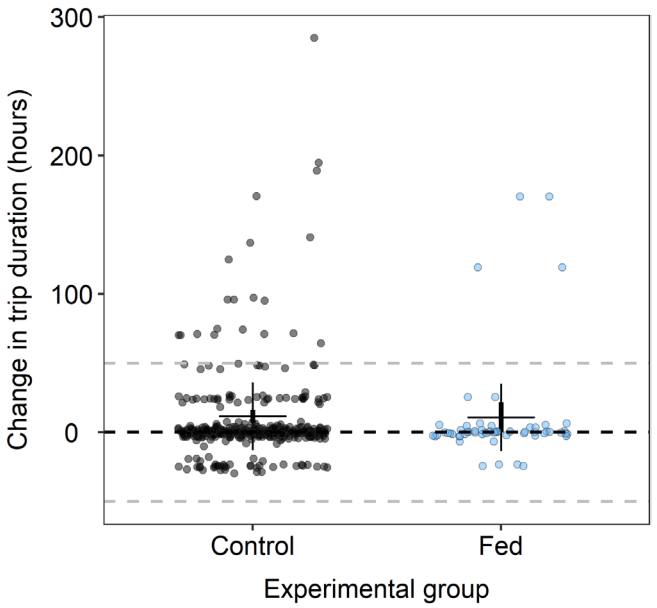

Figure 5. Change in trip duration in hours according to whether short trip parents encountered artificially fed or unfed chicks. Black dotted line indicates 0 change in trip duration; grey horizontal lines indicate +50 and −50 h change in trip duration. Parents whose change in trip durations lay outside these margins were deemed as having switched trip type (short to long). Horizontal line of crosshairs indicates mean, vertical lines indicate 95% CI. Data are jittered in the x-axis for readability.

Discussion

By combining remotely collected observational data and experimental manipulation, we investigated the evidence for the roles of direct communication or indirect signalling mediated by the chick in the coordination of parental care. Despite replicating the finding that care is coordinated (Tyson et al. 2017), neither our observational findings nor experimental results provided support for the role of either mechanism in the maintenance of provisioning coordination.

Manx shearwater pairs almost always reunite at the nest prior to exchanging incubation duties (except during temporary nest desertion) and often overlap in the nest during provisioning (Brooke 1990), which may present an opportunity for communication between the pair. Although we found no difference in the magnitude of trip duration change between parents that overlapped with their partners at the nest and those that did not, only 25% of partners did not meet at the nest. Furthermore, we observed that the first parent to arrive at the nest tended to spend longer waiting at it, even accounting for night time hours available, which could indicate parents were waiting for their partner to return to the nest. However, as reported by Tyson et al. (2017), while we found that parents adjusted trip duration considerably more when they visited the nest on the same night as their partner, the magnitude of this adjustment did not depend on parents overlapping at the nest itself. We further found through an additional experimental manipulation (Supporting information) that parents that were physically prevented from encountering their partners adjusted their trip durations by the amount expected under normal conditions, though our small sample size meant we had limited power to detect an effect, and therefore, this result must be interpreted with caution. We observed that provisioning parents reduced their trip duration as the time since they last encountered their partner increased. This could plausibly reflect parents attempting to maximise the probability of meeting the partner and thus 'reset' their coordinated provisioning as it begins to break down. However, given that our other results clearly do not support the importance of such physical reunion in coordination, this seems unlikely. Possibly, this reduction in trip duration over time might instead reflect deterioration in the physical condition of the parent, which constrains it to collect food for the chick from closer, less productive foraging patches. However, while the effect was statistically significant, it was extremely weak, and so an alternative, possibly more likely, explanation is that this relationship is not of biological relevance in this context at all.

Table 3. Coefficients and test statistics from LMM of change in trip duration (hours) according to experimental group and sex. p-values calculated from likelihood ratio tests comparing the full model to a model without the effect of interest.

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

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

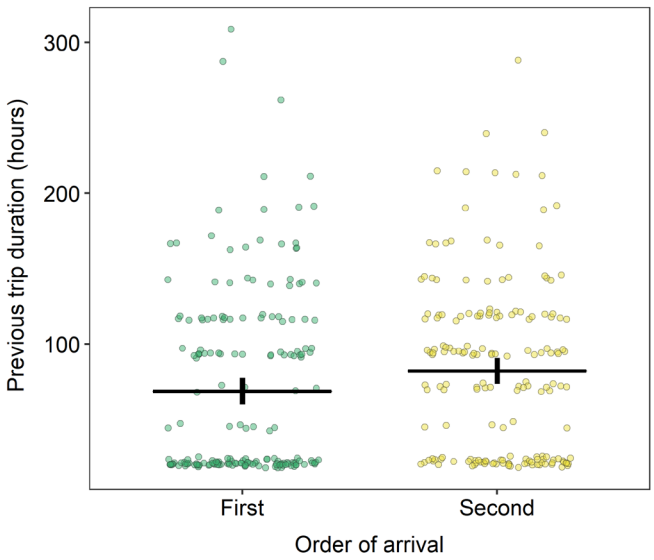

Figure 6. Previous trip duration in hours according to whether the parent was first or second to arrive at the nest. Parents that had been on shorter trips were more likely to arrive at the nest first. Horizontal line indicates mean, and vertical lines indicate 95% CI. Data are jittered in x-axis for readability.

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

Finally, it is possible that parents physically reunite prior to entering the nest, which would not be detected by our RFID detection system. It has been previously suggested (Congdon et al. 2005) that parents may reunite while at sea. Manx shearwaters form large rafting aggregations in

the hours before dusk, which may present an opportunity for such interaction between partners (Brooke 1990, Richards et al. 2019). However, these rafts form for only a few hours and consist of many thousands of shearwaters, and we did not find evidence for individuals rafting in consistent locations (Supporting information), making this hypothesis unlikely. Furthermore, it has been previously observed that shearwaters returning from long, self-maintenance trips tend to return to the nest immediately following their commute, rather than spending any time rafting (Padget et al. 2019). Consequently, they are likely to return to the nest immediately following their foraging trip, eliminating the possibility of meeting their partner in the waters around the colony. This may additionally explain our observation that short-trip parents were more likely to arrive at the nest first, as long trip birds tend to arrive at the colony after dark and are thus more likely to be the second to arrive at the nest. As a result, it is unlikely that parents do not overlap at the nesting raft at the same time at all. While it is possible that shearwaters could instead meet at the colony outside of the nest, parent shearwaters spend little time loafing on the surface (N Gillies, pers. obs.) and are unlikely to spend the average hour-long gap we observed between parent detections waiting outside the nest.

Given these findings, it becomes plausible to consider that apparent coordination during provisioning might actually be the result of some kind of entrainment that develops during incubation and persists into the chick-rearing period. This may occur when parents respond in similar ways to environmental variation or changes in their body condition. During incubation, Manx shearwaters largely sit at the nest until their partner returns, meaning shift duration is ultimately set by the foraging bird, which determines how long to spend at sea based on a combination of its own and its partner's body condition (Gillies et al. 2021a). Over the entire 51-day incubation period, the interdependent contribution of both parents' conditions to determining foraging trip duration might give rise to a consistent pattern of alternating incubation and foraging shifts. If similar decision-making processes are employed with regards to parental body condition during chick provisioning, then these patterns may carry over into this period. For example, a pair in which one parent always incubates for 4 days and the other always incubates for 5 might later be observed to alternate four- and five- day bouts of frequent provisioning visits when feeding the chick. Supporting this is previous theoretical work in which parental provisioning rates were adequately simulated by changes in adult energy reserves alone (Ricklefs and Schew 1994). This may additionally present an alternative explanation for findings by Tyson et al. (2017) that coordination within pairs decreases with chick age. As parents do not always feed nightly, especially as the chick grows older and is less dependent on frequent provisioning (Hamer et al. 1998), then this could lead to a breakdown in this rhythm over time, as provisioning visits are not subject to the same constraints as incubation shifts. Such a mechanism could be an effective way for parents to maintain largely well-coordinated provisioning visits when the opportunities for direct interaction are reduced by the limitations of chick feeding.

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

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Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.wh70rxwp9> (Gillies et al. 2021b).

References

Ahern, T. H., Hammock, E. A. D. and Young, L. J. 2011. Parental division of labor, coordination and the effects of family structure on parenting in monogamous prairie voles *Microtus ochrogaster*. – Devel. Psychobiol. 53: 118–131.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Bebbington, K. and Hatchwell, B. J. 2016. Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. – Behav. Ecol. 27: 652–659.

Boersma, P. D. and Davies, E. M. 1987. Sexing monomorphic birds by vent measurements. – Auk 104: 779–783.

Bolker, B., Skaug, H., Magnusson, A. and Nielsen, A. 2012. Getting started with the glmmADMB package. – R package ver. 2.0-8, <https://rdrr.io/rforge/glmmADMB/>.

Booth, A. M., Minot, E. O., Fordham, R. A. and 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: 144–146.

Boucaud, I. C. A., Aguirre Smith, M. L. N., Valère, P. A. and Vignal, C. 2016. Incubating females signal their needs during intrapair vocal communication at the nest: a feeding experiment in great tits. – Anim. Behav. 122: 77–86.

Brooke, M. 1990. The Manx shearwater. – A & C Black Publishers Ltd.

Chase, I. D. 1980. Cooperative and noncooperative behavior in animals. – Am. Nat. 115: 827–857.

Congdon, B. C., Krockenberger, A. K. and Smithers, B. V. 2005. Dual-foraging and co-ordinated provisioning in a tropical Procellariiform, the wedge-tailed shearwater. – Mar. Ecol. Prog. Ser. 301: 293–301.

Dean, B. 2012. The at-sea behaviour of the Manx shearwater. – Univ. of Oxford.

Drummond, H., Calderón-De Anda, M., Perez, C. and Stamps, J. 2002. Collaborative tactics for nestsite selection by pairs of blue footed boobies. – Behaviour 139: 1383–1412.

Gillies, N., Syposz, M., Wynn, J., Vansteenberghe, C. and Guilford, T. 2021a. Responses of Manx shearwaters to handicapping and its implications for the coordination of care. – Front. Ecol. Evol. 9: 1–12.

Gillies, N., Tyson, C., Wynn, J., Syposz, M., Vansteenberghe, C. and Guilford, T. 2021b. Data from: Exploring the mechanisms of coordinated chick provisioning in the Manx shearwater *Puffinus puffinus*. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.wh70rxwp9>.

Griffioen, M., Iserbyt, A., Muller, W. and Müller, W. 2019. Handicapping males does not affect their rate of parental provisioning, but impinges on their partners' turn taking behavior. – Front. Ecol. Evol. 7: 1–7.

Griffith, S. C. 2019. Cooperation and coordination in socially monogamous birds: moving away from a focus on sexual conflict. – Front. Ecol. Evol., <https://doi.org/10.3389/fevo.2019.00455>.

Grissot, A., Araya-Salas, M., Jakubas, D., Kidawa, D., Boehnke, R., Błachowiak-Samołyk, K. and Wojczulanis-Jakubas, K. 2019. Parental coordination of chick provisioning in a planktivorous arctic seabird under divergent conditions on foraging grounds. – Front. Ecol. Evol. <https://doi.org/10.3389/fevo.2019.00349>.

Guilford, T., Meade, J., Freeman, R., Biro, D., Evans, T., Bonadonna, F., Boyle, D., Roberts, S. and Perrins, C. M. 2008. GPS tracking of the foraging movements of Manx shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. – Ibis 150: 462–473.

Hagelin, J. C., Jones, I. L. and Rasmussen, L. E. L. 2003. A tangerine-scented social odour in a monogamous seabird. – Proc. R. Soc. B 270: 1323–1329.

Hamer, K. C., Lynnes, A. S. and Hill, J. K. 1998. Regulation of chick provisioning rate in Manx shearwaters: experimental evidence and implications for nestling obesity. – Funct. Ecol. 12: 625–630.

Hamer, K. C., Quillfeldt, P., Masello, J. F. and Fletcher, K. L. 2006. Sex differences in provisioning rules: responses of Manx shearwaters to supplementary chick feeding. – Behav. Ecol. 17: 132–137.

Hinde, C. A. 2006. Negotiation over offspring care? A positive response to partner-provisioning rate in great tits. – Behav. Ecol. 17: 6–12.

Johnstone, R. A. and Hinde, C. A. 2006. Negotiation over offspring care – how should parents respond to each other's efforts? – Behav. Ecol. 17: 818–827.

Johnstone, R. A., Manica, A., Fayet, A. L., Stoddard, M. C., Rodriguez-Gironés, M. A. and Hinde, C. A. 2014. Reciprocity and conditional cooperation between great tit parents. – Behav. Ecol. 25: 216–222.

Lehtonen, T. K. 2017. Parental coordination with respect to color polymorphism in a crater lake fish. – Behav. Ecol. 28: 925–933.

Lejeune, L., Savage, J. L., Bründl, A. C., Thiney, A., Russell, A. F. and Chaine, A. S. 2019. Environmental effects on parental care visitation patterns in blue tits *Cyanistes caeruleus*. – Front. Ecol. Evol. 7: 1–15.

Mariette, M. M. 2019. Acoustic cooperation: acoustic communication regulates conflict and cooperation within the family. – Front. Ecol. Evol. 7: 1–8.

Nevitt, G. A. 2008. Sensory ecology on the high seas: the odor world of the procellariiform seabirds. – J. Exp. Biol. 211: 1706–1713.

Padget, O. 2017. Navigation in procellariform seabirds. – Univ. of Oxford.

Padget, O., Stanley, G., Willis, J. K., Fayet, A. L., Bond, S., Maurice, L., Shoji, A., Dean, B., Kirk, H., Juarez-Martinez, I., Freeman, R., Bolton, M. and Guilford, T. 2019. Shearwaters know the direction and distance home but fail to encode intervening obstacles after free-ranging foraging trips. – Proc. Natl Acad. Sci. USA 116: 21629–21633.

Quillfeldt, P., Masello, J. F. and Hamer, K. C. 2004. Sex differences in provisioning rules and honest signalling of need in Manx shearwaters, *Puffinus puffinus*. – Anim. Behav. 68: 613–620.

Raihani, N. J., Nelson-Flower, M. J., Moyes, K., Browning, L. E. and Ridley, A. R. 2010. Synchronous provisioning increases brood survival in cooperatively breeding pied babblers. – J. Anim. Ecol. 79: 44–52.

Richards, C., Padget, O., Guilford, T. and Bates, A. E. 2019. Manx shearwater *Puffinus puffinus* rafting behaviour revealed by GPS tracking and behavioural observations. – PeerJ 7: e7863.

Ricklefs, R. E. and Schew, W. A. 1994. Foraging stochasticity and lipid accumulation by nestling petrels. – Funct. Ecol. 8: 159.
Savage, J. L. and Hinde, C. A. 2019. What can we quantify about carer behavior? – Front. Ecol. Evol., <https://doi.org/10.3389/fevo.2019.00418.
Savage, J. L., Browning, L. E., Manica, A., Russell, A. F. and Johnstone, R. A. 2017. Turn-taking in cooperative offspring care: by-product of individual provisioning behavior or active response rule? – Behav. Ecol. Sociobiol. 71: 162.
Schlicht, E., Santema, P., Schlicht, R. and Kempenaers, B. 2016. Evidence for conditional cooperation in biparental care systems? A comment on Johnstone et al. – Behav. Ecol. 27: e2–e5.
Shoji, A., Aris-Brosou, S., Fayet, A., Padget, O., Perrins, C. and Guilford, T. 2015. Dual foraging and pair-coordination during chick provisioning by Manx shearwaters: empirical evidence supported by a simple model. – J. Exp. Biol. 218: 2116–2123.
Smiseth, P. T. 2019. Coordination, cooperation and conflict between caring parents in burying beetles. – Front. Ecol. Evol. 7, <https://doi.org/10.3389/fevo.2019.00397>.
Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press, Wiley/Blackwell. doi: 10.1046/j.1420-9101.1993.6020304.x
Trivers, R. L. L. 1972. Parental investment and sexual selection. – In: Campbell, B. (ed.), Sexual selection and the descent of man. Aldine, Chicago, IL, pp. 136–179.
Tyson, C., Kirk, H., Fayet, A., Van Loon, E. E., Shoji, A., Dean, B., Perrins, C., Freeman, R. and Guilford, T. 2017. Coordinated provisioning in a dual-foraging pelagic seabird. – Anim. Behav. 132: 73–79.
van Rooij, E. P. and Griffith, S. C. 2013. Synchronised provisioning at the nest: parental coordination over care in a socially monogamous species. – PeerJ 2013: 1–14.
Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? – Deep-Sea Res. II Top. Stud. Oceanogr. 54: 211–223.
Weimerskirch, H., Chastel, O., Ackermann, L., Chaurand, T., Cuenot-Chaillet, F., Hindermeyer, X. and Judas, J. 1994. Alternate long and short foraging trips in pelagic seabird parents. – Anim. Behav. 47: 472–476.
Welcker, J., Harding, A. M. A., Karnovsky, N. J., Steen, H., Strøm, H. and Gabrielsen, G. W. 2009. Flexibility in the bimodal foraging strategy of a high Arctic alcid, the little auk Alle alle. – J. Avian Biol. 40: 388–399.
Wojczulanis-Jakubas, K., Araya-Salas, M. and Jakubas, D. 2018. Seabird parents provision their chick in a coordinated manner. – PLoS One 13: e0189969.