1 Coordinated provisioning in a dual foraging pelagic seabird

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In long-lived species, care-giving parents are expected to balance their own condition 5 6 with that of their offspring. Many species of seabirds display a unique behavioural 7 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 8 9 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 10 11 foraging strategy, chicks might be abandoned for extended periods when the long trips 12 of both partners coincide. Whether partners coordinate their dual foraging strategies, however, is largely unknown. To investigate this possibility, we used radio frequency 13 14 identification readers coupled with passive integrated transponder tags to record 15 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 16 17 between parents, which facilitates consistent provisioning. Additionally, we show that the propensity for pairs to coordinate declines across the chick rearing period. Given 18 19 the potential costs of not coordinating, we expect this behaviour to be widely spread 20 among dual foraging species. 21

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

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

38 During chick care, many seabird species display a unique behavioural adaptation to reconcile these conflicting energetic demands known as "dual foraging" 39 40 wherein long trips are interspersed with one or more short trips (Chaurand & 41 Weimerskirch, 1994). During long trips, parents avoid the high travel costs of repeated 42 commuting and may travel further to utilize more productive foraging grounds, but at 43 the cost of reduced provisioning of the offspring. During short trips, however, the 44 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 45 undertaken by many seabird species, especially those with pelagic foraging habits, and 46 47 the constraints of central place foraging. Numerous studies have documented dual foraging across a variety of taxa, including Procellariiformes (Weimerskirch et al., 1997; 48 49 Granadeiro et al., 1998; Weimerskirch & Cherel, 1998), Sphenisciformes (Saraux et al., 50 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 51 52 as inshore foraging species have also been observed to display dual foraging, e.g. little 53 penguins (Eudyptula minor) (Saraux et al., 2011).

While dual foraging is a widely studied behaviour, it entails a complication that is 54 55 seldom discussed. Namely, if parents independently employ a dual foraging strategy, chicks might be abandoned for extended periods when long trips coincide. As 56 57 prolonged bouts of starvation are likely to increase mortality, especially in young 58 chicks, there should be selection for within-pair coordination in species with variable 59 foraging trip lengths. While there is some evidence that the timing of "long trips" is not independent between partners in some species (Booth et al., 2000; Congdon et al., 60 61 2005), the degree of such coordination and the mechanisms underlying it are poorly 62 understood.

The Manx shearwater Puffinus puffinus is a monomorphic, burrow-nesting 63 seabird that is known to display dual foraging (Shoji et al., 2015; Fayet et al., 2015) and 64 exhibits only minor sex-specific differences in foraging duration and meal size (Gray & 65 66 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 67 68 Procellariiformes, Manx shearwaters have protracted incubation and chick-rearing periods, together lasting approximately 120 days (Brooke, 1990; Harris, 1966), which 69 70 makes the breeding period energetically demanding, and the potential need for 71 coordinated provisioning particularly acute. Given these features, the Manx shearwater 72 is a plausible candidate in which to observe coordination of dual foraging routines 73 between partners.

74 We used an automated nest monitoring system to examine the possibility of coordinated provisioning by monitoring foraging trip durations in Manx shearwater pairs 75 during their chick-rearing period. These data allowed us to examine how individual 76 77 foraging behaviour was adjusted in response to the partner. If pairs coordinate dual 78 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 79 80 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 81 82 Figure 1). While several mechanisms might allow for individuals to coordinate such behaviour, we hypothesized that reuniting at the burrow might trigger a switch between 83 84 foraging strategies. Smaller chicks lack the reserves to withstand prolonged periods of fasting, which makes regular provisioning during the first few weeks post-hatching 85 86 especially critical for chick survival (Phillips & Hamer, 1999). Thus, we also predicted 87 that coordination might be most advantageous during this earlier period and would decline as chick mass increased. 88

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Figure 1 Illustration of expected nest attendance patterns if partners have 91 uncoordinated or coordinated dual foraging routines. In the former case, both partners' 92 93 foraging strategies are completely in phase. This maximizes the interval between 94 feedings for the chick. In the case of coordinated dual foraging routines, each strategy 95 is out of phase, which results in consistent provisioning. On night 1, partner B initiates a long trip and partner A initiates a sequence of short trips. When partner B next 96 97 returns on night 5, partner A initiates a long trip and partner B switches to a series of 98 short trips. This minimizes the interval between feedings. Under this scenario, pair

99 members switch foraging strategies after synchronously returning to the colony with100 their partner.

101 Materials and Methods

102 Ethical Note

All work adheres to the ASAB/ABS Guidelines for the Use of Animals in 103 104 Research, and was conducted after approval by the Countryside Council for Wales, the 105 Skomer and Skokholm Islands Advisory Committee, the British Trust for Ornithology 106 (BTO permit C/5311) and the University of Oxford Local Ethical Review Process 107 (Zoo/LERC/190505). This study was part of the long-term monitoring program carried 108 out by Oxford University since 2006 (see Dean et al. 2012 and Shoji et al. 2015 for 109 details). The combined weight of bio-logging tags was no more than 2.2 g, roughly 110 0.5% of 450 g mean body mass, which is well below the recommended limit of 3% for 111 flying birds (Phillips et al., 2003). Though handling and bio-logging tags may negatively 112 affect birds, we observed that fledging success was not significantly lower between pairs monitored with RFID readers (0.84, n = 39) and other pairs (0.61, n = 38) within 113 our study colony (2-sample binomial test: $X_{1}^{2} = 3.9424$, p-value = 0.977). Furthermore, 114 in a detailed analysis of the impacts of our research on Manx shearwaters at our study 115 116 site, we found that for a sample of 1,321 breeding attempts between 2009 and 2014 117 which led to an egg being laid, fledging success was 0.695 in our experimental nests 118 versus 0.587 in control nests. This suggests that for a large sample our work has no 119 detectable adverse effects on breeding success.

120 Study Site and Birds

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

128 To study foraging coordination between chick-rearing shearwater pairs, we used 129 radio-frequency identification (RFID) readers coupled with passive integrated 130 transponder (PIT) tags (see Naumowicz et al. (2010) for technical details of the sensor 131 network). Our RFID readers broadly consisted of a loop antenna, the computer and a 132 12V battery power supply. The antenna was placed around the opening of the burrow. 133 When a PIT tag passes within approximately 5 cm of the antenna, the tag is energized 134 and transmits a unique identification number, which the RFID reader stores, along with 135 the time of the detection.

136 We deployed RFID readers on 39 burrows nests in March at the start of the 137 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 138 139 cable tie, which was loosely affixed to the tarsus above the metal BTO identification ring. PIT tags including housing material weighed approximately 0.3 g. Five birds with 140 141 PIT tags, each from a different pair, were also equipped with British Antarctic Survey 142 geolocator-immersion loggers (models: Mk13, 14, 15, 18L, and 19), which weighed 1.5 143 - 1.9 g. Loggers were mounted to a Darvic plastic leg ring using two cable ties. All birds 144 were taken from study burrows through an access hatch by hand and weighed at 145 device deployment. Total handling time during the attachment procedure did not 146 exceed ten minutes.

147 Data Analysis

148 All data processing steps and statistical analyses were conducted in R 3.2.3 (R 149 Core Team, 2015). Means are presented throughout as ±1 standard errors. We used 150 RFID readers to record foraging trip patterns within pairs. RFID readers record the PIT 151 tag number and detection time, but not the direction of movement through the burrow. 152 When a bird was detected by the reader, the direction of movement (entry to, or exit 153 from the nest) was inferred as follows: during chick rearing (July to September), 154 breeding shearwaters only visit the burrow for chick provisioning and do so exclusively 155 at night. After feeding, chick rearing shearwaters immediately return to sea. This 156 makes it likely that the first detection after sunset is an arrival at the burrow and the last 157 detection before sunrise is a departure from the burrow. Based on this classification 158 scheme, the time between each departure and arrival was considered the duration of

159 the foraging trip. Similarly, during the interval between each arrival and departure the 160 bird was assumed to be in the burrow. To validate these assumptions, saltwater 161 immersion records from geolocator loggers from a subset of PIT tagged birds were 162 interrogated. During any interval between RFID detections in which saltwater 163 immersion was recorded, the bird was taken to be at sea and similarly, in any detection 164 interval without saltwater immersion, the bird was taken to be at the nest. We used this 165 method rather than manually checking the burrows to reduce potential impacts of 166 visiting nests repeatedly. Our RFID readers also generated a log of the battery voltage. 167 Below 10 volts, the RFID readers would not reliably detect PIT tags. Therefore, 168 foraging trips during which the RFID reader fell below 10 volts for more than one hour 169 were discarded in order to avoid potentially combining multiple trips.

170 Of the 39 RFID readers initially deployed, 24 operated continuously throughout 171 the chick rearing period - the other 15 readers experienced prolonged periods of 172 battery failure. Our foraging trip classification procedure identified 972 foraging trips. 173 After discarding trips with more than one hour of lost battery power, 824 complete 174 foraging trips remained for the 24 pairs. All five geolocators were successfully 175 retrieved. Due to logger failure, however, saltwater immersion data could only be 176 downloaded from four devices. The four individuals with functioning immersion loggers 177 made a total of 37 foraging trips. All of these ostensible trips included periods of 178 saltwater immersion and similarly, none of the intervening ostensible burrow visits 179 contained periods of saltwater immersion, suggesting that our foraging classification 180 scheme was valid.

181 For our analysis of foraging coordination we removed pairs with fewer than five 182 synchronously initiated trips to promote a balanced comparison across pairs. Pairs 183 primarily had insufficient recorded synchronous trips due to a shortened monitoring 184 period. After this step, 17 pairs remained. These made 637 complete foraging trips. 185 Coordination was analysed by examining whether individuals altered trip duration 186 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. 187 188 Large differences in foraging duration between consecutive trips would indicate a shift 189 in foraging behavior, whereas small differences would indicate consistent foraging

190 behavior. We then compared this difference between nights when only one pair 191 member returned to the burrow and when both pair members returned to the burrow. 192 On nights when both pair members returned to the burrow, we considered two 193 scenarios: partners' visits to the burrow either overlapped (synchronous visit to the 194 burrow) or did not overlap (synchronous at the colony). Additionally, we evaluated the 195 influence of sex. The relationship between synchronicity and sex (as independent 196 variables) and the difference in duration between consecutive foraging trips (as the 197 dependent variable) was investigated through linear mixed models with a maximum-198 likelihood fitting method using the Ime4 package in R (Bates et al., 2014). Each model 199 included individual nested within burrow as a random effect and an autoregressive 200 within-group correlation structure representing the dependence between consecutive 201 trip duration. The normality and homoscedasticity of predictor variables was verified by 202 visual inspection. Models were ranked and selected based on AIC and ΔAIC relative to 203 the model with the lowest AIC value (Burnham & Anderson, 2002).

204 If foraging is coordinated in order to minimize the interval between chick 205 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 206 207 long trip, then the other partner should switch in the opposite direction from a long trip 208 to a short trip. By switching foraging duration in the same direction, pairs might either 209 increase or decrease provisioning rates, but would necessarily deviate from the pattern 210 seen in the "Coordinated" panel of Figure 1. We examined how frequently pairs 211 switched foraging strategies in opposite directions after synchronous returns relative to 212 cases where pairs increased or decreased foraging duration in the same direction (i.e. 213 both pairs shifted from a short trip to a long trip or vice versa as is shown in the 214 "Uncoordinated" panel of Figure 1). In some cases, individuals did not alter foraging 215 duration by a day or more between consecutive trips. These cases were not included 216 as our study focuses on the mechanism underpinning switches in foraging strategy 217 between partners, and so cases where birds did not switch strategy were not of 218 interest. We used generalized linear mixed effect models with a binomial error 219 distribution and a logit link function to evaluate the probability of parents switching 220 foraging duration in opposite directions or the same direction as a function of 1) chick

age and 2) the log of chick mass. Burrow was included as a random effect and thesame model selection procedure as before was applied.

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224 Results

225 Visual inspection of the histogram of trip duration suggested a roughly tri-modal 226 distribution with the majority of trips lasting one day (Figure S1). A second, less 227 frequent mode is observed for trips lasting 3-4 days and a third mode with low 228 frequency appears for trips lasting 13 days. The mean trip duration was 50 hours 229 (range of 12 to 309 hours). The difference in mean trip duration for each member of the 230 pair was not significantly different from zero, suggesting that trip duration was similar 231 between sexes (t_{16} = -0.276, P = 0.786). Of the 637 retained chick-rearing trips used 232 to analyse coordinated provisioning, 223 trips were initiated following synchronous 233 visits at the colony (but not at the burrow), and 195 trips were synchronous at the 234 burrow (Figure S2). On synchronous returns to the burrow, males and females were equally likely to arrive at the burrow first. The amount of time that individuals remained 235 236 in the burrow was highly variable, ranging from 10 minutes to six hours. Trip duration 237 between consecutive trips shifted most strongly after synchronous returns to the colony 238 and were not equal between sexes (Model 5, Table 1). Following synchronous visits to 239 the colony, trip duration shifted by a mean of 30 (± 4) hours more than on nights when 240 a trip was initiated in isolation (Figure 3A). Additionally, this shift was not equal 241 between sexes. On average, males adjusted foraging duration between trips by 13 (± 242 6) hours less than females (Figure 3B). This difference between sexes was observed 243 regardless of whether the trip was initiated synchronously with the partner or in 244 isolation.



Synchronous at colony • No * Yes

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



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

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



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

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274 Discussion

275 Life history theory predicts that to maximize long term reproductive success 276 iteroparous animals should balance investment in current offspring with their own 277 condition. Seabird species from several orders are known to alternate between short 278 trips for the purpose of chick provisioning and long trips for self-care. Without 279 coordination between partners, however, this variable foraging strategy would be likely 280 to result in periods of chick starvation when long trips coincide. Protracted bouts of 281 chick neglect are uncommon (Shoji et al., 2015), but it is unclear how this is achieved. 282 Using an automated burrow monitoring system validated using a sample of birds with 283 saltwater immersion loggers, we recorded provisioning trips across the chick rearing 284 period. Using this sequential record of foraging trips for each pair, we show that Manx 285 shearwaters displaying a variable foraging strategy, wherein individuals alternate 286 between long trips and short trips, do indeed coordinate foraging patterns with their 287 partner.

288 Following synchronous returns to the colony, partners tended to shift foraging 289 strategies; either switching from a short trip to a long trip or vice versa. On nights when 290 partners both returned to the colony, the duration of the subsequent foraging trip was 291 shortened or extended by an average of 30 hours more than if the trip was begun 292 following a visit to the colony alone. This shift amounts to a roughly 50% increase over 293 the mean trip duration or the difference between a "short" and a "long" trip. From the 294 other perspective, on nights when individuals returned alone, the duration of the 295 subsequent foraging trip was largely unaltered, indicating that the same foraging 296 strategy was employed.

297 Several mechanisms might plausibly enable partners to coordinate foraging 298 patterns such as endogenous rhythms, e.g. hormonal cycles that govern foraging 299 behaviour (Ricklefs et al. 1985; Weimerskirch, 1998); contact at the burrow, colony or 300 at-sea (Congdon et al., 2005); or indirect cues through chick begging calls or odour 301 (Gray & Hamer, 2001; Riou & Hamer, 2010). We found synchronous colony visits to be 302 a better predictor of foraging shifts than synchronous burrow visits. This suggests that 303 physically reuniting at the burrow is unnecessary for coordinating foraging movements. 304 It is possible that pairs recognize their partner's vocalizations at the colony or meet 305 while rafting offshore prior to coming to land (Brooke, 1990; Booth et al., 2000). While 306 colonially breeding seabirds are known for their ability to locate their partner among 307 numerous conspecifics (reviewed in Falls, 1982), neither of these mechanisms appears 308 likely in this case. Upon returning to the colony, chick-rearing Manx shearwaters 309 quickly go to their burrow and immediately return to sea after provisioning the chick, 310 leaving little time to encounter their partner. It is also unlikely that partners would be 311 able to reunite while rafting offshore as these congregations only form in the last few 312 hours of daylight (Brooke, 1990) and typically consist of thousands of individuals. While 313 our data cannot exclude these mechanisms, some indirect signal mediated through 314 either chick begging or burrow odour would be more feasible as it would not rely on 315 chance contact with the partner. Chick begging intensity may contain information about 316 body condition in shearwaters (Quillfeldt et al., 2004; Granadeiro et al., 2000; Quillfeldt 317 & Masello, 2004) that could act as a signal to the second parent returning to the nest. 318 As this information would only be available to the second partner to return, however, 319 one would expect to see a more pronounced shift in foraging duration for the second 320 partner than the first. While we did not have sufficient data to explore this possibility 321 adequately, this did seem to be the case. Future research will be required to address 322 the specific mechanism that allows partners to coordinate parental duties as we 323 observed.

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

334 Cooperation should be favoured when offspring survival is heavily dependent on 335 contributions from both parents (Clutton-Brock, 1991). We observed that coordination 336 was highest when chick mass was low. During early chick rearing, individuals were 337 most likely to adjust foraging duration in opposite directions, which resulted in 338 consistent provisioning. While the probability of coordination was inversely related to 339 both chick age and mass, we found that the latter was a better predictor. We did not 340 observe any seasonal changes in foraging duration, which could similarly give rise to this pattern. For young procellariiform seabird chicks without accumulated lipid 341 342 reserves, there is an elevated risk of mortality (Boersma et al. 1979; Catry et al., 2006). 343 As such, for a lean, vulnerable chick, coordination is likely to be especially valuable, 344 which is consistent with our findings (Figure 4). This means that breeding pairs can 345 potentially better accommodate environmental changes which may lead to a chick losing body condition despite having grown in terms of developmental stage. 346

347 Reproductive success is positively correlated with pair experience in many avian 348 taxa (Van De Pol et al., 2006; Naves et al., 2007; Sanchez-Macouzet et al., 2014). A 349 variety of mechanisms may account for this relationship such as increased 350 coordination and improved foraging efficiency (reviewed in Ens et al., 1996; see Fayet 351 et al., 2015 for this species). In seabirds, considerable research has focused on 352 mechanisms specifically related to increased coordination that may be advantageous, 353 such as synchronous arrival at the breeding colony (Mills, 1973) and incubation 354 changeovers (Davis, 1988). Our work suggests that coordination in foraging routines 355 may be an important, but overlooked, mechanism underlying reproductive success. 356 Although we were not able here to measure directly the effect of parental coordination 357 on reproductive success, it is known that consistent feedings, especially early during 358 chick rearing, can reduce chick mortality (Boersma et al. 1979; Catry et al., 2006) and

359 optimize chick growth (Schaffner 1990). An alternative explanation is that caregiving 360 parents may directly benefit by coordinating, for instance by determining which partner 361 is in greater need of a long, self-maintenance foraging trip, which could allow pairs to 362 optimise their relationship accordingly. Given the potential costs of not coordinating 363 and the possible benefits of coordinating, we expect that this behaviour is likely to be 364 observed in a wide range of other taxa that engage in a dual foraging strategy. There 365 are considerable prospects for future research that explores how both intrinsic factors 366 such as pair experience or individual quality and extrinsic factors such as resource 367 availability influence the degree of coordination.

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512 Tables

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

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

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

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

	Model / Parameter	3	1	2
	Intercept	5.80 (2.35) *	0.52 (0.35)	0.78 (0.52)
	Log(Mass)	-2.11 (0.93)*		
	Age			-0.01 (0.01)
	AIC	213.84	222.7	223.82
	ΔΑΙΟ	0.00	8.43	9.98
528 529	*** p < 0.001, ** p	< 0.01, * p < 0.05		
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538 Supplemental figures



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



Synchronous at colony • No * Yes

542

543 **Supplemental figure 2** Detection time lines for all analyzed pairs, i.e. those with more 544 than 5 synchronous trips. All detections, save the last, are plotted. Asterisks represent 545 nights when both partners were detected at the colony, while circles represent nights 546 when only one partner was detected. Black lines connecting detections denote foraging 547 trips with less than one hour of lost battery functioning.