



## Coordinated provisioning in a dual-foraging pelagic seabird



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In long-lived species, care-giving parents are expected to balance their own condition with that of their offspring. Many species of seabirds display a unique behavioural adaptation for managing these conflicting demands known as dual foraging, in which long trips, largely for self-maintenance, are alternated with short trips, which are primarily for offspring care. While dual foraging is a widely studied behaviour, it entails a complication that is seldom discussed: if parents independently employ a dual-foraging strategy, chicks might be abandoned for extended periods when the long trips of both partners coincide. Whether partners coordinate their dual-foraging strategies, however, is largely unknown. To investigate this possibility, we used 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.

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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, 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.

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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

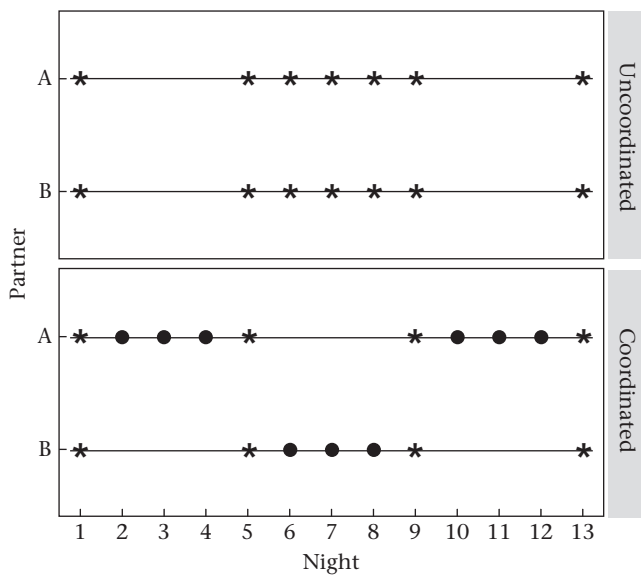
All work adhered to the ASAB/ABS Guidelines for the use of animals in research, and was conducted after approval by the Countryside Council for Wales, the Skomer and Skokholm Islands Advisory Committee, the British Trust for Ornithology (BTO permit C/5311) and the University of Oxford Local Ethical Review 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.

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