Partitioning of diving effort in foraging trips of northern gannets

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Abstract: Many species of seabirds are known to undertake foraging trips that vary in duration, lasting from a few hours up to several days. However, the important question of how individuals allocate their time during foraging trips of different durations has received relatively little attention until recently. Using activity loggers, we examined the foraging behavior of chick-rearing northern gannets, *Morus bassanus* (L., 1758), during trips of different durations, and tested predictions concerning how foraging activity varies across trips. There was no evidence of a relationship between dive frequency during the first 3 h of a trip and trip duration, suggesting that the decision to continue on a longer trip was not affected by an adult’s initial rate of encounter with prey. Flight constituted approximately 50% of total trip time, and the dive rate of birds per daylight hour was apparently unaffected by trip duration. Birds dived at similar rates on the outward and return sections of their foraging trips, which suggests that they may have been “topping up” on food on their return. Overall our results suggest that, unlike other pelagic seabirds, northern gannets at the Bass Rock do not adjust their individual foraging strategies among trips of different durations.

Résumé: De nombreuses espèces d’oiseaux marins entreprennent des excursions de recherche de nourriture de durée variable, allant de quelques heures à plusieurs jours. Jusqu’à récemment, la question importante de l’allocation du temps par les oiseaux individuels durant les excursions de différentes durées n’a été que peu étudiée. L’utilisation d’enregistreurs d’activité nous a permis d’analyser le comportement de recherche de nourriture chez des fous de bassan, *Morus bassanus* (L., 1758), en période d’élevage des poussins, durant des excursions de diverses durées et de vérifier certaines prédicitions relatives à la variation des activités alimentaires en fonction des excursions. Il n’y a pas de relation évidente entre la fréquence des plongées durant les trois premières heures d’une excursion et la durée de cette excursion, ce qui laisse croire que la décision de prolonger l’excursion n’est pas affectée par le taux initial de rencontre de proies par l’adulte. Le vol représente environ 50 % de la durée de l’excursion et le taux de plongée des oiseaux par heure d’éclairement ne semble pas affecté par la durée de l’excursion. Les oiseaux plongent au même rythme à l’aller et au retour des excursions, ce qui laisse croire que les oiseaux font peut-être « le plein » de nourriture durant le retour. Dans leur ensemble, nos résultats indiquent que, contrairement à d’autres oiseaux marins pélagiques, les fous de basson de Bass Rock n’ajustent pas leurs stratégies individuelles de recherche de nourriture en fonction de la durée des différentes excursions alimentaires.

[Traduit par la Rédaction]

Introduction

Among species exhibiting parental care, adults must collect enough food to satisfy their own requirements and those of their offspring, and behavioral strategies during foraging reflect these competing needs (Roff 1992; Stearns 1992; McNamara and Houston 1996). Among central-place foragers (Orians and Pearson 1979), in addition to the spatial component to this parent–offspring trade-off (where to forage), there is a temporal component (when to forage). Although recent technological advances mean that we now have a reasonably good idea of where seabirds go on foraging trips, from satellite telemetry (Jouventin and Weimerskirch 1990; Prince et al. 1992; Weimerskirch et al. 1993), our understanding of how they allocate their time during these trips is limited. Using activity loggers, we examined the foraging behavior of chick-rearing northern gannets, *Morus bassanus* (L., 1758), during trips of different durations, and tested predictions concerning how foraging activity varies across trips.
1997; Putz et al. 2003) or global positioning system loggers (Weimerskirch et al. 2003; Grémillet et al. 2004), we still know relatively little about their foraging routines or search strategies during trips (but see Ropert-Coudert et al. 2004; Weimerskirch et al. 2005).

Dual foraging strategies during chick-rearing have been recorded in several species of Procellariiformes, whereby adults alternate long self-feeding trips with shorter chick-feeding trips. However, among species that do not show bimodality in trip duration, there may still be differences in the foraging routine of parents that is dependent on trip duration. In this study, we examined foraging behavior in relation to trip duration in the northern gannet, Morus bassanus (L., 1758). There is no obvious bimodal pattern to trip duration in this species in the British Isles (Lewis et al. 2001, 2002), and its foraging trips are known to be highly variable in duration, making it an excellent model species to examine whether foraging behavior is related to trip duration.

Gannets are plunge divers, locating prey visually from the air (Nelson 1978), and therefore the number of dives is a good proxy for prey-encounter rate. First, we evaluate how foraging birds choose the length of trip they undertake. To do this, we determine the number of dives carried out in the first 3 h of the trip in relation to the resultant trip duration. A negative relationship would suggest that birds carry out a longer trip because the prey-encounter rate was lower during the first phase of foraging. A positive or no relationship would suggest that the cue for trip duration may be primarily factors other than early foraging success, such as the longer term physiological requirements of parents and (or) offspring, or the risk associated with leaving young chicks unattended at the nest (Lewis et al. 2004a). Second, we examine how the total time spent flying during a foraging trip and the number of dives vary with trip duration. Finally, we examine when dives are performed during trips of all durations and evaluate the strength of evidence for the following alternative scenarios. (i) Birds fly straight out to a foraging site, feed there, and then come straight back to the nest (i.e., foraging activity is mainly confined to the middle of a trip). (ii) Birds fly straight out but feed opportunistically on the way back (i.e., foraging activity is mainly confined to the middle and end of a trip). (iii) Birds feed opportunistically on the way out but fly straight back (i.e., foraging activity occurs mainly at the beginning and in the middle of a trip). (iv) Birds feed opportunistically at any time (i.e., there is no difference in foraging activity across the beginning, middle, and end of a trip).

Materials and methods

Study site and study birds

The study was carried out between 19 June and 28 July 2001 at the northern gannet colony on the Bass Rock, southeast Scotland (56°6′N, 2°36′W), which currently contains over 40 000 breeding pairs (Nelson 2002). During the study, sunrise and sunset occurred at approximately 0230 and 2130 GMT (0330 and 2230 BST), respectively. Twenty-two adults with young chicks (age range 2–6 weeks) were captured at the nest using a 6 m long telescopic pole and noose and were equipped with activity loggers (width 22–33 mm; height 13–19 mm; length 62–80 mm; mass 19–28 g, ca. 1% of adult body mass). Only one member of a pair was sampled from each nest. All loggers contained a flight sensor (a small modified microphone), which was activated by wing beats, and the majority of loggers also contained a depth meter (operating range 0–70 m, resolution 0.3 m). Further details of these loggers are given by Benvenuti et al. (2001). The sampling rate was set at 4 s for the depth meter / water switch and 8 s for the flight sensor, which allowed data to be collected for approximately 4 days before the memory was full.

The loggers were attached to the tail feathers of each bird with self-amalgamating tape and cable ties. To minimize drag during flight and prevent tags being displaced during plunge diving, tags were attached to the underside of the four central tail feathers, close to the base of the tail. The attachment process took approximately 5 min and, after release, birds returned to their nest site within a few minutes. The loggers represented approximately 1% of body mass and a previous study on gannets at the same colony with similar devices showed no significant differences in mean trip duration between birds equipped with loggers and controls (Hamer et al. 2000). All birds were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care (1984, 1993).

Each bird was equipped with a logger for 2–4 days to record at least one foraging trip (mean trip duration at the Bass Rock is ca. 24 h; Hamer et al. 2000; Lewis et al. 2001, 2002). After this time the bird was recaptured and weighed and the device removed. Recorded data were downloaded from the loggers to a portable computer and analyzed using specially designed software.

Logger analysis

Four activities could be distinguished from the distinct signals that the sensors produced: (1) nest attendance: weak variable signals from the flight sensor; (2) flight: strong regular signals from the flight sensor; (3) resting on the sea surface: moderately strong irregular signals from the flight sensor; (4) diving: strong noisy signal from the flight sensor and activation of the depth sensor (see Fig. 1). Dives of less than 1 m were excluded because such shallow depths often occur during bathing or other movements not believed to be related to feeding. Our sampling interval (4 s) may have prevented us from recording some of the shortest dives. However, on average, 50% of 2-s dives and 75% of 3-s dives will be recorded using this sampling interval, and we have no reason to believe that these shorter dives would have been distributed differently through the trip than longer dives. Further details on the methodology and accuracy of these instruments for this species are given in Garthe et al. (2000).

Statistical analyses

Time spent on a trip has three main components: flying, diving, and sitting on the sea surface. However, time spent diving was ca. 0.2% of total trip time (Lewis et al. 2002) and so was not considered a separate variable in analyses of composition and duration of trips. In 8 cases, we recorded more than one trip per bird. To control for potential pseudo-replication, our analyses were performed using linear mixed models (using the method of residual maximum likelihood; Patterson and Thompson 1971) or generalized linear mixed
models (Schall 1991) as appropriate, with bird identity as a random factor. To assess whether the decision to carry out a long trip was dependent on foraging patterns early in a trip, we fitted a linear mixed model with trip duration as the dependent variable and the number of dives carried out during the first 3 h of a trip as the independent variable. The proportion (arcsine transformed) of time spent flying was analyzed by fitting a linear mixed model with total trip time as an independent variable. We examined the relationship between the total number of dives carried out on a trip and trip duration by fitting a generalized linear mixed model with a Poisson error distribution and logarithm link function. The fitted model corrected for overdispersion by inclusion of a random effect for trip within bird, rather than as a multiple of the Poisson variance. To examine the distribution of dives throughout each trip recorded. Overall, there was no significant difference in the proportions of dives carried out during the beginning, middle, and end of a trip (generalized linear model deviance ratio: $\chi^2 = 1.12$, df = 1, $p = 0.28$). There was no effect of chick age on trip duration (Table 1; $\chi^2 = 0.42$, df = 1, $p = 0.51$), indicating that gannets that made longer trips did not have a significantly lower (or higher) initial dive rate. This was not simply a reflection of our arbitrary 3-h cut-off — there was also no effect if we used the number of dives made in the first 2, 4, or 6 h of a trip as our independent variable ($\chi^2 = 0.63$, df = 1, $p = 0.43$, and $\chi^2 = 0.14$, df = 1, $p = 0.71$, respectively). Secondly, there was a highly significant relationship between trip duration and flight duration (Fig. 3a; $\chi^2 = 135.07$, df = 1, $p < 0.001$). The fitted least squares equation (constrained to pass through the origin) was:

$$\text{Flight duration (h)} = 0.45 \pm 0.021 (\text{mean} \pm \text{SE}) \times \text{trip duration (h)}$$

Flight therefore accounted for, on average, approximately 50% of trip time (empirical range 22%–72%), as was found previously (Hamer et al. 2000; Lewis et al. 2002), with time spent on the sea surface making up almost all of the remaining time. Accordingly, there was no significant difference in the proportion of time spent flying (and thus on the sea surface) among trip durations ($\chi^2 = 0.35$, df = 1, $p = 0.56$). There was a highly significant relationship between the total number of dives performed during a foraging trip and foraging-trip duration (Fig. 3b; $\chi^2 = 7.41$, df = 1, $p = 0.006$), and the mean (±SD) dive rate on a trip was 1.35 ± 1.09 dives/h (range 0.25–3.79). Figure 4 illustrates the timing of dives throughout each trip recorded. Overall, there was no significant difference in the proportions of dives carried out during the beginning, middle, and end of a trip (Fig. 5; generalized linear model deviance ratio: $F_{[2,40]} = 0.42$, $p = 0.7$). There was also no influence of trip duration on the distribution of dives between the three thirds of the trip (generalized linear model deviance ratio: $F_{[2,40]} = 1.12$, $p = 0.3$). Finally, there was no effect of chick age on trip duration in our study ($\chi^2 = 0.04$, df = 1, $p = 0.8$).

**Discussion**

Northern gannets are visually hunting predators (Nelson 1978) and although we do not know the foraging success of dives, it is probable that dive rate is a good proxy for prey-encounter rate in this species. Our first finding was that the number of dives carried out within the first few hours of a trip did not influence the final length of that trip. Therefore, we have no evidence to suggest that birds extend their forag-
Secondly, we have shown that northern gannets foraging from the Bass Rock dived at approximately equal rates during daylight hours throughout trips, irrespective of trip duration. Furthermore, there was no effect of trip duration on the distribution of dives across trips, suggesting that birds do not change their foraging strategies between trips of different durations. The simple finding that birds feed on the way home suggests that either they did not collect enough food at the farthest point from the colony, or they were opportunistically “topping up” to replace food that had already been digested. Food consumed on the way back to the colony may be either for birds’ own needs, or it may enable them to feed their chick relatively fresh food on returning to the nest.

Gannets do not fly or forage during the hours of darkness (Garthe et al. 1999, 2000, 2003; Hamer et al. 2000, 2001; Lewis et al. 2002), but spend the night sitting on the sea surface. However, Fig. 4 shows that there was no systematic pattern in the occurrence of nighttime during a trip that might have affected the distribution of diving throughout a foraging trip.

Both the dive rate (number of dives per trip hour) and the proportion of time spent flying and sitting on the water remained approximately equal across all trip durations. This result is interesting because it has been shown that for albatrosses and petrels, short foraging trips were more energeti-

Table 1. Trip duration and total time spent flying, sitting on the sea surface, and diving for each trip, number of dives per trip, and number of dives made during the first 3 h of a trip for 22 chick-rearing northern gannets, Morus bassanus, on the Bass Rock in 2001, in decreasing order of trip duration.

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<th>Total time at sea (h)</th>
<th>Total dive time (h)</th>
<th>No. of dives</th>
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*Trips made by birds equipped with a logger without a depth meter.

Fig. 2. Frequency distribution of durations of 30 trips carried out by 22 chick-rearing northern gannets on the Bass Rock in 2001.
cally costly than longer trips (Shaffer et al. 2003; Weimerskirch et al. 2003), therefore one might also expect to observe differences in time–activity budgets between trips of different durations in other species. Brown boobies, *Sula leucogaster* (Boddaert, 1783), and red-footed boobies, *Sula sula* (L., 1766), dive at a higher rate with decreasing trip duration (Lewis et al. 2004b). However, these two species, unlike northern gannets, are constrained to return to the colony at night, and adjust their foraging effort to the amount of time remaining in the day.

The distribution of dives in our study contrasted with those of Garthe et al. (2003), who suggested that northern gannets in the northwest Atlantic Ocean (Funk Island) foraged mainly in the middle of both 1-day and 2-day trips and very little at the beginning or end of trips. Figure 4 illustrates clearly that birds from the Bass Rock also forage at the beginning and end of a trip, irrespective of trip duration. Intercolony differences in chick-provisioning rates may be important. For example, gannets at the Bass Rock have a trip duration approximately twice that of birds at Funk Island and, owing to rapid digestion rates (Jackson 1992), may have to feed at the end of trips in order to have sufficient food for the chick. These differences may also reflect a greater food requirement for adults at the Bass Rock during their longer chick-attendance periods, to reduce the risk of leaving the chick unattended (see Lewis at al. 2004a).

Data from a closely related species, the Cape gannet, *Morus capensis* (Lichtenstein, 1823), reveal that a period of rest on the sea surface at the midpoint of a daily foraging trip is typical in the majority of individuals (Ropert-Coudert et al. 2004). The authors suggest that adults may need to allocate time to digest some food at the midpoint of the trip, usually in the middle of the day for Cape gannets, before returning home to feed the chick later in the day. The longest periods of rest on the sea surface in our study were driven by nightfall, which fell randomly within a trip. Thus, extended
periods without foraging are evident in both species. Time allocated to digestion may therefore be important in northern and Cape gannets, but whether this is self-imposed or coincides with periods when foraging is not possible may depend on trip duration, which differed markedly in the two species (ca. 24 h for northern gannets in this study, 9 h for Cape gannets).

Northern gannets locate prey from the air, so the evidence that they dive throughout the trip, not just at the midpoint of the trip, is consistent with the observation that they may actively displace the food of conspecifics by disturbing “communal” prey shoals (Kees Camphuysen, personal communication). This activity may drive birds farther from the colony in search of less disturbed shoals (Lewis et al. 2001).

Conclusions

Using activity loggers we examined how chick-rearing northern gannets allocate their time during foraging trips of different durations. We found that individuals foraged at similar rates throughout trips of all durations, and that the times spent flying and resting on the sea surface were each approximately 50% of total trip time, irrespective of trip duration. Birds feed opportunistically throughout foraging trips, and the occurrence of dives during the return flight to the colony suggests that parents may need to forage at this time for their chicks, or for themselves whilst they are attending their young, because food caught earlier in the trip may have been digested. We suggest that, overall, northern gannets do not adjust their individual foraging strategies among trips of different durations, in contrast to a number of other seabird species.

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