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At-sea-activity and foraging efficiency in chick-rearing northern gannets *Sula bassana*: a case study in Shetland

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ABSTRACT: Chick-rearing northern gannets *Sula bassana* from Hermaness, Shetland (UK), were equipped with both stomach temperature loggers and external temperature loggers (attached to the leg). Detrimental device effects on the birds could not be detected. Three complete data sets covering several foraging trips by 3 birds showed that the logger-equipped birds spent 39 to 49% of their time in the colony, 22 to 30% flying and 22 to 34% swimming. Foraging trips lasted between 2 h 45 min and 27 h 08 min, with a mean length of 13 h. Maximum foraging range was estimated to be 128 km. Dives lasted between 1 s and 7.5 s, with a mean of 4.4 s. Median food quantity swallowed per feeding event was 101 g (n = 32), with 745 g being the maximum. No foraging activity occurred at night. Catch per unit effort was assessed to range between 0.9 and 2.8 g fish min^{-1} flying and between 0.5 and 1.3 g fish min^{-1} at sea. Foraging efficiency varied between 0.6 (negative energy budget) and 1.5 (positive energy budget). More data on foraging efficiency, preferably from different colonies and different years, could show how efficiently this top predator utilises food resources.

KEY WORDS: Northern gannet · Seabird · Activity · Foraging efficiency · Top predator

INTRODUCTION

The northern gannet *Sula bassana* is the largest pelagic seabird of the North Atlantic. Since the first half of this century, its total population size has been increasing, with a concurrent expansion of its range (Nelson 1978, Lloyd et al. 1991, Siorat & Rocamora 1995). The continuous growth of numbers in colonies at an overall rate of ca 3% yr^{-1} (del Hoyo et al. 1992) suggests that this species is not affected by population regulating factors at the moment. This phenomenon might be attributed to the fact that the population is probably still recovering from earlier persecution by humans (del Hoyo et al. 1992) but may also be attributed to improved food availability (e.g. Furness et al. 1992, Montevecchi & Myers 1997). Studies of seabirds scavenging at fishing vessels in the North Sea have shown that northern gannets utilise discards very efficiently and that they have strong competitive capabilities (e.g. Furness et al. 1992, Garthe & Hüppop 1998). Although several dietary analyses indicated that lipid-rich pelagic fish such as herring *Clupea harengus*, mackerel *Scomber scombrus* and sandeel *Ammodytes marinus* are the main prey in the eastern North Atlantic (e.g. Wanless 1984, Martin 1989), the behaviour of northern gannets when feeding on these pelagic fish has hardly been studied, and thus potential keys to population expansion and role in the marine food chain of the North Atlantic may remain unknown.

Very recently, there have been significant advances in the use of miniaturised data loggers on seabirds, enabling measurements over time of parameters such as location, and feeding activity (e.g. Wilson et al. 1992a, 1992b). We applied this technology in a study of northern gannets in Shetland (UK) to obtain novel data on the feeding ecology of this species. In particular, we attempted to assess the foraging efficiency of these birds during the chick-rearing stage.

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METHODS

The study was conducted in the Hermaness National Nature Reserve at the northernmost tip of Unst, Shetland (Fig. 1). The reserve holds a gannetry of about 12 000 pairs of northern gannets (1994; Murray & Wanless 1997).

Breeding adult northern gannets were equipped with 2 types of data loggers, a stomach temperature logger and an external temperature logger. The stomach temperature was recorded by a SICUP (Single Channel Unit Processor), manufactured by Driesen & Kern GmbH (Bad Bramstedt, Germany). This device consisted mainly of a PT 100 temperature sensor, a quartz clock, a 128 KByte RAM-chip and a Lithium battery. The electronics were encapsulated in a titanium housing of 91 mm length and 16 mm diameter (total mass in air: 30 g), which transmitted temperature changes rapidly to the sensor due to its high conductivity (Wilson et al. 1995a). The stomach temperature was recorded every 16 s. Loggers were fed to the birds after capture at nests where there were small chicks. They were recovered from the gannets, several days later, when the birds spontaneously regurgitated their food on being recaptured. The data were read out into a laptop computer. Timing of feeding can be derived

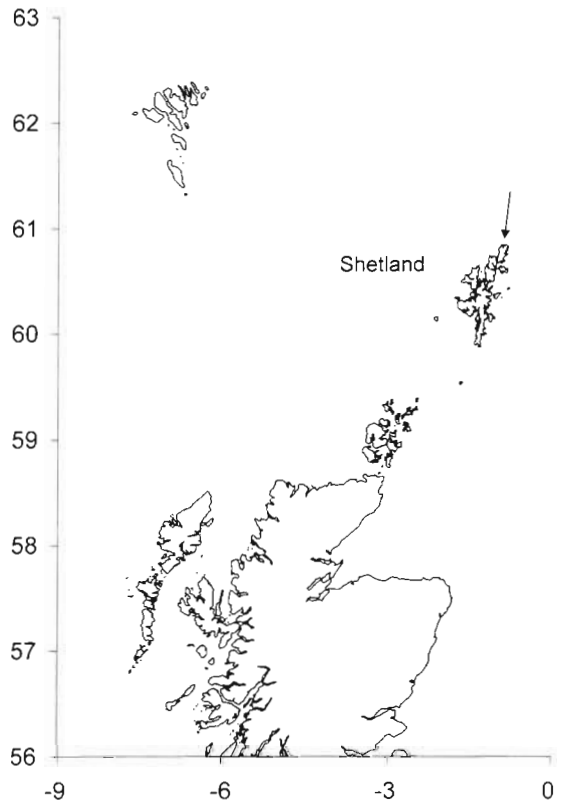

Fig. 1 Location of the gannetry in the Hermaness National Nature Reserve, Shetland (UK)

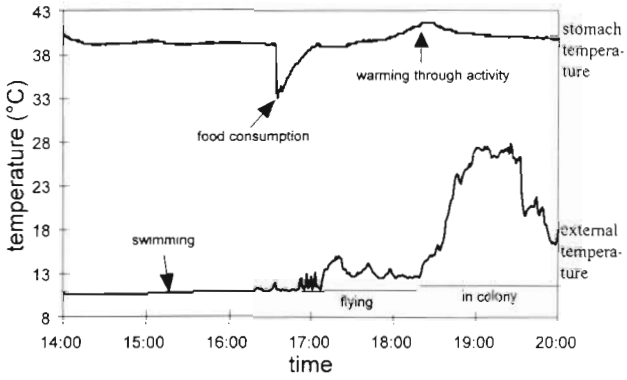

Fig. 2. Six hour example of temperature patterns measured by the 2 temperature sensors on one bird

from the stomach temperature recordings based on the principle that each ingestion of cold food from the sea leads to a sudden drop in the stomach temperature (Fig. 2; Wilson et al. 1992a). From the magnitude of the temperature drop and the time it takes to re-warm the stomach and contents, the amount of food can be calculated (e.g. Wilson et al. 1995a). We used the TRIM method (temperature rise integral method) presented by Grémillet & Plös (1994) and corrected for active birds according to Wilson et al. (1995a).

The external temperature loggers were 17 × 31 × 41 mm and weighed about 20 g. They had a memory of about 8 kBytes and were manufactured by Onset Computer Corporation. The logger was attached by waterproof cloth adhesive tape to a plastic (Darvic) ring put on the bird's tarsus. From the fluctuations in temperature, which was recorded every 60 s, the activity of the bird could be deduced (following Wilson et al. 1995b; Fig. 2). When the temperature remained constant, the bird was considered to be swimming or resting on the water surface with the logger itself being submerged, so indicating sea temperature. When the temperature varied slightly within the range recorded for air temperature (a few degrees higher than sea temperature), the bird was considered to be flying. When the temperature varied in other temperature ranges (mostly being much higher as the logger was warmed by the body heat of the bird) and with other rhythms, then the bird was considered to be in the colony (i.e. on the nest most of the time). The last deduction was validated by frequent visits to the colony to record which birds carrying loggers were present.

Eight gannets rearing chicks approximately 2 to 4 wk old were caught between 9 and 23 July 1997. All these birds were equipped with both stomach temperature loggers and external temperature loggers. We were unable to recapture 4 birds. These birds returned to their nests but were too difficult to recapture due to the location of their nest sites. One recaptured bird had

lost its stomach temperature logger (probably regurgitated at sea), and also the external temperature logger malfunctioned. Three birds provided complete data sets, for a total of 220 h of activity budget and 32 prey ingestions (Table 1).

Dive durations, which could not be derived from the data loggers, were determined by direct observation of unmarked gannets on 12 July 1997, when we observed a few hundred gannets feeding on unidentified fish school(s) close to the breeding colony. Since individuals could not be individually identified the data could comprise (some) replicates.

The foraging range was calculated from the flight time between departure from the colony and the first feeding event, and from the time between taking flight after the last dive and arrival at the colony. Flight speed of 14.9 m s^{-1} was taken from Pennycuick (1997; observed speed) and multiplied by the flight time to give the foraging range. Direct flights between the last feeding site and the colony are probably the most reliable measures of foraging range because the chick-rearing adults are assumed to feed their chicks as soon as possible (Nelson 1978). Wind speed was not taken into account for these calculations but remained largely low (Force 2 to 3 on the Beaufort Scale) within the study period.

Catch per unit effort was calculated for each bird over all foraging trips recorded. Two measures were used; one was assessed food intake per minute flying, the other assessed food intake per minute at sea (i.e. either flying or swimming). In addition, gross foraging efficiency (according to Weathers & Sullivan 1991) was calculated for each bird over the respective foraging trips. Gross foraging efficiency is defined as the energy gain by the food swallowed during the foraging trips divided by the energy loss through the bird's activities, assuming that all food gathered would have been used to cover the energy costs of the adults. Mean energy content of the food was taken as 6 kJ g^{-1}, assuming the food to consist of mackerel, sandeel and clupeids (herring *Clupea harengus* and sprat *Sprattus sprattus*).

Table 1. *Sula bassana*. Sex, duration of equipment and number and duration of foraging trips of 3 northern gannets

	Gannet 1	Gannet 2	Gannet 3
Sex	♀	♂	♀
Duration of equipment	45 h 11 min	73 h 46 min	96 h 25 min
Number of foraging trips	2	3	4
Duration of foraging trips	10 h 52 min 12 h 10 min	9 h 20 min 11 h 15 min 17 h 28 min	2 h 45 min 8 h 33 min 18 h 19 min 27 h 08 min

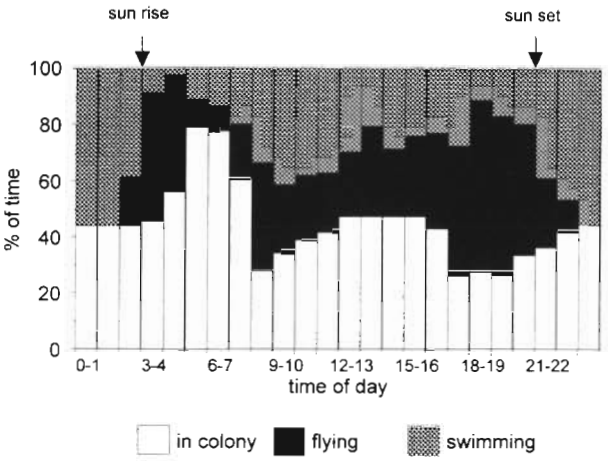

Fig. 3. *Sula bassana*. Diel pattern of the activity of 3 northern gannets, distinguishing between swimming, flying and staying in the colony. Percentages are means of the 3 birds

Mean assimilation efficiency was set at 0.75 (Castro et al. 1989, Brekke & Gabrielsen 1994). Energy expenditure of northern gannets was taken from Birt-Friesen et al. (1989), with 144 kJ h^{-1} while swimming and 349 kJ h^{-1} while flying.

RESULTS

Activity

All logger-equipped birds spent almost half of the time in the colony, ranging from 39 to 49%. The rest of the time the birds were at sea, where they were either flying (22 to 30%) or swimming (22 to 34%). Flight activity was highest in the early morning and in the evening but was not recorded between 22:35 and 02:15 h UTC (Fig. 3).

Foraging trips and foraging range

A total of 9 foraging trips were recorded from 3 birds (Table 1). Apart from 2 extremes (2 h 45 min and 27 h 08 min, respectively), the trips lasted between ca 8.5 and 18.5 h, with a mean length of 13 h.

From continuous flights between the last feeding event and the nest, foraging ranges were estimated to be 32, 80, 122 and 128 km.

Dive duration

Dives lasted between 1 and 7.5 s, with a mean dive duration of 4.4 s (n = 100; Fig. 4).

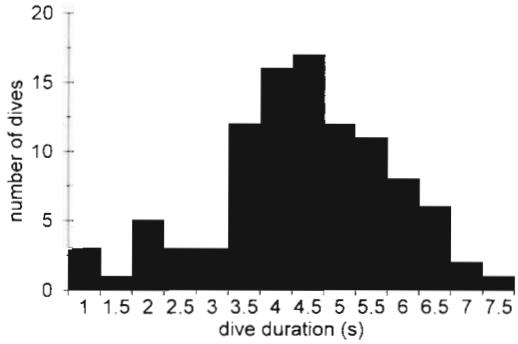

Fig. 4. *Sula bassana*. Frequency distribution of the duration of 100 dives of northern gannets observed near the breeding colony

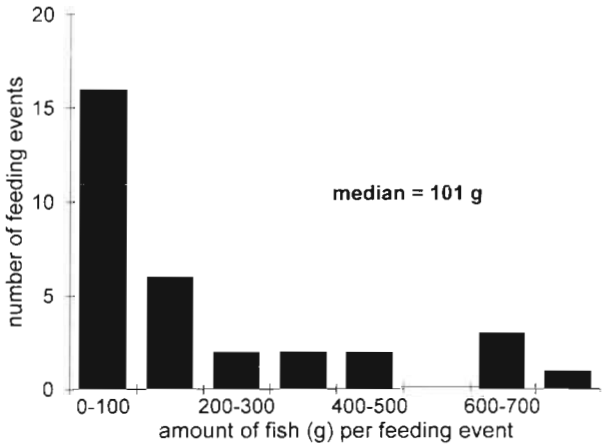

Fig. 5. *Sula bassana*. Amounts of food swallowed by the northern gannets during the respective feeding events

Food intake

Most quantities of food swallowed by northern gannets during feeding events were lighter than 100 g, with 101 g the median (n = 32) and 745 g the maximum (Fig. 5). The diel patterns of feeding events and amounts of food ingested do not show a very distinct variation through the day, apart from a nocturnal lack of foraging activity (Fig. 6).

Catch per unit effort and foraging efficiency

Catch per unit effort statistics revealed values of between 0.9 and 2.8 g fish min^{-1} flying and between 0.5 and 1.3 g fish min^{-1} at sea (including both flying and swimming; Table 2). Foraging efficiency varied between 0.6 (negative energy budget) and 1.5 (positive energy budget). In all 3 parameters, the bird listed in the third column in Table 2 was much more efficient than the 2 others.

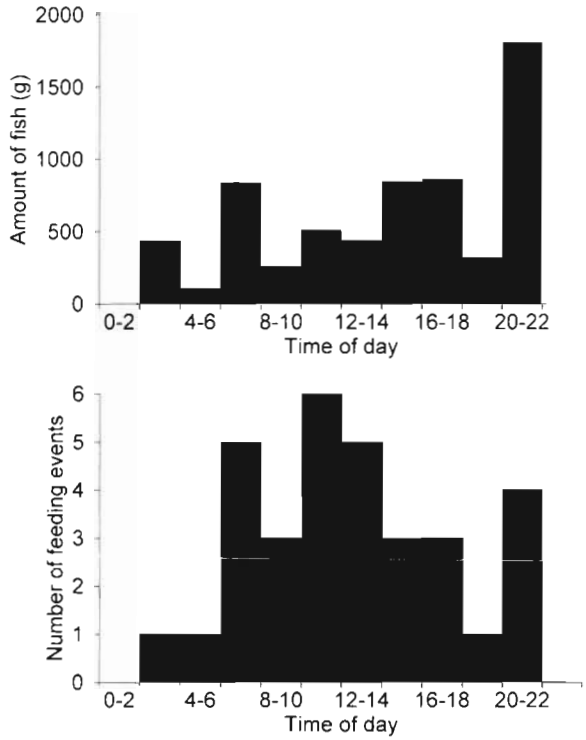

Fig. 6. *Sula bassana*. Diel pattern of the amounts of food swallowed by the northern gannets and the number of feeding events that occurred

Table 2. *Sula bassana*. Catch per unit effort and foraging efficiency of 3 northern gannets. The values are summed for each bird over the respective foraging trips

	Gannet 1	Gannet 2	Gannet 3
Food swallowed (g)	828	1235	4388
Catch per unit effort:			
g fish per min flying	1.4	0.9	2.8
g fish per min at sea	0.6	0.5	1.3
Foraging efficiency	0.7	0.6	1.5

DISCUSSION

Equipment and behaviour of the birds

To the best of our knowledge, no negative effects of the devices on the birds could be detected. First, at the feet, bill and pharynx there was no visible external damage. Second, the birds which could be recaptured showed similar behaviour to all birds during their first capture; all of them were very aggressive. Presence-absence patterns of birds carrying loggers were similar to those of their partners which were not equipped with devices ($\chi^2 = 7.59$, df = 7, 2×8 contingency table.

m.s.) also in those birds which could not be recaptured (due to unfavourable selection of nest sites for the study). Third, all 3 individuals equipped with devices gathered food during each of the 9 foraging trips.

Activities and foraging efficiency

Deducing the activities of the birds from the 2 temperature patterns was fairly simple (see 'Methods'). Difficulties in the interpretation of activity only occurred for some minutes when there were sudden and frequent changes between flying and swimming. Misinterpretations would nevertheless not have affected time budgets to any major extent.

There was a tendency for low flight and high swimming activity in the morning which should not be overinterpreted at this stage realising that data could only be gathered from 3 birds. Feeding was fairly uniform through daylight hours. Most interestingly, feeding as well as flying did not occur at darkness, confirming strongly that northern gannets are visual foragers. Information on the amount of time seabirds spend on the sea surface is very important in assessing their vulnerability to oil pollution. Our data show that about half of their time at sea was spent on the sea surface, so gannets have a fairly high risk of coming into contact with oil spills within their foraging area. Mean and maximum amounts of food per feeding event are somewhat larger than regurgitates recorded by Martin (1989), which could originate from the different methods employed. The estimated foraging ranges lay well between those estimated by Tasker et al. (1985) for Noss, Shetland (<40 km for most birds, up to 150 km at maximum) and Camphuysen et al. (1995) for the western North Sea (300 km). Nelson (1978) estimated from foraging trip duration the maximum foraging range to be 320 to 480 km. Foraging trip durations are similar to those recorded at Ailsa Craig (Clyde, west Scotland), slightly longer than on the Bass Rock and much longer than at Bempton (both North Sea; Nelson 1978).

In contrast to many previous studies on seabirds, foraging efficiency could be determined directly by considering all food consumed during the foraging trips, not only from the amount of food brought back to the nest (which might have been lost to kleptoparasites or might have been partly digested already) or solely derived from energetic calculations (e.g. Adams et al. 1991). Two of the 3 birds had negative foraging efficiencies for the period they were equipped with the 2 types of device. Effects on the birds by handling and/or by the devices were not detectable (see above). However, we cannot exclude the possibility that the devices caused the birds to forage less efficiently than normal. The equipment of the birds for 2 to 4 d represents only a very short part of the whole chick-rearing period of about 13 wk (Nelson 1978, Montevecchi & Porter 1980). It is quite probable that fluctuating food availability leads to different success rates of all birds in the colony (Grémillet 1997). Furthermore, the period of our study was characterised by low winds which may have increased the energy expenditure during flight (sensu Furness & Bryant 1996). Finally, the energetic cost given by Birt-Friesen et al. (1989) might be an overestimate. This can especially be due to the fact that doubly labelled water studies may generally tend to overestimate field metabolic rates because the behaviour of the birds is affected (Wilson & Culik 1995).

The values of foraging efficiency found in this study appear to be low compared to those of great cormorants *Phalacrocorax carbo* (3.3 to 3.5; Grémillet 1997) but are close to those of African penguins *Spheniscus demersus* (2.1; Nagy et al. 1984) and Adélie penguins *Pygoscelis adeliae* (1.6; Chappell et al. 1993).

Use of the marine environment

Northern gannets use a particular feeding technique, plunge-diving, which is a unique feeding method in all the highly productive shelf waters of the North Atlantic. By plunge-diving, gannets can exploit the uppermost few meters of the water column, e.g. up to 12.6 m (mean dive depth: 5.9 m) in the case of the closely related but slightly smaller cape gannet *Sula capensis* (Adams & Walter 1993). In this regard, they might be considered to attain depths intermediate to those achieved by alcids and cormorants on one hand which are able to dive much deeper, and gulls and fulmars on the other hand which can only feed on or near the water surface. The disadvantage of not being able to dive deep is compensated by the particular wide range of fish lengths exploited by the northern gannet (Hudson & Furness 1988, Garthe & Hüppop 1994, Montevecchi & Myers 1997). This range of prey size, from small fish such as sandeels *Ammodytes* spp. and capelin *Mallotus villosus* to large pelagic fish like mature mackerel and herring distinguishes this species from many other species such as the common guillemot *Uria aalge* and the razorbill *Alca torda*. Another major advantage of the northern gannets is their large flight range, much larger than that of cormorants, which are relatively restricted to the coast (e.g. Stone et al. 1995), but also larger than that of alcids, which exhibit high flight costs due to their heavy wing loading (e.g. Pennycuick 1987). The large flight range should enable northern gannets to circumvent local shortcomings in food availability. Studies on the Shetland Islands have shown that surface-feeding

species with restricted foraging range, in particular arctic terns *Sterna para disaea* and black-legged kittiwakes *Rissa tridactyla*, have suffered most strongly from reduced food supply whereas deeper-diving species such as the European shag *Phalacrocorax aristotelis* and the common guillemot *Uria aalge* have generally performed much better (e.g. Monaghan 1996, Monaghan et al. 1996).

The methods and results presented in this paper should form the basis of a more comprehensive study to evaluate from larger data sets how efficient this species is able to exploit food resources, particular so in different oceanographic regions and under different food conditions.

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