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Review

Foraging strategies of breeding seabirds studied by bird-borne data loggers

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Abstract: Our research group has devised and manufactured a data logger which glued on the back of a bird, can detect and memorise the direction in which the bird is heading during a flight. Given the birds' constant cruising speed, the memorised data can be used to reconstruct the whole flight path. Subsequent versions of this direction recorder, equipped with new sensors (depth meter and flight sensor), were used to investigate the foraging behaviour of several species of breeding marine birds (Balearic shearwater, Brünnich's guillemot, common guillemot, razorbill, black-legged kittiwake, Audouin's gull, northern gannet, blue-footed booby). The data recorded at different colony sites allowed us to identify the birds' feeding grounds and record the most relevant events occurring in the foraging trips, including the duration of the trips, total flight time, number and duration of the stops where feeding actually occurred, dive profiles and diving behaviour. Differences in the foraging strategies between sexes and between incubating and brooding birds were also investigated.

key words: foraging, marine birds, data loggers

Introduction

In the late '80s, our research team devised and manufactured a data logger which records at pre-set intervals the flight direction of the bird which carries it on its back. On the basis of the relatively constant flying speed of birds, directional data allowed us to reconstruct the whole flight path (Bramanti *et al.*, 1988). This direction-recorder was originally devised to investigate the navigational abilities of homing pigeons (Papi *et al.*, 1991; Ioalè *et al.*, 1994; Dall'Antonia *et al.*, 1999; Holland *et al.*, 2000; Bonadonna *et al.*, 1997, 2000). The instrument was subsequently modified to be used in studies of the homing abilities of wild marine birds displaced from the home colony (Dall'Antonia *et al.*, 1995). The good performance of the device induced us to design new generations equipped with additional sensors, which were used to monitor the foraging behaviour of several species of seabirds, and their functional role in the marine ecosystem in relation to sex, breeding status and environmental conditions. In the present paper, we report a brief review of the main results achieved by equipping breeding seabirds with our data loggers.

The instruments

Table 1 reports the various types of loggers manufactured by our research group, the sensors which they are equipped with, the size and mass, and the bird species on which they were mostly used. The original prototype (Table 1, type 1) recorded the main axis of the bird's body with respect to geomagnetic north at pre-set time intervals (mostly 6 or 10 s). The basic component of this direction recorder is a traditional compass equipped with a transducer to convert the angular values into electrical resistance values (see Bramanti *et al.*, 1988; Dall'Antonia *et al.*, 1993). The compass compensated for the effect of deviation from a horizontal position and thus was sufficiently accurate even if the birds' back was not horizontal during flight. Flight data were easily distinguishable from the stable and stereotypic data acquired while the birds were at their nest. Flight-path reconstruction was possible because birds have a sufficiently constant flight speed (further details on flight-path reconstruction and correction for wind-drift are reported in Benvenuti *et al.*, 1998). By modifying the original direction recorder (type 1), and adding other sensors, other types of data loggers were obtained (Table 1). In order to distinguish data recorded during flight from data recorded during swimming or diving, we used a saltwater switch consisting of two electric wires connected to the instrument. The distal ends of the wires were glued to the feathers of the bird's abdomen and thus were short-circuited by seawater whenever the bird was swimming or diving (Table 1, types 1a and 1b).

Type 2, the largest and heaviest instrument, was equipped with a compass sensor and a depth gauge (operative range 0–70 m, resolution 30 cm). In addition, the saltwater switch which had been added to types 1a and 1b, to allow the study of marine birds, was replaced by

Table 1. Data loggers devised and used by our research group. T=Device type. Cs, Fs, Dm, Ss=Compass sensor, Flight sensor, Depth meter and Saltwater-switch, respectively. Size; the size refers to the container (mm: width, height, length); minimum and maximum width and height of the streamlined containers are given. M=total mass (g).

T	Cs	Fs	Dm	Ss	Size	M	Species
1	X				18×15×70*	13*	Pigeon
1a	X			X	24×15×87	29	Cory's shearwater
1b	X			X	22–24×14–21×97	29	Brünnich's guillemot
2	X	X	X		23–33×15–20×93	33	Brünnich's guillemot, Gannet
3	X	X			22–31×13–22×90	25	Brünnich's guillemot, Razorbill, Gannet, (Common guillemot), (Blue-footed booby)
4		X	X		22–33×13–19×80	28	Brünnich's guillemot, Razorbill, Gannet, (Common guillemot), (Blue-footed booby)
5		X		X	22–26×13–18×62	19	Kittiwake

*The size and mass of the earlier prototypes was variable; measurements given here refer to one of the loggers frequently used on pigeons. Species=Bird species on which each device type was mainly used; for the species in parenthesis, only unpublished data are available.

an internal flight (or motion) sensor. This is a small modified microphone whose signals allowed us to graphically distinguish flight activity (continuous high-level vibration 'noise signal') from activity at nest (absent or weak and irregular signals) and swimming (low-intensity signals with irregular spikes). Types 3 and 4 were obtained from type 2 by removing the depth gauge and the compass sensor, respectively, in order to reduce the size and weight of the device when it was used on medium sized alcid. Type 5, especially suited for non-diving small gulls, such as the black-legged kittiwake (*Rissa tridactyla*), was equipped with flight sensor and a saltwater switch consisting of two short electric wires (1 cm) emerging from the housing plug of the device. Short-circuiting of the wires occurred when the bird was fully submerged in water during foraging activity. The signals produced by the flight sensor and saltwater switch during a foraging trip of a black-legged kittiwake are reported in Fig. 1.

In most cases, the time between successive recordings was set at 6–10 s for the compass, 4 s for the depth gauge and saltwater switch, 6–8 s for the motion sensor; these sampling frequencies allowed continuous recording for 3–4 days. The devices were attached to the birds' back by means of cyanoacrylate glue or Tesa tape and cable ties (see Benvenuti *et al.*, 1998; Daunt *et al.*, 2002). Recorded data were downloaded from the loggers to a portable computer and analysed using specially designed software (A. Ribolini, unpubl. data).

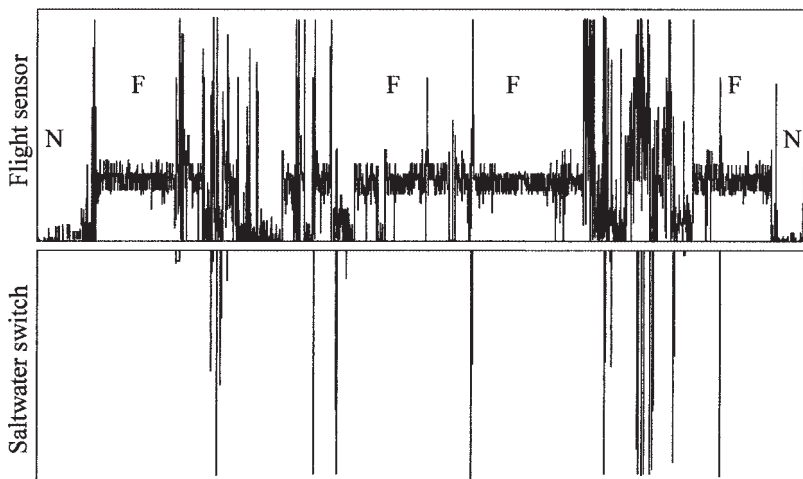


Fig. 1. A foraging trip of a black-legged kittiwake, which lasted about 5 hrs, is shown. Data collected by the flight activity sensor and the saltwater switch from the bird-borne logger allow us to distinguish different activities: N=Nest attendance, F=travelling flight, which consists of high, stable signals. Foraging flights consist of strong signals of variable intensity together with frequent activation of the saltwater switch. Presence on the sea surface between flights consists of weak frequent signals.

Results and discussion

Experiments on homing pigeons

Type 1 loggers were used for studying the homing strategies of pigeons (Papi *et al.*, 1991; Ioalè *et al.*, 1994; Dall'Antonia *et al.*, 1999; Holland *et al.*, 2000; Bonadonna *et al.*,

1997, 2000). These experiments will not be mentioned in the present paper which deals with marine birds.

Experiments on procellariiforms

The excellent performance of the instruments in investigations on homing pigeons induced us to extend our study to a wild bird, the Cory's shearwater (*Calonectris diomedea*). The shearwaters' homing strategies were investigated by moving some birds, fitted with direction recorders, to five different release sites 46–248 km from the colony (Dall'Antonia *et al.*, 1995). In order to reconstruct the birds' flight paths, a flight speed of 30 km/h was assumed (Massa and Lo Valvo, 1986). Directional data recorded by the compass during flight were corrected for wind drift; corrections for wind drift were calculated automatically by a specially designed software package that incorporated wind data collected every hour from five weather stations in Sicily.

The birds' routes turned out to be oriented homeward soon after release, thus revealing that the homing process was not based on a random search for familiar landmarks. The birds were able to assume and maintain a homeward directed flight over large areas of open sea, completely devoid of guiding features. This ability, which was exhibited during both day and night, is presumably based on a true navigation system, whose nature was however not revealed by our study.

Our instruments were also used in preliminary tests on the foraging ecology of Balearic shearwaters (*Puffinus mauretanicus*). The instruments have recorded data on the pattern of nest attendance (including departure time to foraging trips and return time) and the diurnal pattern of flight and dive activity (including dive profiles) (Aguilar *et al.*, 2003). It is worth noting that this species can perform 26 m deep dives, which last over 60 s, much longer than the duration reported in previous observations (Rebassa *et al.*, 1997).

Experiments on alcids

The foraging pattern of two alcid species, at 4 different colony sites, were investigated: the razorbill (*Alca torda*) and Brünnich's guillemot (*Uria lomvia*). In both species, foraging trips mainly consisted of a number of straight flights interrupted by a series of dives by which the birds seemingly explored areas for prey availability. Foraging occurred at sites where razorbills stopped, dived and rested for a longer time before returning to the nest by a single flight or a sequence of a few flights. The razorbills' diving pattern and depth, and the location of foraging areas, turned out to be very different from that reported for Brünnich's guillemot breeding in the same colony. Considerable differences between populations of the same species at different colonies and successive breeding seasons were also observed (Dall'Antonia *et al.*, 2001). These differences mainly regarded the duration of foraging trips and global time allocation (Benvenuti *et al.*, 1998, 2001; Dall'Antonia *et al.*, 2001; Falk *et al.*, 2000, 2001, 2002).

In a study carried out on Brünnich's guillemot breeding at Coats Island (Canada), the use of data loggers was complemented by visual observations, in order to verify some aspects of birds' foraging ecology within the framework of "central place foraging theory". Guillemots are "single prey loaders", owing to the fact that they use their bill to both capture and carry food items. The size and mass of prey items delivered to chicks were visually assessed and related to individual travelling distance reported by the data loggers. This rela-

tionship between mass and travel distance resulted in a highly significant positive correlation, according to the prediction made by Orians and Pearson (1979) on the principles of "central place foraging theory" (increased selectivity at greater distances). The data also allowed us to relate dive pattern and depth with prey species delivered to the colony in relation to sex and time of day (Benvenuti, Gaston and Woo, unpubl. data).

The use of bird-borne data loggers brings up the problem of possible negative bird reactions, and consequent disturbance of its behaviour as a consequence of severe experimental manipulations, increased wing loading and thereby decreased flight efficiency, and increased drag during both swimming and flight. The risk that results of data logger experiments are biased by non-controlled factors can be reduced by carrying out comparative studies of two bird groups equipped with the same device types, and thus burdened equally. These comparative studies were aimed at investigating possible differences in the foraging ecology and behaviour between birds of the same species breeding at different colony sites, between sexes, and between incubating and brooding birds within the same colony. As regards the former point, we investigated the foraging behaviour of Brünnich's guillemot breeding in the high Arctic in two different sectors (about 220 km away from each other) of the North Water polynya (Falk *et al.*, 2002). While the foraging range was equal at the two colonies, significant differences were observed in the diving behaviour; dives of birds on the western (Greenland) side of the polynya were significantly deeper than those performed by birds on the eastern (Canadian) side, and spent a greater share of each trip actively diving. The trips of Canadian birds had longer duration than the Greenland birds, but they also spent more time 'resting' on the sea surface, indicating a spare capacity for additional work. Given that the growth rate of Greenland chick was higher than that on the other side of the polynya, it remains unclear why the Canadian guillemot did not use their spare capacity to increase foraging efforts.

In Northern Greenland, we also carried out a study aimed at verifying possible differences between incubating and brooding Brünnich's guillemot (Benvenuti *et al.*, 2002). Our data, which were collected in parallel (within a period of 10 days) on incubating and brooding birds, showed that brooding birds dived significantly deeper than incubating birds, indicating that self-maintenance of adult birds is based on prey items different from those delivered to chicks (fish). Self-maintenance is possibly based on food less nutritious than fish (crustaceans?), which however requires shallower dives, providing a more efficient energy return to cover individual foraging costs. Incubating birds tended to distribute their diving activity more or less homogeneously during the day, whereas brooding birds exhibited a preference for the first part of the day. This shift in the feeding-time preference may reflect a difference in the accessibility of the selected prey type during the day.

At Coats Island, female Brünnich's guillemots turned out to dive significantly deeper than males; this difference, however, was not due to sex-specific foraging strategies, but to the fact that males and females exhibited a different pattern of nest attendance. As a consequence, males were nocturnal foragers whereas females were diurnal foragers. Therefore, low light penetration and positive vertical migration of plankton during the night were the cause of the sexual difference in the diving depth (Woo *et al.*, 1999).

Experiments on gulls

Our devices were used to record the foraging routes of Audouin's gulls (*Larus*

audouinii) and the foraging strategies and maximum foraging range of the black-legged kittiwake (*Rissa tridactyla*) breeding in the Isle of May (Scotland, UK). Incubating Audouin's gulls were captured at two different Sardinian (Italy) colonies; from data recorded for three days it turns out that birds foraged at night and daytime, at distances up to 70 km from the colony. Nocturnal foraging occurred only with calm weather conditions. The foraging routes showed that different Sardinian colonies rely on overlapping foraging areas. Therefore, competition for resources might contribute to determine local colony size and distribution (Baccetti *et al.*, 2000).

For the kittiwake, we used a small data logger, equipped with flight sensor and saltwater switch (Table 1); short circuiting of the saltwater switch occurred when the bird was fully submerged in water during foraging. The loggers allowed us to distinguish 4 key behaviours: travelling flight, foraging flight, rest on the sea surface, attendance at the nest (Fig. 1). The relationship between travelling time and trip duration provided evidence for a maximum foraging range (about 70 km from the colony). Given that this range includes a large sand bank complex, with high concentration of lesser sandeels (*Ammodytes marinus*), the upper limit seems to be related to the distribution of prey rather than any energetic constraint on flight costs (Daunt *et al.*, 2002).

Experiments on gannets

The experiments on gannets were carried out at two colony sites: Funk Island (Newfoundland, Canada) and Bass Rock (Scotland, UK). While the experiments at Funk Island were run to verify general aspects of the foraging ecology of brooding birds (Garthe *et al.*, 2000, 2003), data recorded at Bass Rock were aimed at verifying possible sexual differences in the foraging behaviour. Radio-tracking procedures showed that males and females tended to forage in different directions; while females flew mainly southeast, males went from northeast to southeast equally frequently. In addition, data from loggers showed that females made deeper and longer dives than males. This difference was not related to a different pattern of nest attendance, as reported for the Brünnich's guillemot breeding at Coats Island. We found significant differences in the dive depth between males and females operating under the same light conditions, in the middle of the day (Lewis *et al.*, 2002). It is worth noting that the gannet is a monomorphic species; therefore, the reported differences between sexes in foraging behaviour cannot be due to a difference in body size. The observed sexual difference in a monomorphic seabird brings up the possibility that the differences reported in dimorphic species are not mediated exclusively by differences in body size.

In conclusion, our results show that the data loggers originally designed by our research group for investigation on homing pigeons are also useful in studies of the foraging behaviour of breeding marine birds. The use of bird-borne devices inevitably interferes with their behaviour; however, it has previously been argued that the effects of instruments of this size and weight have relatively little impact on the behaviour of birds (Croll *et al.*, 1992; Benvenuti *et al.*, 1998, 2001; Falk *et al.*, 2000; Lewis *et al.*, 2002). In addition, our instruments were mostly used in comparative studies of two groups of birds (males *versus* females, incubating *versus* brooding birds, birds at one colony *versus* birds at another colony) burdened equally with the same device types, thus reducing the risk of biased results and conclusions.

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