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When do wandering albatrosses Diomedea exulans forage?

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ABSTRACT: Five free-living wandering albatrosses *Diomedea exulans* were fitted with stomach temperature sensors to detect when birds fed. Three birds went to sea for a total of 24 d during which time they ingested 159 prey items which were calculated to have a total mass of 45.65 kg. These results were lumped with results from another study to show that 89 % of all prey (by mass) were caught during the day when wandering albatrosses fly the greatest distances. We suggest that birds generally rest during periods of darkness but actively search for widely-spaced prey during the day during which time they use dynamic soaring to enable them to cover the requisite large distances with minimal energy expenditure.

Seabirds are top predators in the marine environment and there is increasing interest in their relationship with their prey and their role in community ecology (e.g. Croxall 1987). Procellariiformes (albatrosses and petrels) are the most abundant seabirds in terms of number and of species, especially in the Southern Ocean. Most are surface-seizing species that feed extensively on squid. However, how and when these birds catch their prey has been the subject of extensive speculation (Prince & Morgan 1987).

In a recent review of nocturnality in seabirds, Brooke & Prince (1991) consider that squid-eating Procellariiformes generally feed at night. Bioluminescence (Imber 1973, Clarke et al. 1981) and diel vertical migration (Hardy 1956) in some species of squid taken by Procellariiformes have also been invoked to substantiate the argument that these birds feed at night, since apparently such prey species are only visible and accessible near the surface at this time. Direct observations of birds foraging at night come from individuals feeding adjacent to a floodlit ship (e.g. Harper 1977), a situation which cannot be described as natural. Otherwise, some species are considered to forage nocturnally because they have rarely been seen to feed during the day. Finally, activity recorders logging the amount of time spent on the water's surface by wandering (*Diomedea exulans*), black-browed (*D. melanophris*) and grey-headed albatrosses (*D. chrysostoma*) demonstrate that these species spend from 3 to 13 times more time on the sea by night than by day (Prince & Morgan 1987). Results from satellite tracking studies show a similar pattern (Jouventin & Weimerskirch 1990). Since these large albatrosses must alight on the water to feed, Brooke & Prince (1991) interpret this as demonstrating that these birds feed predominantly at night. That albatrosses might spend time on the water's surface for other reasons, such as sleep, was not discussed.

Using a recently-developed archival recorder that logs the timing of feeding by marine endotherms, Cooper et al. (in press) determined that 2 wandering albatrosses, at sea for a total of 4 d, fed both during the day and at night. Sample size was, however, too small to determine whether birds fed preferentially during any particular period. We used these same units on a larger sample of birds to examine the extent to which wandering albatrosses feed during the day and during the night.

Materials and methods. We used a stomach temperature logger to determine the time of feeding in free-living wandering albatrosses. The logger (termed an EATL – Einkanaliger Automatischer Temperatur Logger) had a mass of 100 g (101×22 mm diameter) and was composed of a temperature sensor linked to an archival unit (32 kB) encapsulated within a titanium housing. Full details are given in Wilson et al. (1992). The EATLs are designed to be retained in the stomach until recovered by stomach flushing (Wilson 1984). While in the stomach a temperature reading can be recorded every 32 s up to a maximum of 12 d. Ingestion of prey or water (at ambient temperature) is recorded by the EATL as a characteristic precipitous temperature drop followed by an exponential temperature rise as the ingesta is warmed to normal body temperature (a PDER event as defined by Wilson et al. 1992). Integration of the area underneath the asymptote allows estimation of the mass of prey ingested at each PDER event (Wilson et al. 1992). The time when the prey was ingested can be calculated from the known start time of the unit and the sampling interval.

During January and February 1992, 6 wandering albatrosses incubating eggs at Possession Island (46° 25' S, 51° 40' E), Crozet Islands, were induced to swallow EATLs. One bird was then fed prey of known mass at ambient sea temperature in order to examine the relationship between prey mass and integrated area under the asymptote (Wilson et al. 1992). This bird was then stomach pumped immediately. The other 5 birds were allowed to continue normal incubating behaviour undisturbed. Units were recovered after 8 to 18 d. One bird did not go to sea and incubated for 10 d before the EATL was recovered and another bird regurgitated the EATL at sea. The other individuals all executed 1 foraging trip at sea lasting 6, 8 and 14 d, respectively. During this time the birds recorded 39, 67 and 53 PDER events corresponding to total masses ingested of 15.35, 15.74 and 14.55 kg. During their foraging trips wandering albatrosses can move over thousands of kilometres (Jouventin & Weimerskirch 1990). The hours of sunrise and sunset were corrected appropriately to accord with the birds' geographic locations as determined every 2 to 4 h with

miniature satellite transmitters (45 g) connected to the Argos system (Jouventin & Weimerskirch 1990). In order to increase sample size, these results were lumped with results of foraging activity from 2 wandering albatrosses studied by Cooper et al. (in press) using EATLs. Cooper's birds were equipped with EATLs during the brooding period, in April, for short trips lasting ca 2 d. A total of 99 h of recording at sea was added to our results.

Results and discussion. Ingestion of prey was recorded by obvious sharp temperature drops followed by slower temperature rises as the ingesta was warmed to body temperature (Fig. 1). Combined results from all birds that had been foraging demonstrate that a greater mass of food was ingested by day than by night (Fig. 2). After correcting for the timing of day and night [periods delimited by the centre of the sun's disk crossing the 6° below the horizon mark (onset and end of civil twilight)] according to time of year and locality we found that 89 % of the mass of all prey was taken during the day and only 11 % was taken at night (dusk to dawn), even though the period of darkness represented on average 33 % of the available time. In addition, 83 % of the total number of prey items was captured during the day and 17 % at night.

There was no indication that wandering albatrosses preferentially feed during periods of dawn and dusk, since only 1 % of the mass of all prey was caught during twilight (defined as the period when the sun is

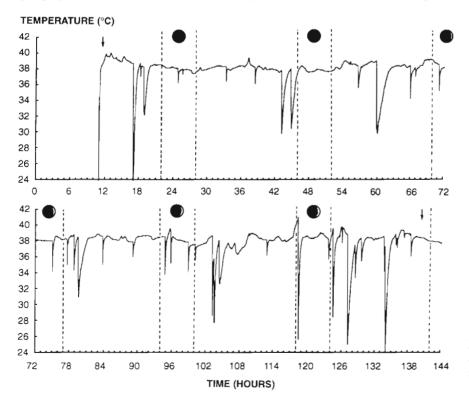


Fig. 1. *Diomedea exulans*. Stomach temperature of a male wandering albatross during a 6 d foraging trip. Arrows indicate the times when the bird left and returned to the colony. Dashed lines show the periods of darkness

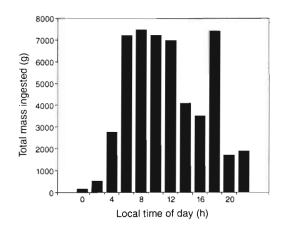


Fig. 2. *Diomedea exulans.* Calculated total mass of food ingested by 5 wandering albatrosses during a total of 29 d at sea as a function of time of day

between 0 and 6° below the horizon). Extension of this period by 5° either side of these boundaries did not alter this conclusion. Over 50 % of all prey items were calculated to be less than 200 g with larger prey items becoming progressively less common. Prey larger than 200 g, however, represented 82 % of the total mass ingested. During 637 h at sea, the birds ingested 179 items, i.e. 1 item every 3.6 h. The satellite-tracked Crozet Island birds, which ingested almost 90 % of all prey items considered, foraged in areas not frequented by fishing vessels and had flight patterns which showed movement far too extensive to indicate ship following (e.g. La Cock & Schneider 1982). It thus seems likely that most, if not all, prey ingestion recorded came from birds feeding on a natural food source.

During incubation and the brooding period wandering albatrosses appear to forage and feed principally during the day. Extended time spent on the water's surface such as occurs during periods of darkness (Prince & Morgan 1987, Jouventin & Weimerskirch 1990) therefore clearly has little to do with foraging. The 2 different activities associated with day and night (flying or sitting on the water's surface, respectively) would imply 2 very different prey distributions if both phases were to be associated with foraging. One option, that proposed for nocturnal foraging, necessitates that the birds essentially remain in a relatively fixed spot and wait for prey to vertically migrate within reach (cf. Hardy 1956, Brooke & Prince 1991). This implies, however, that prey densities per m² of water column are very high since the birds move little. That flying is associated with foraging indicates that birds actively search extensive areas for prey that are spatially far apart. Wandering albatrosses move continuously during daytime (Jouventin & Weimerskirch 1990) when they catch most of their prey. Alba-

trosses are able to do this since, despite flying rapidly, they use very little energy due to their ability to use the wind to dynamically soar (Pennycuick 1987, Jouventin & Weimerskirch 1990). Results from satellite tracking studies show that birds average 500 km d⁻¹ (Weimerskirch unpubl.) and may travel up to 900 km in any 1 d (Jouventin & Weimerskirch 1990). At average flight speeds of 30 km h^{-1} (a substantial underestimate because wandering albatrosses do not travel in straight lines as has been assumed; Weimerskirch unpubl.) our results indicate that wandering albatrosses encounter 1 prey item for a minimum of every 107 km travelled. Thus, prey do indeed seem to be rare. There is no indication that these prey are locally abundant because birds wearing satellite transmitters did not ingest multiple prey items in 1 locality.

In the Crozet sector of the Southern Ocean wandering albatrosses feed predominantly on squid (Weimerskirch et al. 1986, Ridoux in press). Our birds returning with EATLs were stomach flushed (Wilson 1984) and also contained only squid beaks. These squid must have been caught at the surface since wandering albatrosses catch their prey by surface seizing and are clearly ill-adapted for diving. It is perplexing that vertically-migrating squid species should be at the surface at all during the day (Clarke 1966, Imber 1973). Either our understanding of the prey species is at fault or the individuals taken were sick or moribund exhibiting abnormal behaviour (Weimerskirch et al. 1986, Brooke & Prince 1991). This latter suggestion has been reinforced by Lipinski & Jackson (1989), who showed that cephalopods eaten by Procellariiformes are mostly species that float after death, whereas those species that sink are rarely caught despite their greater abundance (see also Cooper et al. 1992). Although dead squid may not be common, wandering albatrosses are well able to cover extensive distances during the day to search for them.

With wandering albatrosses, as is the case with many pelagic seabirds, deductions about foraging habits are based on our knowledge of the ecology of prey. Such information is often sadly inadequate. Stomach temperature sensors such as the EATL may turn the tables and enable us to enhance our understanding of the habits of prey species by examining the ecology of seabirds.

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