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Vol. 139, No. 2, April 1997

Satellite tracking of seabirds: interpretation of activity pattern from the frequency of satellite locations

The ARGOS system provides accurate information on large-scale migratory and foraging movements of wild birds and mammals. Foraging strategies have been studied via satellite telemetry in several seabirds, such as the Wandering Albatross *Diomedea exulans* (Jouventin & Weimerskirch 1990), Emperor Penguin *Aptenodytes forsteri* (Ancel *et al.* 1992), Adélie Penguin *Pygoscelis adeliae* (Davis & Miller 1992), King Penguin *Aptenodytes patagonica* (Jouventin *et al.* 1994) and Light-mantled Sooty Albatross *Phoebetria palpebrata* (Weimerskirch & Robertson 1994). Recent studies used ARGOS tracking to predict the diving behaviour of penguins because fixes are obtained only when the animals are on the sea surface or on land (Davis & Miller 1992, Jouventin *et al.* 1994). These studies suggested that there were reductions in the number of fixes at various hours of the day, and these reductions indicated that the birds were diving and, consequently, probably feeding. However, the ARGOS system may not be adequate for predicting the diving behaviour of seabirds like penguins because observed gaps in fixes may be a direct consequence of less frequent satellite passes at certain times of the day.

In this paper, we investigate this question using data on the satellite pass calendar, which corresponds to the times and dates when the satellites passed overhead, and ARGOS data on diving and nondiving seabirds for a better interpretation of their foraging activity in relation to the distribution in time of the satellite passes.

METHODS

This study used satellite fixes obtained for three seabird species, the Wandering Albatross, Sooty Albatross *Phoebetria fusca* and King Penguin, breeding on Possession Island, Crozet Archipelago (46°25'S, 51°50'E), Southern Indian Ocean. Sooty Albatrosses were tracked from 1 to 23 January 1994 and Wandering Albatrosses from 1 January 1994 to 7 March 1994. King Penguins were tracked during austral summer in 1992 and 1993 for a total period of 61 days (Jouventin *et al.* 1994). We used T2028C and T2038C platform transmitter terminals (PTTs), which were programmed for continuous transmission at a pulse interval of 90 s. Because several PTTs could be used for the same species on the same day, we calculated the total PTT-days for each species (the sum of the number of days the PTTs were used on one species over each study period). Over the 66 days of tracking, we obtained 179 PTT-days for the Wandering Albatross, 30 PTT-days for the Sooty Albatross and 114 PTT-days for the King Penguin. The ARGOS system permitted the calculation of a fix if the satellite received at least two messages during its pass over the PTT. The pass calendars over 48°50'S, 52°00'E were calculated for the two satellites NOAA-D and NOAA-H. We used this geographic point because it coincided with the centre of the area used for foraging by the birds. Satellite pass calendars were calculated for 1994 by ARGOS-CLS Services according to the orbital cycle of the two satellites. An orbital cycle is the period between two successive passes vertically above the same point on the Earth, i.e. 5 days (ARGOS-CLS Services, pers. comm.). The precision of the pass time calculation was within 2 min (ARGOS-CLS Services, pers. comm.). We could not retrocalculate the precise satellite pass calendar for the 1992 and 1993 summers, but because of a 5-day periodicity of the NOAA satellites, we assumed that the distribution of satellite coverage of the study area was identical to that observed in 1994. The minimum elevation angle used was 5°, i.e. each satellite simultaneously "sees" all PTTs within a circle of 5000 km diameter on the earth surface. Only the fixes within the 2500-km radius centred at 48°50'S, 52°00'E were considered, although the satellite elevation angle was always greater than the 5° value. Time is given in Greenwich Meridian Time (GMT). Data were regrouped into 4-h classes, and this allowed both an easy partition of the journey into six periods and a separation between night and day. Because the study took place in summer, the times of sunrise and sunset were given average values of 01.00 h and 17.00 h, respectively. A day was divided into a daytime (01.00–17.00 h) and a nighttime (17.00–01.00 h) period, i.e. nighttime was only half the duration of daytime. The nighttime period is indicated by a black bar in Figure 1.

RESULTS

At latitude 48°S, satellite coverage corresponded to a total of 60 passes during one orbital cycle, each satellite passing six times per

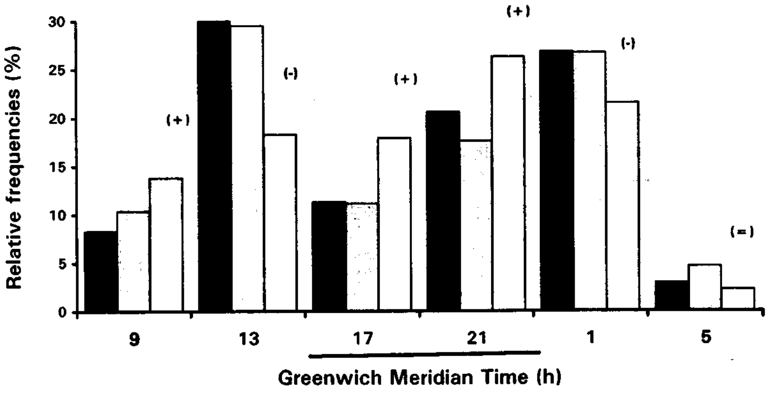

Figure 1. Frequency distribution of NOAA satellite coverage (black), Wandering Albatross and Sooty Albatross fixes (grey) and King Penguin fixes (white) with respect to 4-h periods. Night is represented by the dark bar. The figure shows that the albatross distribution was similar with NOAA satellite coverage but the penguin distribution was not. (=) indicates that the number of fixes was equivalent to the expected value, (−) significantly less ($P < 0.05$) and (+) significantly more ($P < 0.05$) than the expected value (contrast test; Neu *et al.* 1974).

Table 1. *Total satellite passes and fixes for the Wandering Albatross, Sooty Albatross and King Penguin obtained during the study period*

Time of day (GMT)	NOAA satellite passes	Satellite fixes: Wandering Albatross	Sooty Albatross	King Penguin
01.00–05.00 h	220	316	65	126
05.00–09.00 h	24	55	11	13
09.00–13.00 h	68	129	19	81
13.00–17.00 h	246	360	61	107
17.00–21.00 h	93	144	15	105
21.00–01.00 h	169	223	28	154
Total	820	1227	199	586

day. The coverage of the study area by the two satellites was not constant through the day (Table 1). The observed distribution of frequencies during 4-h periods was not homogeneous ($\chi^2_5 = 11.16$, $P < 0.05$). Contrast tests (Neu *et al.* 1974) showed that the middle of the day and the beginning of the night were undersampled, while other periods of the journey were oversampled. This coverage pattern was similar whether considering one orbital cycle (i.e. 5-day period) or incomplete parts of the cycle. In the same way, the pattern of satellite coverage during one orbital cycle was similar to the coverage during 23 days ($\chi^2_5 = 0.0$, n.s.), 61 days ($\chi^2_5 = 0.1$, n.s.) and 66 days ($\chi^2_5 = 0.2$, n.s.), so it is possible to compare one orbital cycle coverage with fix distributions obtained for the Sooty Albatross (23-day period), King Penguin (61-day period) and Wandering Albatross (66-day period).

Tracking of the three species provided 1227 fixes over 66 days for the Wandering Albatross (179 PTT-days), 199 fixes over 23 days for the Sooty Albatross (30 PTT-days) and 586 fixes over 61 days for the King Penguin (114-PTT days). The numbers of fixes per day obtained for the Wandering Albatross, Sooty Albatross and King Penguin were 6.8, 6.6 and 4.0, respectively. Because satellites pass over the study area 12 times per day, we obtained fix efficiency rates of 56%, 55% and 33% for the Wandering Albatross, Sooty Albatross and King Penguin, respectively. On average, a PTT fitted on a King Penguin provided 40% fewer fixes than if fitted on an albatross. The numbers of fixes obtained for both the Wandering and Sooty Albatrosses were positively and closely correlated with the number of satellite passes ($r_4 = 0.99$, $P < 0.001$ and $r_4 = 0.93$, $P < 0.001$), unlike the number of fixes obtained for the King Penguin ($r_4 = 0.73$, n.s.).

Distributions of frequencies of fixes with respect to time periods (Table 1) were not homogeneous for the Wandering Albatross ($\chi^2_5 = 181$, $P < 0.001$), Sooty Albatross ($\chi^2_5 = 40.7$, $P < 0.001$) and King Penguin ($\chi^2_5 = 83.3$, $P < 0.001$), suggesting that gaps occurred during certain hours of the day. However, two types of distribution patterns of the seabirds could be differentiated. The distributions of fixes for the Wandering Albatross and Sooty Albatross were not significant different ($\chi^2_5 = 8.1$, n.s.), but the two differed from the distribution of fixes for the King Penguin (Wandering Albatross *v* King Penguin: $\chi^2_5 = 54.6$, $P < 0.001$; Sooty Albatross *v* King Penguin: $\chi^2_5 = 45.7$, $P < 0.001$). Whilst the data from the two species of albatross were associated, the distribution of fixes for the albatrosses differed significantly from the distribution of fixes for the penguin ($\chi^2_5 = 65.1$, $P < 0.001$). The distribution of fixes for the albatrosses did not differ from the satellite pass distribution ($\chi^2_5 = 6.6$, n.s.), unlike the distribution of fixes for the penguin ($\chi^2_5 = 45.5$, $P < 0.001$; Fig. 1). Contrast tests indicated that location sampling anomalies were derived from differences between penguin-type and satellite pass distributions and resulted from undersampling in the first and last quarters of the day and oversampling at noon and throughout the night (Table 1, Fig. 1).

DISCUSSION

The two NOAA satellite systems used did not give constant coverage on a daily scale. This lack of passes at certain times results from the orbital scheme of the two satellites. NOAA-D and NOAA-H satellites do not run on an exact polar orbit, so it is not possible to have a global coverage of the Earth's surface. In the vicinity of Crozet Archipelago, gaps in passes occurred during the 06.00–11.00-h and 20.00–21.00-h periods.

Two groups of seabirds have been defined according to the analyses of the fix frequency distributions with time. On the one hand, albatrosses are flying seabirds that dive occasionally and for a few seconds only (Weimerskirch & Wilson 1992). All their movements can be recorded optimally with satellite tracking. The location frequencies of the birds are similar to satellite coverage during the whole day. So despite the fact that locations are less numerous and of lower quality when the birds move rapidly (Weimerskirch *et al.* 1992), especially during the daytime, the interpretation of their behaviour seems not to be affected by the number of fixes received per day.

Our study shows that diving behaviour is not directly predictable using only ARGOS data. The lower number of locations around 05.00 h was not necessarily related to the diving behaviour, as was assumed in previous studies (Davis & Miller 1992, Jouventin *et al.* 1994), but could have resulted from the low number of satellite passes at that time of the day. To interpret diving behaviour of penguins, it is important to analyse the frequency distributions of satellite passes as well as those of bird fixes. For the King Penguin, the analysis of frequency distributions of bird fixes indicated that, during the night as well as at noon, there were proportionally more fixes of King Penguins than expected from the satellite passes (Fig. 1). Conversely, at the beginning of the day and just before nightfall, there were proportionally fewer fixes of King Penguins than expected from the satellite passes, suggesting that penguins were diving at those times (Table 1). These observations could indicate that early morning and late afternoon are the most favourable periods for foraging in this species in summer. Results suggest that King Penguins spend more time than expected on the sea surface at midday and during the night and are thus easier to locate at these times.

This study has shown that care must be taken when analysing ARGOS data. Recent studies indicated that ARGOS data can be reinterpreted with the use of an alternative index of ARGOS location errors (Keating 1994). Because of a nonsynoptic coverage of NOAA satellites, the same number of fixes cannot be obtained at each hour of the day. Consequently, the use of ARGOS data to gain insight into the diving activity of diving seabirds is more complicated than suggested by Davis and Miller (1992) for Adélie Penguins and Jouventin *et al.* (1994) for King Penguins. To overcome this problem, ARGOS Services have proposed the association of the two pre-existing satellites with a third satellite, NOAA-F. The orbit scheme of NOAA-F fits between the two other orbits and would increase global coverage by 50%. Fixes would also be more abundant and regularly distributed during the journey (ARGOS-CLS Services, pers. comm.) and would allow a better understanding of the activity pattern of the species tracked by satellite.

This study was part of the program Ecologie des Oiseaux et Mammifères Marins Antarctiques, supported financially and logistically by the Institut Français pour la Recheche et la Technologie Polaire and the Territoire des Terres Australes et Antarctiques Françaises. We are grateful to our field assistant Frank Cuenot-Chaillet and Christophe Boiteau. We are also grateful to a referee and to J. Coulson for his editing work and for correcting the English.

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Submitted 13 February 1996; revision accepted 1 June 1996