

SHORT COMMUNICATION

DETERMINATION OF MOVEMENTS OF AFRICAN PENGUINS *SPHENISCUS DEMERSUS* USING A COMPASS SYSTEM: DEAD RECKONING MAY BE AN ALTERNATIVE TO TELEMETRY

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Determination of animal movements is essentially achieved by a temporal sequence of positional fixes. Currently, evaluation of animal positions depends on energy transmission between the animal and the perceiver. The distance between animal and perceiver and the type of medium separating them determine the proportion of energy transmitted in relation to that received. Visual localization of animals is most used, but transmission of optical images is highly variable and rarely effective over decametres. Superior sonic transmission in water and radio-transmission in air have led researchers to fit animals with power sources so that positional information can be obtained by triangulation with specialized receivers (Priede, 1983; Kenward, 1987). This increases perceptive range, but the 'distance' and 'medium' problems still apply (Kenward, 1987). Moreover, the accuracy of positional fixes decreases with increasing transmitter/receiver distance (Heezen and Tester, 1967; Springer, 1979) so that, for far-ranging animals, only gross movements can be determined. Satellite tracking systems (Jouventin and Weimerskirch, 1990) set a specific limit on this form of error but, even so, extended transmitter/receiver distances require large power sources to allow reception of a viable signal despite attenuation by the intervening medium. Ultimately, the viability of most telemetric systems is a balance between having a small enough power source so that animal behaviour is minimally altered (Holliday *et al.* 1988; Wanless *et al.* 1989) but large enough to enable signal transmission.

Animal movements can, however, be theoretically determined by methods other than those dependent on signal transmission. An animal's position at any time ($T+1$) is determined by the animal's position at time T and the distance and directional vectors incurred between T and $T+1$ (dead reckoning). In theory, therefore, the movements of an animal fitted with a system to sense information on heading and speed as a time function could be determined without telemetry if the

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animal could be recaptured (Bramanti *et al.* 1988; Wilson and Wilson, 1988). The need for prohibitively large power sources may thus be eliminated.

We deployed a simple compass system on African penguins *Spheniscus demersus*. Our unit recorded basic bird heading over specified time intervals. We then used data on penguin swimming speeds and the principles of dead reckoning to attempt to reconstruct penguin movements at sea. African penguins, when foraging for their chicks, spend well-defined periods (about 10 h) at sea before returning to the nest (Wilson and Wilson, 1990). Deployed devices can thus be easily recovered. There is extensive information on the distribution of breeding penguins at sea (Wilson *et al.* 1988), but visual tracking of individuals at sea is virtually impossible because birds may spend up to 90 % of their time under water (Wilson and Wilson, 1990). Movements of African penguins at sea have been determined using radio-tracking (Heath and Randall, 1989). However, to overcome the problems of effective signal transmission, battery packages were prohibitively large (Wilson *et al.* 1986) and aerials were almost a full body length (Heath and Randall, 1989; cf. Wanless *et al.* 1989) so that foraging durations were almost twice that expected (Heath and Randall, 1989; Wilson and Wilson, 1990).

Our compass system (92 mm×27 mm×17 mm; mass approx. 48 g) was based on a pivoted neodymium/boron magnet surrounded by four equatorially mounted Hall generators. The Hall generators were pulsed by two mono-stable multivibrators and linked, *via* an oscillator-controlled timer, to a 4×7 light-emitting diode (LED) matrix positioned adjacent to a photosensitive film (Fig. 1). The complete unit was powered by two 3 V lithium/manganese dioxide cylindrical coin cells with

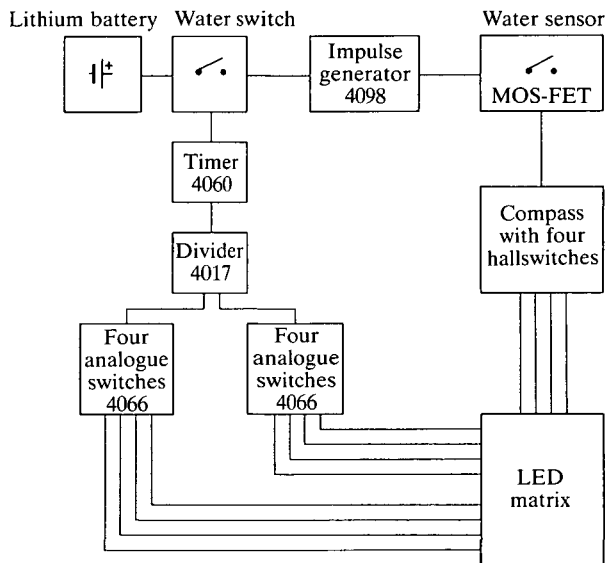


Fig. 1. Logical diagram of the compass system.

a nominal capacity of 160 mA h. After initial activation of the system, the orientation of the magnet within the compass housing was relayed, *via* the Hall generators, to the LED matrix so that one diode in the first row of four was activated. Changes in device orientation were accompanied by differential LED activation, with each diode corresponding to one of the four major orientations (NWSE). After 2 h, the magnet positional information was relayed to the second LED row and 2 h later to the third LED row etc., until all seven rows had been used after 14 h. LED activation exposed adjacent film. All film, Agfapan 100 (100 ASA), was developed in a 1:5 Neofin Blue:water solution at 20°C. Exposure of this film to the LEDs induced predictable changes in optical density as a function of total exposure time (Wilson *et al.* 1989a). Optical density of the exposure spots on the film was determined with a modified Uvikon 810 P spectrophotometer set at 600 nm with a detection window of 0.5 mm × 0.05 mm. For standardized film development procedures applied to a specific film type exposed to one particular LED type, the optical density, OD, of the exposed film is related to exposure time, T (min), by $OD = A + \phi \ln T$, where ϕ is a constant, but A varies according to the luminous intensity of individual LEDs (Wilson *et al.* 1989a). The logarithmic nature of the response curve means that changes in film optical density are less apparent with longer exposures so that light intensity, pulse length, film type and development procedures must be chosen to maximize reading accuracy over the appropriate time interval. With our system, we incurred a maximum error of less than 3% in time estimates over a maximum of 2 h exposure. Initial activation of the timer was achieved by dissolution of a sugar crystal separating two sprung-together electrodes. The 14-h timing system then ran through to completion irrespective of bird activity. The matrix diodes, however, were only activated when the system was under water, being triggered by salt-water contact between two spaced external electrodes (Fig. 1). Since penguins only travel appreciably when under water and then almost invariably at a constant speed (Wilson and Wilson, 1990) [calculated to be 1.9 m s^{-1} after correcting for device-induced drag (Wilson *et al.* 1986)], densitometric analysis of our exposed film permitted approximate calculation of the distance covered by swimming in a particular direction per 2 h time interval. Swim direction per interval was assumed to be derived only from headings of 0°, 90°, 180° or 270°. The total displacement over any 2-h interval was calculated by using vectors on the product of the swim speed and the time spent swimming per heading. Since our system only indicated four headings, each encompassing an arc of 90°, potential for directional error is high, particularly if birds choose to swim at absolutely invariant headings close to, but not crossing, arc boundaries. Conversely, errors of this type are liable to be reduced if swimming penguins constantly alter heading so that arc boundaries are often crossed. Previous pilot studies using a range-finder and goniometer to quantify swimming speed and heading variability in African penguins swimming near islands (Wilson, 1985) indicate that penguins may change heading as often as every 5 s and by as much as 60° (R. P. Wilson, unpublished data). Wilson *et al.* (1989b), using data derived from telemetry, calculated that travelling

penguins deviate from their overall heading to an extent that results in at least a 25 % increase in distance travelled between two specific points.

During August 1989, 10 adult penguins, breeding at Marcus Island (33°03'S, 17°58'E) (now joined to the mainland by a man-made peninsula), South Africa, were fitted with compass recorders using tape (Wilson and Wilson, 1989) and allowed to go to sea for one foraging period. To test the accuracy of our system, one bird was additionally fitted with a radiotransmitter (55 mm×20 mm diameter; mass 28 g) with an operating frequency of 151 MHz. A 35 cm long antenna was curved away from the back of the bird to project above the water when the animal surfaced. We were aware that this bird was unlikely to be able to forage normally (Wilson *et al.* 1986), but hoped that it would enable comparison between telemetry-determined movements and those derived by dead reckoning. We attempted to triangulate the penguin's position using radio-receivers coupled to null-peak, five-element double Yagi antennae. Receiving stations were located on two hills, 55 m and 111 m above sea level and 3.3 km apart (Fig. 1).

All 10 penguins fitted with compass systems returned to their nest (eight birds spent 1 day at sea, one 2 days and one 3 days). Nine birds were seen to feed chicks and maximum mass gain per adult was 900 g (30 % of body mass), although the bird fitted with both the compass recorder and radiotransmitter did not appear to have fed. In none of our birds fitted with compass recorders did we get full utilisation of the LED matrix. The 14 h timers were designed to cover the normal period at sea (Wilson and Wilson, 1990), but device-fitted birds invariably went into the water for a short period for a drink some hours before they went foraging. The timers thus started running before the birds actually left the island.

The radio-tagged penguin transmitted a very intermittent signal and the lower radio-receiving station could only determine that the bird went approximately West and disappeared around the headland at approximately 09:30 h (Fig. 2). The station at higher altitude managed to get fixes estimated to be within 10° of true position (Heezen and Tester, 1967; Springer, 1979) at approximately hourly intervals. The telemetric positional fixes indicated that the bird swam out of the bay approximately West, rounded the headland, and then swam North until approximately 13:00 h when it subsequently moved little. The penguin was considered to be close to the coast because the signal was very strong. These movements accord well with those determined by our compass system (Fig. 2). Other birds appeared to forage within a few kilometres of Marcus Island (Fig. 3). At sea, transects indicate that this behaviour is expected (Wilson *et al.* 1988). Compass-fitted penguins had two distinct types of swimming behaviour apparent over the 2-h measurement intervals; directed swimming, where the distance actually moved was approximately equal to the distance swum, and 'random-walk type' behaviour, where birds swam extensively, but did not move far (Fig. 4). We interpret these two behaviours as travelling and foraging, respectively. African penguins at sea have already been classified as either foraging or travelling on the basis of dive durations (Wilson and Wilson, 1990), but differences in directionality for the two behaviours have only been assumed.

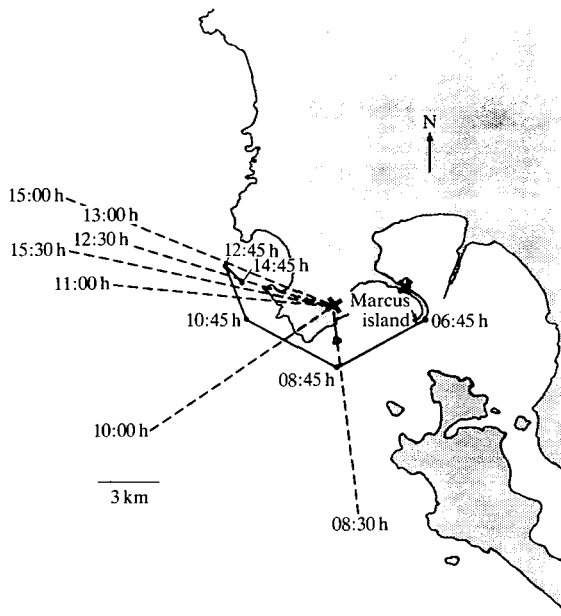


Fig. 2. Movements of an African penguin as determined by a compass system (unbroken line) with periodic bearings taken by telemetry. The two telemetric receiving stations are indicated by crosses.

Although our compass system was crude, it enabled us to elucidate area utilisation by foraging African penguins using the principles of dead reckoning. This was only possible because penguins travel at a relatively constant known speed while under water. A similar assumption was made by Bramanti *et al.* (1988) for determining flight paths of homing pigeons. In fact, although many birds have invariant flight speeds (Meinertzhagen, 1955), effective determination of animal movements in general will necessitate both speed and directional information incorporated in a single dead-reckoning unit. Some remote-sensing units for measuring speed have already been deployed (e.g. Ponganis *et al.* 1991) and microprocessor dead reckoners are now being tested (B. Culik, R. Link and R. P. Wilson, unpublished data). Such systems should enable us to gain new insights into the behaviour and movements of many animals that are unsuitable subjects for radio or sonic telemetry.

The greatest source of inaccuracy in dead reckoning is drift, being relatively unimportant in terrestrial animals, but becoming significant in marine, and especially volant, animals. This can be partially compensated by knowledge of the environment and correcting for currents, winds etc. (Bramanti *et al.* 1988), or by initially plotting the known start and finish positions and minimally adjusting the course so that they accord (Wilson and Wilson, 1988).

Unlike dead reckoning, in telemetric systems, larger distances between transmitter and receiver make positional fixes more inaccurate (Kenward, 1987), so

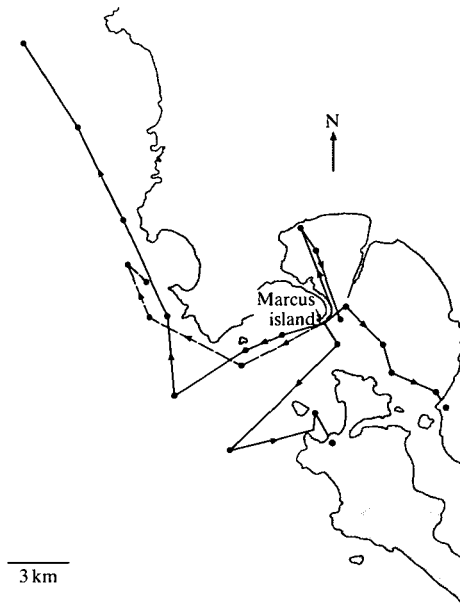


Fig. 3. Movements of five foraging African penguins as determined by a compass system. The dashed trace indicates the route taken by the bird fitted with an additional radiotelemeter (Fig. 2). Timers in all devices ran to completion before birds returned to the island to feed their chicks (see text). Foraging tracks recorded for less than 5 h are omitted.

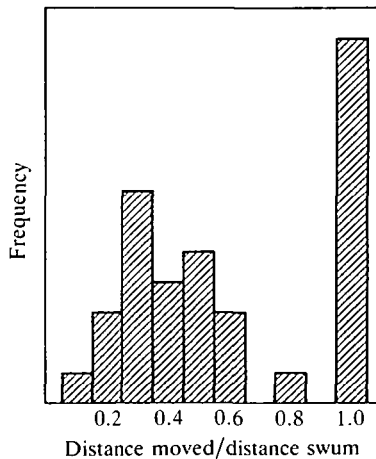


Fig. 4. Bimodal directionality in swimming by African penguins foraging for their chicks and carrying compass systems. To obtain this figure the straight-line distances between starting and finishing positions over 2-h intervals (distance moved) were divided by the total distance swum (speed \times Σ times spent swimming at any heading) during the respective intervals (distance swum). This figure includes all data from all device-fitted birds.

Table 1. *Relative properties of dead reckoners compared to telemetry*

Property	Dead reckoning	Telemetry
Viability (range-dependent)	No (+)	Yes (-)
Viability (medium-dependent)	No (+)	Yes (-)
Resolution of activity (range-dependent)	No (+)	Yes (-)
Accuracy of fixes (range-dependent)	No (+)	Yes (-)
Accuracy of fixes (time-dependent)	Yes (-)	No (+)
Subject to drift errors	Yes (-)	No (+)
Power consumption	Low (+)	High (-)
Battery size	Small (+)	Large (-)
Likelihood of animal disturbance	Low (+)	High (-)
Possible animal disturbance from antenna	No (+)	Yes (-)
Labour intensive	No (+)	Yes (-)
Expense	Low (+)	High (-)
Animal recovery imperative	Yes (-)	No (+)

Positive assets are indicated by (+), negative by (-).

that only gross movements over larger time intervals can be determined. This will tend to cause an apparent reduction in animal travelling speed since few animals travel in a perfectly straight line; in a perfectly accurate telemetry system, maximum travelling speeds will be recorded over the shortest time intervals. Telemetrically recorded 'stationary' behaviour may be periods of either rest or activity where no large-scale directional vector is taken (Fig. 4). Dead reckoning systems differentiate between these possibilities, although positional fixes become more inaccurate with time.

Although both telemetry and dead reckoning permit determination of animal movements, the two methods result in very different applicabilities (Table 1). The applicability of a particular system depends principally on the quality of signal transmission in the animal's environment. Particularly powerful would be a combination of both systems so that an infrequent telemetric signal could be used periodically to correct for dead reckoning drift incurred over time. In this way, power consumption and receiving station attendance would be reduced, but animal activity and movements could still be resolved in detail.

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