

BEYOND RINGS ON BIRDS FOR DETERMINATION OF MOVEMENTS: WITHER THE ARCHIVAL TAG?

RORY P. WILSON¹

Wilson R.P. 2001. Beyond rings on birds for determination of movements: wither the archival tag? *Ardea* 89(special issue): 231-240.

Two methods for determining the movement of birds are discussed; Global Location Sensing (determination of position by consideration of day length and local timing of mid-day) and dead reckoning (calculation of routes by vectors). These are examined for their utility over a number of scales. Work conducted on penguins demonstrates that, although global location sensing is not subject to drift errors, its temporal and spatial resolution makes the system only applicable for large scale movements over at least tens of km. Dead reckoning, however, can be used over scales ranging from tens of kilometres to centimetres. Positions derived from dead reckoning are relatively more accurate the closer they are in time and distance to each other although drift over time can be problematic. The high temporal and spatial resolution of dead reckoning means that animal decisions leading to their movements can be determined and this is examined for penguins over a scales ranging from tens of kilometres to metres. Future work is likely to concentrate on small scale movements in 3 dimensions which, to date, cannot be resolved with other systems.

Key words: global location sensing - dead reckoning - vectors - movements - archival tags - animal decisions

¹Institut für Meereskunde, Düsternbrooker Weg 20, D-24105 Kiel, Germany; E-mail rwilson@ifm.uni-kiel.de.



INTRODUCTION

The successful development of ringing schedules has considerably enhanced our understanding of many aspects of bird biology (e.g. Freeman & Morgan 1990; Bub 1996). While bird ringing has become a discipline in itself, it is seldom acknowledged that the concept of attaching foreign bodies to free-living animals was essentially proposed for the first time in the form of rings and indeed found to be tenable. Today many modern-day studies of some of the more enigmatic of the world's creatures are virtually entirely dependent on this type of philosophy (e.g. Priede & Swift 1992).

One of the aspects of bird biology to which ringing substantially contributed was that of bird movements (e.g. Harris 1984). Recovery of an identifiable bird at a site distant from that at which it was ringed meant that the animal had traversed

at least the intervening distance and travel speed and overall direction could be derived from the data (e.g. Winkel & Frantzen 1991). This has given very useful base line data for many species, particularly as concerns migration patterns (Noer 1991). Initially, most ring recoveries were from dead birds so that only two points in the bird's route could be used. However, bird ringers have been instrumental in providing temporally-spaced sightings of living ringed birds so that travelling routes can be sometimes resolved with three or more points (Brenning 1989) and migration routes and migration timing have been documented by pooling data from many individuals. The thinking behind this methodology is that of reconstruction of the bird route after it has taken place because only then are the positional data available.

With the inception of instantaneous tracking systems such as radio, and later, satellite telemetry, researchers were able to ask where a particu-

lar bird was at any precise moment in time (for review see Kenward 1987; Weimerskirch 1998). This was a powerful alternative to simple ringing and has enormously improved our understanding of bird movements over a large range of scales (Taillade 1992). Such systems are, however, not without their drawbacks (e.g. White & Garrot 1990) and satellite tracking systems are, due to their size, currently limited to use on comparatively large birds (e.g. Weimerskirch 1998)

More recently, alternative systems have been developed for determining bird movements. In a manner similar to that used by rings, these systems are based on the premise that we do not need to know the instantaneous position of the bird to be able to derive its movements but rather we can do that by back-calculating. In this case, data stored by an electronic tag allow calculation of the bird's position. This paper presents two of these new methods and considers the temporal and spatial utility of these systems for resolving animal movements as well as a brief discussion of some of their advantages and disadvantages with respect to conventional telemetry (cf. Wilson *et al.* 1991). Exhaustive discussion of conventional telemetry (radio or satellite) used on birds will not be undertaken since such treatises already exist (e.g. Kenward 1987).

STUDY AREAS AND METHODS

Data presented are derived from various field trips, all conducted in the southern hemisphere and all concern free-living penguins. Details will be furnished as appropriate. The data are selected to illustrate specific points whose general validity holds true almost irrespective of bird type. Penguins are, however, excellent models for demonstrating these points because they are flightless (which aids their capture) large, robust, nest-site-faithful (which facilitates deployment and recovery of electronic tags) and demonstrate a variety of complex movements and behaviours over scales ranging from fractions of a metre to hundreds of kilometres.

Archival tags were placed on the mid-line of the lower back of birds, to reduce hydrodynamic drag (Bannasch *et al.* 1984), and attached using waterproof tape (Wilson *et al.* 1997). Only birds associated with nests were used to ensure that they were likely to return to the colony after deployment so that the devices could be removed and the data accessed. Essentially two archival tag types will be presented; the Global Location Sensor and the Dead Reckoner. Both are started and the data accessed by computers linked to appropriate interfaces.

Global Location Sensing

The Global Location Sensor (also termed a geolocator - see Hill 1994) consists of an archival tag that measures and stores data on light intensity at regular intervals (typically between once every 30 s and once every 2 min). The time base is controlled by a highly accurate quartz crystal and set for a stable time zone within the world e.g. Greenwich Mean Time. Available units currently range in size from 44 X 14 mm dia (16 g) upwards and have memories of up to 2 Mbyte with resolution ranging between 8 and 16 bit giving a total of up to one million data points or a recording lifetime of over 3.8 years for data being stored once every 2 min. The latitude of the unit on any given day during the wearing period can be determined by consideration of the local time of dawn and dusk because day length is a function of Julian day and latitude. In addition, the Greenwich Mean Time of local noon, or midnight, (this being the mid-point between dawn and dusk) is dependent on longitude. Various algorithms are available to describe the precise mathematical process of positional calculation (e.g. Wilson *et al.* 1992; Hill 1994; Wilson *et al.* 2001). There is enormous variability in errors in positional fixes, these being dependent on (i) non-variable processes such as algorithm, sampling regime, type of light sensor used and the orientation of the light sensor with respect to the sky and (ii) processes which vary from day to day such as bird orientation, distance travelled per day (albatrosses may travel up to 1000 km/day and thus incur highly variable daylight regimes al-

though this can be corrected for by software (Wilson *et al.* 2001)), diving behaviour and cloud cover. Typically, though, the errors in positional fixes vary between 20 and 150 km (e.g. Wilson *et al.* 1995a; Wilson *et al.* 2001).

Dead reckoners

The Dead Reckoner (Wilson & Wilson 1988; Wilson *et al.* 1993; cf. Benvenuti *et al.* 1998) is an archival tag that records speed, heading and height (or depth) at intervals generally between once a second and once every 15 s. Speed is variously sensed (paddle wheels, differential pressure sensors) and is generally accurate to better than 0.25 m/s (cf. Ponganis *et al.* 1990; unpubl. data), heading can be resolved to within 5° by either flat, two dimensionally-operating compasses (Benvenuti *et al.* 1998) or more complex 3-dimensional versions (Davis *et al.* 1999, cf. Hochscheid *et al.* 1999), while depth can typically be resolved to within 30 cm (> 8 bit resolution on pressure transducers with a range up to 10 Bar). Memories currently range from 32 Kbyte to 4 Mbyte with electronic resolutions between 8 and 16 bit. The smallest commercially-available dead reckoners are of the order of 100 mm long X 40 mm wide and 18 mm high and weigh *ca.* 80 g. The routes of device-carrying animals are determined by calculating movements from a known start point using vectors (Wilson *et al.* 1993). Consideration of 63 tracks of Pygoscelid penguins, Adélie *Pygoscelis adeliae*, Gentoo *P. papua* and Chinstrap Penguins *P. antarctica*, breeding at Ardley Island (62°13'S, 58°55'W), King George Island, Antarctica in 1991, showed that for wearing periods between 3 and 24 h for foraging trips with a mean length 18.9 km (SD 17.5) the mean error incurred due to drift (derived by comparing known start and end positions of the birds with calculated data) was 1.2 km (SD 1.8). This error can be reduced to less than half, with maximum errors occurring at the mid-point of the foraging trip, by superimposing the known start and end points and correcting the track to accord.

RESULTS AND DISCUSSION

Our ability to determine bird movements lies, to a large extent, on the scale over which we have to operate and the temporal resolution which we can achieve. Temporal and spatial resolution cannot always be easily separated from each other but, in general, the greater the resolution in either of these parameters the more likely we are to be able to determine the reason for the movements we observe, assuming that we have data of equivalent quality on the environment through which the animal moves. Thus we may go beyond simple description of habitat use, moving into the realms of behaviour and the way in which the study animal interacts with the environment. This is particularly true when we consider movements over a scale of metres and will be examined below.

Determination of scale-dependent processes in bird movements using transmission telemetry.

In order to put archival tag tracking technology into perspective, however, it is appropriate to give a brief over-view of the qualities and limitations of transmission telemetry, this currently being the major methodology being used to determine bird movements.

Radio-telemetry can theoretically adhere to a methodology that advocates taking a positional fix of the radio-tagged bird very often (e.g. once every 15 s) but such temporal precision is generally meaningless due to the quality of the spatial resolution. This latter is dependent *inter alia* on the angular resolution of the emitted signal by both receivers, the reception angles of the two receivers relative to each other and the distance between the transmitter and the receivers. All these factors result in an error polygon which may be up to several kilometres in any one dimension (for discussion of this see White & Garrot 1990). Ultimately, radio-telemetry can only be used where the receivers have line of sight contact to the transmitters so that where the curvature of the earth, or intervening mass (e.g. Wanless *et al.* 1993), hinders transmission, other systems must be deployed.

Satellite tracking telemetry (e.g. Jouventin & Weimerskirch 1990) has proved invaluable for elucidating movements of birds ranging hundreds of kilometres although intervening mass between transmitter and receiver can still effectively stop transmission (e.g. Bost *et al.* 1997). Spatial resolution is good to within a hundred metres or so for the best quality fixes but such high quality fixes occur relatively rarely (Brothers *et al.* 1998 for discussion - but see also Burns & Castellini 1998). The number of potential fixes is determined by the path of the orbiting satellite and the position of the bird. There are markedly less fixes at the equator than at the poles due to the polar orbit of the satellite (Taillade 1992) and the number of fixes per unit time is not constant which tends to give an apparent temporal bias in the resolution of movements and derived parameters (such as travelling speed) if the user is not careful (e.g. Hull 1997, Wilson 2001).

Global Positioning Systems (GPS) have not, to date, been used on seabirds although they have been deployed on some marine mammals (e.g. Sisak 1998). They can only operate when the animal is above the surface but can acquire a positional fix (stored on board) within about 30 s with an accuracy of some tens of metres or even metres if differentially corrected (Kaplan 1996). These systems are not dependent on overpasses from Argos satellites, as are satellite tracking systems (see above), and thus can acquire fixes at any time virtually anywhere in the world (Kaplan 1996). Although currently too large to be deployed on most seabirds the rate at which units are being reduced in size means that they are likely to be deployed for this purpose within a year or two.

Determination of scale-dependent processes in bird movements using archival tags

Although archival tags are theoretical particularly useful for determining animal movements over long periods and when the surrounding environment does not lend itself to transmission of radio waves, the units have to be recovered in order to access the data. This is a serious drawback and means that it is inappropriate to equip

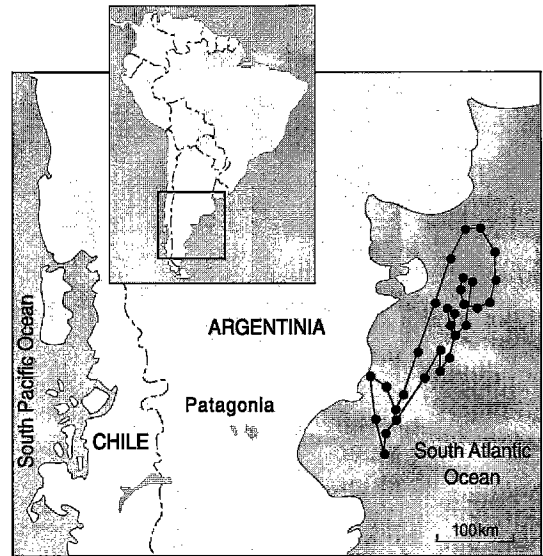


Fig. 1. Movements of a Magellanic Penguin during October and November 1996 as determined by a GLS unit. The bird was engaged in a foraging trip which lasted 21 days during which time its mate incubated the clutch at Punta Loberia, Argentina.

nomadic animals with this technology. The extent to which birds associated with a particular area can be recovered varies substantially between species. In those species which have well-defined nest sites recovery of units may be problematic but ultimately, the necessity of recovery acts as a policing policy often not present in transmission studies; only in those individuals equipped with appropriate minimum stress (e.g. Krause 2000), and which do not incur device-induced aberrant behaviour (Calvo & Furness 1992) will it be possible to recover the units and thus access the data.

Global Location Sensing (geolocation)

Global Location Sensing gives low spatial and temporal resolution, although the temporal resolution is constant, being two fixes every 24 hours (Wilson *et al.* 2001; Fig. 1). The main advantage in GLS technology is that it is relatively small and can thus be deployed on increasingly smaller birds for longer periods with less likelihood of aberrant device-induced effects (Calvo & Furness

1992 for review). This technology has proved able to resolve, for example, that Magellanic Penguins *Spheniscus magellanicus* breeding at or near Peninsula Valdes (42°04'S, 63°37'E), Argentina during the course of *ca.* three weeks foraging trips selectively visit fronts during the incubation period (Wilson *et al.* 1995) as well as to document the large scale movements of Gentoo *Pygoscelis papua* and Chinstrap *Pygoscelis antarctica* penguins and Black-browed Albatrosses *Diomedea melanophris* over 8 months during winter when these birds are fully pelagic (Wilson *et al.* 1998a, b; Grémillet *et al.* 2000). More recently, Wandering Albatrosses *Diomedea exulans* that abandoned breeding have been tracked for 13 months during their notoriously long subsequent sojourns at sea (Weimerskirch & Wilson unpubl. data). Tracking albatrosses continuously over such long periods using other technology has not yet been possible.

Dead Reckoning

For really fine scale resolution of movement in 3 dimensions (over a scale of m) the only system that is currently applicable to birds is dead reckoning. The absolute quality of the positional fixes depends critically on knowing the location of start and/or end point of the track since without this the determined movements cannot be put into a geographic context. Irrespective of this, however, the relative position of each fix compared to other fixes within the same track is dependent on the distance and time elapsed between compared fixes; as fixes get closer together in space and time, so their relative errors diminish. This occurs because drift errors and sensor inaccuracies tend to accumulate over time. Comprehension of this is critical for interpretation of behaviours exhibited by the animal in question both in terms of behaviour in response to the environment and behavioural sequencing. If the position of the animal with respect to its environment is not known, then observed movements cannot be correlated with environmental features, however, certain movement patterns may become apparent as characteristic of a species irrespective of this. This will be

examined for penguins over a variety of scales resolvable using dead reckoning technology.

Penguins foraging for chicks typically describe a looping course, generally over a scale of kilometres or tens of kilometres, consisting of rapid movement away from the colony, a period where birds tend to move approximately parallel to the colony and a final phase where the birds move virtually directly back to the colony (Fig. 2a - cf. Bost *et al.* 1997). The necessity of outward- and inward-moving phases is given by all central place foragers (Orians & Pearson 1979). The directness and extent of both these phases, however, is determined by the likelihood of prey encounter at different distances from the colony (cf. Birt *et al.* 1987) and the time and energetic costs and benefits of effectively foraging at particular distances from the central place (Kamil *et al.* 1987). Even at the complete foraging trip scale, some aspects of the decision processes responsible for the observed movements can be alluded to by examining the extent to which penguins allocate time to searching, rather than moving to and from the colony, during the various phases of the trip, even in the absence of prey encounter. This can be done by considering depth utilisation with respect to the directness of the course taken by the bird (Fig. 2b) because, for a given distance swum underwater, more distance allocated to vertical displacement results in less effective horizontal movement away from the colony. Similarly, birds can decide to invest energy by moving laterally rather than directly away from the colony (Fig. 2b). It can be seen in the example shown in Fig. 2, that the monitored Adélie penguin *Pygoscelis adeliae* sometimes invested considerable effort in searching for prey at a site proximate to the colony (e.g. at time $t = ca. 7$ h), without finding any, before giving up to move quickly to a site further away and searching again. Note, however, that in this example the allocation of distance with respect to vertical movement does not mirror that of lateral displacement indicating that the bird was essentially moving directly away from the colony in the horizontal plane during much of the outward phase while allocating proportionately

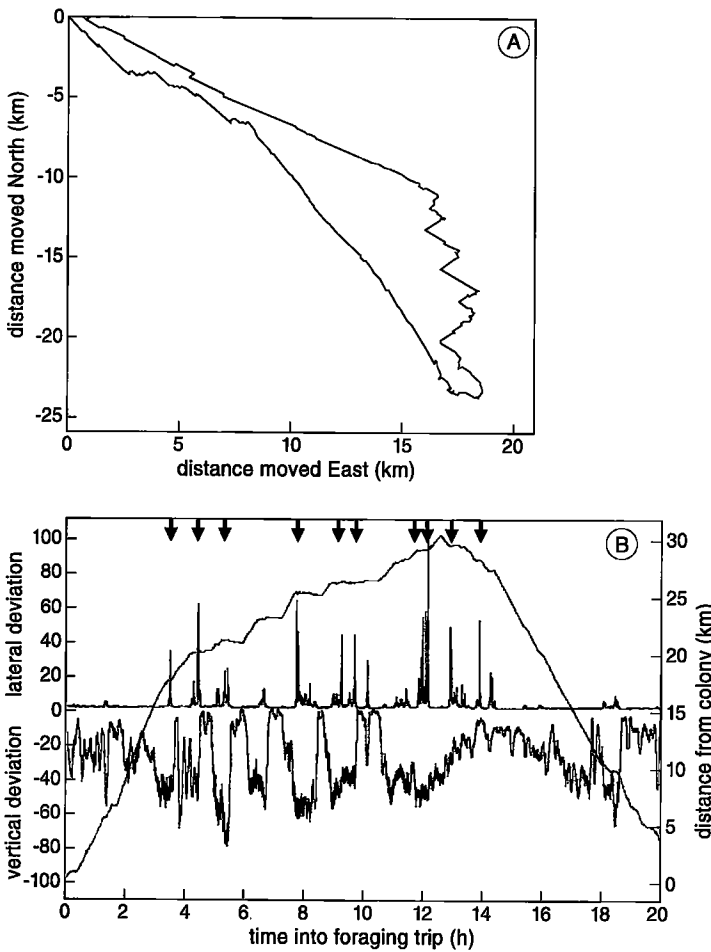


Fig. 2. (A) Movements of an Adélie Penguin foraging for small chicks at Ardley Island, Antarctica as determined by a dead reckoner during December 1991. The bird was a sea for *ca.* 20 hours. (B) Vertical (lower line) and lateral (centre line repeatedly departing from the 0 mark) deviation from a straight line course from the bird whose foraging movements are shown in (a). The lateral deviation is given by the total distance swum over five minutes divided by the straight line distance swum over that time. The vertical deviation is the sum of the vertical distance swum over five minutes divided by four (to allow comparisons over different scales). Both deviations are shown as running values. The upper line shows the distance of the bird from the breeding site and arrows show where prey was captured.

more time searching the depths. That, in this case, the penguin initially preferentially deviated vertically rather than laterally has implications for the bird's perceived prey distribution *viz.* that the vertical distribution of the prey is not constant down the water column, prey being more likely to occur in deeper waters than closer to the surface (cf. Wilson *et al.* 1996). In fact, consideration of *Pygoscelis* penguin foraging tracks in general indicates that birds generally do not deviate laterally substantially from a direct heading away from the breeding site unless they have actually encountered prey (prey encounter being determined by stomach temperature loggers; Wilson *et al.* 1995).

Most penguins feed on aggregating prey species (Williams 1995) so that encounter and exploitation of prey until oxygen reserves are depleted does not preclude subsequent exploitation during future dives, provided the patch can be re-located. Again, dead reckoning can be used to examine the decisions that foraging penguins make that result in movements apparently geared to re-locating a previously exploited patch. This occurs over a scale of tens or hundreds of metres. In fact, after having encountered a prey patch, penguins appear to search selectively the area in which they encountered prey by exhibiting considerable non-directional movement and meandering resulting in a more effective quartering of the area (Fig. 3).

This behaviour continues for a specific period before the bird abandons its localised search (cf. 'giving up time' - Krebs 1978) and begins to exhibit directional movement again (Fig. 2). Note, however, that subsequent to prey encounter, birds often change their highly directional movement away from the colony to a more parallel course.

To consider how penguin movement changes after prey have been located we have to examine movement on a much finer scale with high resolution. Penguins are pursuit divers and, for the most part, are considered to catch their prey by swimming after them (e.g. Rand 1960; Zusi 1975; Wilson 1996) although penguins of the genus *Spheniscus* are reported to engage in herding behaviour (Wilson *et al.* 1987). This means that the penguin movement recorded during prey pursuit and capture will be primarily determined by the movements of the prey itself and would be carried out over a scale of metres. This being the case, we would expect, perhaps, that penguin movements during prey pursuit would differ according to prey type. To date we do not have enough data to examine this in detail. However, after encountering krill *Euphaussea superba*, *Pygoscelis* penguins apparently move rapidly and erratically around within the swarm, picking up individuals at a high rate (Falla, quoted in Zusi 1975). This behaviour results in a movement with little overall displacement in the otherwise well-ordered, fairly directional movement of searching penguins (Fig 3). The extent to which information recorded by dead reckoning systems genuinely represents the movements of the feeding individual depends, however, largely on the recording frequency. Data from a Magellanic Penguin *Spheniscus magellanicus*, recorded at a frequency of 0.5 Hz show the movements for a bird taking what was apparently a single lone prey item (Fig. 4) although clearly, even here, the resolution of movements would be greatly enhanced by higher recording frequencies.

Thus, examination of the movement of foraging penguins over a series of different scales, ranging from tens of kilometres to fractions of a metre enables us to identify the processes that are responsible for observed changes in movement as

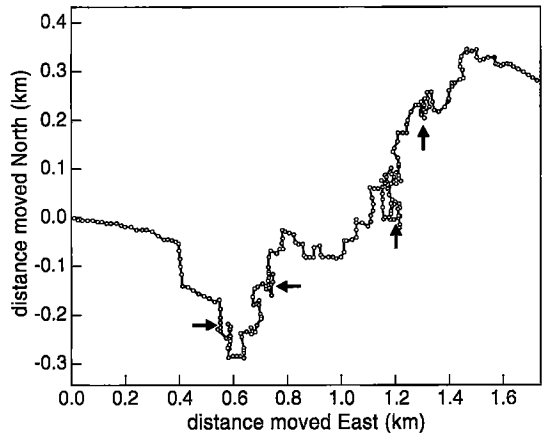


Fig. 3. Virtual straight line travel by an Adélie Penguin followed by meandering subsequent to prey encounter (shown by arrows). After a period of encountering no prey during a meandering phase the bird switches to straight line travel again (top right of figure). This bird was foraging for small chicks at Ardley Island and was equipped with a dead reckoner during December 1991.

well as to elucidate 'ground rules' by which birds operate during the searching process.

For future work, very high sampling frequencies of dead reckoning systems will allow examination of movement on a scale of centimetres. This has just recently been done on free-living birds (sampling frequencies of 30 Hz on systems used during December 1999 on Magellanic Penguins in Argentina by A. Steinfurth, unpubl. data). Here, minute changes in body orientation brought about by the muscular process involved in the generation of movement can be determined and in the data set referred to above it is even possible to determine flipper beat frequency (A. Steinfurth, unpubl. data). Thus, the process of dead reckoning can be used to examine the dynamics of movement in an anatomical sense. This may prove useful for those workers attempting to understand the complexities of locomotion (e.g. Bannasch 1995).

Although archival tags for determination of bird movement are subject to a number of errors, they are highly complimentary to existing radio-

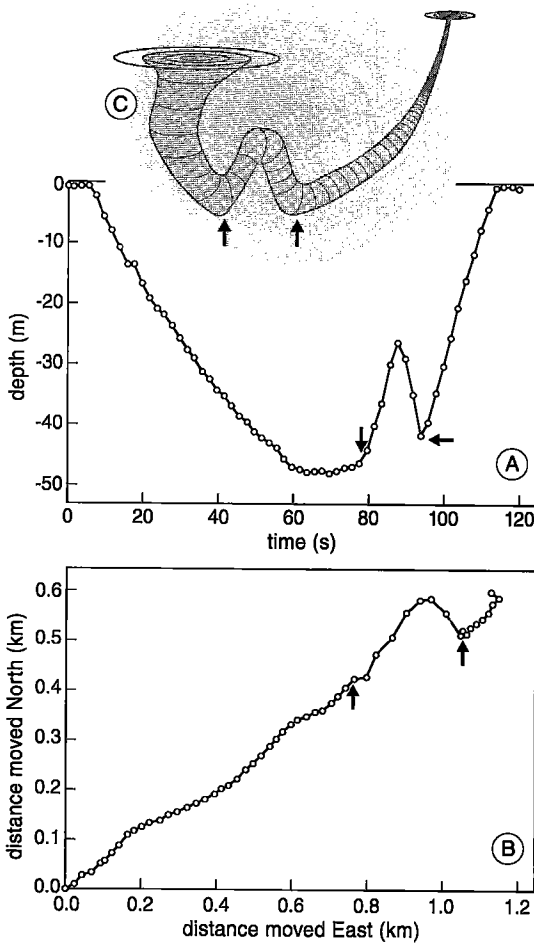


Fig. 4. (A) Dive profile for a single dive where a Magellanic Penguin chased (arrow) and caught (arrow) a prey item. Recording frequency was 0.5 Hz. The bird was equipped with a dead reckoner at Peninsula Valdes ($42^{\circ}04'S$, $63^{\circ}37'E$), Argentina during November 1997 and was foraging for two chicks. (B) Lateral displacement for the bird whose dive profile is shown in (b). The onset of the chase and capture are shown by arrows. (C) Schematic diagram showing the three-dimensional movements of the bird whose movements are defined in (a) and (b).

telemetric methodologies currently being used and are likely to compliment e.g. video records and other techniques currently being developed (Davis *et al.* 1999). The future development of

archival tags promises to reveal exciting new aspects of bird decision making processes and, in order to put such decisions in an accurate environmental context as possible, workers should consider combining systems so that the weakness on one system can be eliminated by the strengths of the other.

ACKNOWLEDGEMENTS

Much of the work presented in this paper was conducted under the auspices of projects funded by the Deutsche Forschungsgemeinschaft. I am grateful to Dieter Adelung, Rudi Bannasch, Boris Culik, Gunther Dorn, Stefan Garthe, Mandy Kierspel, Uwe Lenz Alejandro Scolaro and Antje Steinfurth for help at various stages of the project. I am also grateful to Yan Ropert-Coudert for using his skills to bail me out when the postal service dropped me in it.

REFERENCES

- Bannasch R., R.P. Wilson & B. Culik 1984. Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J. exp. Biol.* 194: 83-96.
- Bannasch R. 1995. Hydro-dynamics of penguins - an experimental approach. In: Dann P., I. Norman & P. Reilly (eds) *The penguins - ecology and management*: 141-176. Surrey Beatty & Sons, Chipping Norton, Australia.
- Benvenuti S., F. Bonadonna, L. Dall'Antonia & G.A. Gudmundsson 1998. Foraging flights of breeding Thick-billed Murres (*Uria lomvia*) as revealed by bird-borne direction recorders. *Auk* 115: 57-66.
- Birt V.L., T.P. Birt, D. Goulet, D.K. Cairns & W.A. Montevecchi 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. *Mar. Ecol. Progr. Ser.* 40: 205-208.
- Bost C.A., J.Y. Georges, C. Guinet, Y. Cherel, K. Pütz, J-B. Charrassin, YX. handrich, T. Zorn, J. Lage & Y. Le Maho 1997. Foraging habitat and food intake of satellite-racked King Penguins during the austral summer at Crozet Archipelago. *Mar. Ecol. Progr. Ser.* 150: 21-33.
- Brenning U. 1989. Der Zug des Alpenstrandläufers (*Calidris alpina*) auf der Grundlage von Beringungen, Wiederfinden und Kontrollen in der DDR. *Ber. Vogelwarte Hiddensee* 9: 16-38.
- Brothers N., R. Gales, A. Hedd & G. Robertson 1998.

- Foraging movements of the Shy Albatross *Diomedea cauta* breeding in Australia; implications for interactions with long-line fisheries. *Ibis* 140: 446-457.
- Bub H. 1996. Bird trapping and bird banding. Cornell University Press, USA.
- Burns, J.M. & M.A. Castellini 1998. Dive data from satellite tags and time depth recorders: a comparison in Weddell Seal pups. *Mar. Mamm. Sci.* 14: 750-764.
- Calvo B. & R.W. Furness 1992. A review of the use and the effects of marks and devices on birds. *Ringling & Migr.* 13: 129-151.
- Davis R.W., L.A. Fuiman, T.M. Williams, S.O. Collier, W.P. Hagey, S.B. Kanatous, S. Kohin & M. Horning 1999. Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 283: 993-996.
- Freeman S.N. & B.J.T. Morgan 1990. Studies in the analysis of ring-recovery data. *Ring* 13:271-288.
- Grémillet D., R.P. Wilson, S. Wanless & T. Chater 2000. Mesoscale movements in breeding and non-breeding Black-browed Albatrosses foraging over the Patagonian Shelf. *Mar. Ecol. Progr. Ser.* 195: 269-280.
- Harris M.P. 1984. Movements and mortality patterns of North Atlantic Puffins as shown by ringing. *Bird Study* 31: 131-140.
- Hill R.D. 1994. Theory of geolocation by light levels. In: Le Boeuf B.J. & R.M. Laws (eds) *Elephant Seals: population ecology, behavior and physiology*: 227-236. Univ. California Press, Berkeley, California, USA.
- Hochscheid S., & R.P. Wilson 1999. A new method for the determination of at-sea activity in sea turtles. *Mar. Ecol. Progr. Ser.* 185: 293-296.
- Hull C.L., M.A. Hindell & K. Michael 1997. Foraging zones of Royal Penguins, and their association with oceanographic features. *Mar. Ecol. Progr. Ser.* 153: 217-228.
- Jouventin P. & H. Weimerskirch 1990. Satellite tracking of Wandering Albatrosses. *Nature* 232: 746-748.
- Kamil A.C., J.R. Krebs & H.R. Pulliam 1987. Foraging behaviour. Plenum Press, New York.
- Kaplan E.D. (ed.) 1996. *Understanding GPS: principles and Applications*. Artech House, Norwood, MA.
- Kenward R.E. 1987. *Wildlife radio tagging*. Academic Press, San Diego.
- Krause M. 2000. Entwicklung einer Betäubungsmethode zur Streßminderung beim Fang von Vögeln zu wissenschaftlichen Zwecken. Ph.D.-thesis Tierärztlichen Hochschule, Hannover.
- Krebs J. R. 1978. Optimal foraging: Decision rules for predators. In: Krebs J.R. & N.B. Davies (eds) *Behavioural Ecology*: 23-63. Blackwell Scientific Publications, Oxford.
- Noer H. 1991. Distributions and movements of Eider *Somateria mollissima* populations wintering in Danish waters analysed from ringing recoveries. *Dan. Rev. Game Biol.* 14: 1-32.
- Orians G.H. & N.E. Pearson 1979. On the theory of central place foraging. In: Horn D.J., R.D. Mitchell & G.R. Stairs (eds) *Analysis of Ecological Systems*: 154-177. Ohio State University Press, Columbus, USA.
- Priede G. & S.M. Swift. 1996. *Wildlife telemetry: remote tracking and monitoring of animals*. Ellis Horwood, Chichester.
- Prinzinger R. & E. Bezzel 1990. *Ornithologie*. 2nd ed. Ulmer, Stuttgart.
- Rand R.W. 1960. The biology of guano-producing seabirds. The distribution, abundance and feeding habits of the Cape Penguin *Spheniscus demersus* off the southwestern coast of the Cape Province. Investigational Report 41, Department of Commerce and Industries, Division of Sea Fisheries, Union of South Africa. Cape Town, South Africa.
- Sisak M.M. 1998. Animal-borne GPS and the deployment of a GPS based archiving datalogger on Hawaiian Monk Seal. *Mar. Techn. Soc. J.* 32: 30-36.
- Taillade M. 1992. Animal tracking by satellite. In: Priede I.M. & S.M. Swift (eds) *Wildlife Telemetry*: 149-160. Ellis Horwood, Chichester.
- Wanless S., T. Corfield, M.P. Harris, S.T. Buckland & J.A. Morris 1993. Diving behaviour of the Shag *Phalacrocorax aristotelis* (Aves: Pelecaniformes) in relation to water depth and prey size. *J. Zool., Lond.* 231: 11-25.
- Weimerskirch H. 1998. Foraging strategies of Indian Ocean albatrosses and their relationships with fisheries. In: Robertson G. & R. Gales (eds) *Albatross biology and conservation*: 168-179. Surrey Beatty & Sons, Chipping Norton.
- Weimerskirch H., A. Catard, P.A. Prince, Y. Chereil & J.P. Croxall 1998. Foraging White-hinned Petrels *Procellaria aequinoctialis* at risk: from the tropics to Antarctica. *Biol. Conserv.* 87: 273-275
- White G.C. & R.A. Garrot 1990. *Analysis of wildlife radio tracking data*. Academic Press, San Diego, USA.
- Williams T.D. 1995. *The penguins*. Oxford University Press, Oxford.
- Wilson R.P., P.G. Ryan, A. James & M-P. Wilson 1987. Conspicuous colouration may enhance prey capture in some piscivores. *Anim. Behav.* 35: 1558-1560.
- Wilson R.P. & M-P. Wilson 1988. Dead reckoning: a new technique for determining penguin movements at sea. *Meeresforschung* 32: 155-158.
- Wilson R.P., M-P. Wilson, R. Link, H. Mempel & N.J. Adams 1991. Determination of movements of Afri-

- can Penguins using a compass system: Dead reckoning may be an alternative to telemetry. *J. exp. Biol.* 157: 557-564.
- Wilson R.P., J.-J. Ducamp, G. Rees, B.M. Culik & K. Niekamp 1992. Estimation of location: Global coverage using light intensity. In: Priede, I.M. & S.M. Swift (eds) *Wildlife Telemetry*: 131-134. Ellis Horwood, Chichester.
- Wilson R.P., B.M. Culik, R. Bannasch & H.H. Driesen 1993. Monitoring penguins at sea using data loggers. *Biotelemetry* 12: 205-214.
- Wilson R.P., J.A. Sclaro, G. Peters, S. Laurenti, M. Kierspel, H. Gallelli & J. Upton 1995a Foraging areas of Magellanic Penguins *Spheniscus magellanicus* breeding at San Lorenzo, Argentina during the incubation period. *Mar. Ecol. Progr. Ser.* 129: 1-6.
- Wilson R.P., K. Pütz, D. Grémillet, B.M. Culik, M. Kierspel, J. Regel, C. Bost, J. Lage & J. Cooper 1995b. Reliability of stomach temperature changes in determining feeding characteristics of seabirds. *J. exp. Biol.* 198: 1115-1135.
- Wilson R.P. 1996. Foraging and feeding behaviour of a fledgling Magellanic Penguin *Spheniscus magellanicus*. *Mar. Orn.* 24: 55-56.
- Wilson R.P., G. Peters, B. Culik & R. Bannasch 1996. Diving behaviour of Gentoo penguins at Ardley Island, Antarctica. *Mar. Biol.* 126: 153-162.
- Wilson R.P., K. Pütz, G. Peters, B. Culik, J.A. Sclaro, J.-B. Charrassin & Y. Robert-Coudert 1997. Long term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl. Soc. Bull.* 25: 101-106.
- Wilson R.P., B. Alvarez, L. Latorre, D. Adelung, B. Culik & R. Bannasch 1998a. The movements of Gentoo Penguins *Pygoscelis papua* from Ardley Island, Antarctica. *Polar Biol.* 19: 407-413.
- Wilson R.P., B.M. Culik, P. Kosiorek & D. Adelung 1998b. The over-winter movements of a Chinstrap Penguin. *Polar Record* 34: 107-112.
- Wilson R.P., G. Rees, J. Lage, K. Pütz, M. Kierspel, J. Cooper, C.A. Bost & B. Culik 2001. Determination of animal position using changes in diel light intensity. *Proc. V. European Conference on Wildl. Telemetry* (in press).
- Wilson R.P. 2001. Determination of foraging behaviour of free-ranging endotherms at sea: geographic position, local movement and ingestion. *Proc. V. European Conference on Wildl. Telemetry* (in press).
- Winkel W. & M. Frantzen 1991. Ringfund-Analyse zum Zug einer niedersächsischen Population des Trauerschnäppers *Ficedula hypoleuca*. *Vogelkdl. Ber. Niedersachsen* 23: 90-98.
- Zusi R.L. 1975. An interpretation of skull structure in penguins. In: Stonehouse B. (ed.) *The biology of penguins*: 59-84. Macmillan Press, London.

SAMENVATTING

Twee methoden voor het volgen van verplaatsingen van vogels worden besproken: *Global Location Sensing* (waarbij de positie van het dier wordt bepaald uitgaande van de daglengte en de lokale vaststelling van het midden van de dag) en *Dead Reckoning* (berekeningen van vliegroutes aan de hand van kompaskoersen). Beide technieken worden besproken met het oog op hun bruikbaarheid op verschillende schalen. Onderzoek aan pinguïns liet zien dat, ofschoon de eerste methode niet bloot staat aan fouten door verdrijving, de temporele en ruimtelijke resolutie zodanig is, dat dit systeem alleen gebruikt kan worden om verplaatsingen over ten minste enkele tientallen kilometers in kaart te brengen. De tweede methode is veel preciezer en zou gebruikt kunnen worden over zowel afstanden van enkele tientallen kilometers als enkele centimeters. Posities die met deze methode worden berekend, zijn preciezer naarmate de onderlinge afstand kleiner is, maar in de loop van een lange reeks kan door 'verdrijving' een steeds grotere fout ontstaan. De hoge temporele en ruimtelijke resolutie van 'dead reckoning' betekent dat beslissingen van het dier met betrekking tot zijn verplaatsingen kunnen worden gevolgd en dit kan worden gedemonstreerd aan de hand van bij pinguïns verzamelde gegevens over afstanden variërend van tientallen kilometers tot enkele meters. Toekomstig onderzoek zal zich concentreren op kleinschalige verplaatsingen in een driedimensionale omgeving (onder water), zoals dat, althans tot op dit moment, nog niet met andere systemen kan worden opgelost. (CJC)

Received 2 October 1999, accepted 10 May 2000
Corresponding editor: Lukas Jenni