J. Field Ornithol., 58(2):118–125

TRAVELING SPEED AND FORAGING RANGE OF MACARONI AND ROCKHOPPER PENGUINS AT MARION ISLAND

CHRISTOPHER R. BROWN
Percy FitzPatrick Institute of African Ornithology
University of Cape Town
Rondebosch 7700
South Africa

Abstract.—Traveling speeds of breeding Macaroni and Rockhopper Penguins at Marion Island averaged 7.5 and 7.4 km/h, respectively. Macaroni Penguins rearing old chicks and Rockhopper Penguins rearing younger chicks spent 38% and 30% respectively of their time at sea traveling. Foraging ranges were 59 to 303 km for Macaronis during late chick rearing and 4 to 157 km for Rockhoppers during early chick rearing. Diet, chick feeding rates, traveling speed and probably foraging range are very similar for both species, and the principal factor segregating the two species at this time appears to be the three week difference in the onset of breeding.

VELOCIDAD DE MOVIMIENTO Y EXTENSIÓN DE LAS ÁREAS DE FORRAJEO DE LOS PINGÜINOS *EUDYPTES CHRYSOLOPHUS* Y *E. CHRYSOCOME*

Sinopsis.—En la isla Marion del Océano Índico, se encontró que la velocidad de movimiento de los pingüinos *Eudyptes chrysolophus* y *E. chrysocome* en sus viajes en búsqueda de alimentos para sus crías, promedió 7.5 y 7.4 km/h respectivamente. Durante la cría de polluelos maduros, *E. chrysolophus* pasa el 38% de su tiempo en el mar, el otro tipo de pingüino el 30% en la cría de pichones más jovenes. Las áreas de forrajeo se extienden de 59 a 303 km para *E. chrysolophus* durante la cría de polluelos maduros y de 4 a 157 km en *E. chrysocome* al criar pichones jovenes. La dieta, cantidad de alimento llevado a los polluelos, velocidad de movimiento y probablemente hasta las áreas de forrajeo son similares para ambas especies de pingüinos. El factor que aparentemente segrega estos pingüinos, parece ser las tres o cuatro semanas de diferencia que hay entre el comienzo de la reproducción de estas especies.

Penguins are difficult to observe at sea because of their low profiles, and observations of their foraging behavior are rare. However, recent development of remote sensing devices has greatly increased our potential for understanding penguin behavior at sea (e.g., Kooyman et al. 1971, 1983; Lishman and Croxall 1983; Wilson and Bain 1984a,b). In this study, I investigated the traveling speed and foraging range of breeding Macaroni (*Eudyptes chrysolophus*) and Rockhopper Penguins (*E. chrysocome*) at Marion Island, southern Indian Ocean, using an autoradiographic speed meter (Wilson and Bain 1984b), with the aim of determining any species specific differences.

An estimated 405,000 pairs of Macaroni and 93,000 pairs of Rockhopper Penguins breed sympatrically at Marion Island (Williams et al. 1979, FitzPatrick Institute, unpubl. data). Considerable overlap occurs in their breeding periods and, especially, in their chick rearing. Feeding rates of chicks (Williams 1982) and the diets fed to chicks (Brown and Klages 1987, Horne 1985, Williams and Laycock 1981) are broadly similar. Williams (1982) suggested, however, that potential interspecific

competition for food could be reduced during chick rearing by differences in type or size of prey, foraging depth, or speed at which the parents travel. Traveling speed in part determines foraging range, which for both species at Marion Island has been estimated at about 95 km (Williams and Siegfried 1980). At South Georgia, the potential foraging range of Macaroni Penguins has been estimated at up to 115 km, although the birds may in fact forage on the edge of the continental shelf only 50 km away (Croxall and Prince 1980). These figures are generally based on estimated traveling speed and time spent away from the nest between chick feedings.

Traveling speeds reported for penguins range from 7 to 12 km/h (Clark and Bemis 1979, Kooyman 1975). Macaroni and Rockhopper Penguins reportedly swim at 8.2 and 7.8 km/h respectively (Clark and Bemis 1979). These are maximum speeds measured for penguins swimming in a tank and may not represent speeds attained at sea. Furthermore, it is now apparent that penguins do not swim all the time they are at sea and neither do they necessarily swim a straight course. The ratio of time spent swimming to time at sea in Gentoo (*Pygoscelis papua*), Chinstrap (*P. antarctica*) and Adélie Penguins (*P. adeliae*) is highly variable (Adams and Wilson 1987, Wilson et al. 1986). Consequently, large overestimates may occur when estimating foraging range from chick feeding rates if the parents are assumed to be traveling for the entire time they are away from the nest.

METHODS

The study was carried out at Marion Island (46°52′S, 37°51′E) between 7 January and 24 February 1985. A colony of Rockhopper Penguins breeds near the research station and a small colony of Macaroni Penguins breeds about 1 km away. Both species were rearing chicks during the course of the study. Ages of Rockhopper chicks ranged from about 7 to 30 d, whereas Macaroni chicks ranged from 26 to 62 d.

Twenty-six speed meters (Wilson and Bain 1984b) were attached to Rockhoppers and 16 to Macaronis. Each meter consisted of a spring-mounted, polyurethane bung enclosed in a tube. A radioactive, phosphorus-32 bead was inserted into the bung and a sachet of X-ray sensitive film was taped to the outside of the tube (see Wilson and Bain 1984b for illustrations and operation details). In contrast to Wilson and Bain (1984b), who attached their devices to the front of their penguins using harnesses, the devices in the present study were attached with hose-clamps to the feathers on the dorsal midline of the penguins. The mass of each device in air was about 2.5 g.

Penguins were caught at their respective colonies, weighed, and, after attachment of meters, were released. The Rockhopper colony was checked frequently each day for metered birds departing and returning: the Macaroni colony was checked once or twice daily. When next observed, birds with meters were recaptured, weighed, and the meters removed. Because of low isotope activity in some beads and the short feeding interval of

Rockhopper Penguins during early chick rearing, some birds were allowed to make two or more foraging trips before recapture to ensure sufficient film exposure time.

The film (Kodak Direct Exposure Film) was processed for 3 min at 24 C in Kodak GBX developer and fixed for 3 min in Kodak GBX fixer. Optical density of the developed film was measured with a transmission densitometer. Traces typically showed two discrete blackened patches corresponding to the traveling speed and the zero position when the bung was stationary. The traveling speed and total distance traveled were calculated from the traces (see Wilson and Bain 1984b). Wilson et al. (1986) report that devices attached to free-ranging Jackass Penguins (*Spheniscus demersus*) affect traveling speed. The magnitude of the effect was related to the cross-sectional area of the device as a percentage of penguin cross-sectional area. Meters attached to Macaroni and Rockhopper Penguins had cross-sectional areas less than 2.0% that of the birds, and the reduction in traveling speed was estimated to be less than 5%.

Foraging range was estimated from total distance traveled and number of foraging trips made between release and recapture. A number of assumptions were necessary. For Rockhopper Penguins, when devices were left on for more than one foraging trip, the birds were assumed to have traveled the same distance on each trip. If the durations of two or more foraging trips differed, distance traveled was assumed to be proportional to duration of each trip (i.e., if a bird made one 12 h trip followed by one of 36 h before recapture, that bird traveled three times farther during the longer trip than the shorter one). Because visits to the Macaroni colony were less frequent and adults did not remain long at the colony when feeding older chicks (pers. obs.), the birds usually completed several foraging trips before recapture. The number of foraging trips made was estimated from the approximate age of chicks in the colony and the known feeding frequency of chicks of this age (Williams 1982). The birds were assumed to have traveled the same distance each trip and in all cases were assumed to have traveled directly to and from the feeding grounds on a constant heading. Consequently, foraging range was overestimated.

RESULTS AND DISCUSSION

Thirteen of 16 devices on Macaroni Penguins and 19 of 26 on Rockhopper Penguins were recovered, but only five films from Macaroni and seven from Rockhopper Penguins had useable traces. Water or light leaks in the sachets were the major cause of ruined traces, and some films showed no traces because the bung twisted about its axis as the spring was compressed so that the radio-isotope no longer exposed the film.

Three meters from Macaroni Penguins were recovered 9 to 16 d after deployment, whereas all those from Rockhopper Penguins were recovered within 7 d. A further two devices were recovered from Macaroni Penguins 53 d after release and included the pre-molt foraging trip which

lasts between 4 and 5 wks. Results obtained from the developed traces from Macaroni and Rockhopper Penguins are presented in Tables 1 and 2, respectively.

Traveling speed.—The mean (±1 SD) measured traveling speed of Macaroni Penguins was 7.5 ± 0.5 km/h (range 7.0–8.2 km/h) and that of Rockhopper Penguins was 7.4 ± 0.5 km/h (range 6.9–8.1 km/h), both within the range recorded for several other penguin species (Adams and Wilson 1987, Clark and Bemis 1979, Kooyman 1975, Wilson and Bain 1984b). The traveling speeds obtained from free-ranging Macaroni and Rockhopper Penguins in the present study are only slightly lower than the maximum speeds measured by Clark and Bemis (1979) and, presumably, represent the most economical speeds.

There was no perceptible variation in individual traveling speed, each bird showing typically only one discrete traveling trace even when devices were carried for several foraging trips and, in the case of two Macaroni Penguins, for the extended pre-molt foraging trip. Adams (in press) and Adams and Wilson (1987) observed the same for King Penguins (*Aptenodytes patagonicus*) and Gentoo Penguins and concluded that they forage solitarily since, if birds foraged in groups, traveling speed would have to vary to maintain group cohesion. Macaroni and Rockhopper Penguins both leave and return to their colonies in groups (pers. obs.), but these may only be maintained while they pass through the inshore area where predators, in particular Killer Whales (*Orcinus orca*), are likely to be encountered. Individuals of both species, returning ashore in conspecific groups, frequently have totally different food in their stomachs (pers. obs.), further suggesting that they forage individually.

Time spent traveling.—Macaroni and Rockhopper Penguins feeding older chicks spend little time ashore. Consequently, the time between release and recapture of the Macaronis was a reasonable estimate of the time spent at sea. The amount of time Rockhoppers spent at sea was estimated from their presence at the colony during the frequent checks for returning birds. Macaroni Penguins spent 38.0 ± 23.0% of their estimated time at sea swimming at speed, whereas Rockhopper Penguins spent 29.8 ± 18.0%. The difference is not significant ($P > 0.5$).

The amount of time at sea spent traveling, calculated from the density of the traveling trace, included time spent commuting to and from the feeding area plus time spent feeding underwater, but did not include time spent swimming on the surface or porpoising, when the meters are out of the water and not recording. However, Adélie Penguins spend less than 6% of their total swimming time porpoising (Wilson et al., in press), and penguins probably travel only short distances by surface swimming (Adams and Wilson 1987, Trivelpiece et al., in press), so errors in time spent traveling and, consequently, in distance traveled are probably small.

Rockhopper chicks during the present study were 7–30 d old. Chicks of this age are fed only by females and guarded by males (Warham 1963). The feeding interval is short, usually less than 36 h in the first 2

TABLE 1. Time spent traveling, traveling speed, distance traveled and estimated foraging ranges of Macaroni Penguins.

Time at sea (h)[a]	Time spent traveling (h)	% time spent traveling	Speed km/h	Total distance traveled (km)	No. foraging trips	Estimated foraging range (km)
218.0	47.2	21.7	7.5	354	3	59
310.0	242.0	78.0	7.5	1815	3	303
386.3	125.0	32.4	8.2	1025	3	171
1269.0	306.0	24.1	7.0	2142	2 + PM	180[b]; 711
1269.0	428.0	33.7	7.2	3082	2 + PM	180[b]; 1180

[a] Assuming time spent ashore feeding chicks is negligible in relation to time spent at sea.
[b] Assuming an average foraging range of about 180 km, calculated from the three foraging ranges estimated above.
PM = Pre-molt foraging trip.

wks and less than 60 h for chicks between 16 and 30 d of age (Williams 1982). Females spend the night ashore and forage during the day, usually leaving just before first light (about 04:00) and returning in the late afternoon or soon after dark at about 19:00 (pers. obs.). Macaroni chicks during the study were older than Rockhopper chicks and were fed at longer intervals by both parents. Consequently, the breeding adult Macaroni Penguins spent more time at sea, foraged farther afield and spent a relatively greater proportion of their time traveling than did Rockhopper Penguins. Similarly, King Penguins feeding large chicks spend about 36% of their time at sea traveling, whereas those with small chicks requiring brooding spend only 19% of their time at sea traveling (Adams 1987). Gentoo Penguins, which are diurnal foragers that usually return ashore each evening, spend about 19% of their time at sea swimming and feeding (Adams and Wilson 1987).

Foraging range.—Estimated foraging ranges of Macaroni Penguins feeding chicks vary between 59 and 303 km (Table 1), although the latter estimate was from a bird which spent an unusually large proportion of its time swimming. Rockhopper Penguins ranged from about 4 to 157 km away (Table 2). Since the traveling speeds and chick feeding rates of the two species are almost identical, it seems likely that Rockhoppers forage at distances similar to Macaroni Penguins later in the season when the chicks are older. Indirect evidence for this comes both from the species composition of the Rockhopper Penguins' diet, which becomes increasingly similar to that of Macaroni Penguins later in the season, as well as from the increasing degree of digestion of the stomach contents as the season progresses (Brown and Klages 1987). Similarly, Macaroni Penguins almost cerainly forage closer to shore when their chicks are small and the feeding interval shorter. Stomach contents of Macaroni Penguins are less well digested with many intact prey items during early chick rearing (pers. obs.).

The relatively short foraging range of 95 km estimated by Williams

TABLE 2. Time spent traveling, traveling speed, distance traveled and estimated foraging ranges of Rockhopper Penguins.

Time at sea (h)[a]	Time spent traveling (h)	% time spent traveling	Speed km/h	Total distance traveled (km)	No. & duration of foraging trips	Estimated foraging range (km)
15.0	0.9	6.0	7.6	7.1	1	3.5
43.0	6.5	15.1	7.2	46.8	3 × 12 h	7.8
40.0	18.0	45.0	7.8	140.4	3 × 12 h	23.4
53.9	15.1	28.2	6.9	104.2	1 × 12 h 1 × 36 h	17.4, 34.8
54.5	17.1	31.4	7.0	119.7	2 × 12 h 1 × 24 h	15.0, 30.0
70.5	16.6	23.6	8.1	134.5	1 × 12 h 1 × 36 h	16.8, 50.4
148.0	88.2	59.6	7.1	626.2	2	156.6

[a] Estimated from observations of the approximate arrival and departure times of the birds at the colony.

and Siegfried (1980) is explained by their underestimate (4.5 km/h) of traveling speed. Croxall and Prince (1980) estimated a potential foraging range of 115 km for Macaronis at South Georgia but this was based on a chick feeding rate of once every 2 d, more typically associated with younger chicks (Williams 1982).

Two Macaroni Penguins made pre-molt foraging trips before being recaptured. These birds covered 2142 and 3082 km respectively in a period of 53 d. Both were estimated to have made two foraging trips before their pre-molt trip and these were assumed to have averaged 180 km in range (Table 1). Consequently, the estimated distances covered during the pre-molt trips were 1422 and 2362 km, with potential maximum ranges from their colony of 711 and 1181 km, respectively.

Weight changes.—Four of 5 recaptured Macaroni Penguins lost weight while at sea, the maximum weight loss being 850 g over a period of 16 d. One bird gained 1200 g over a 13-d period. Mean weight change was −20 g. Ten Rockhopper Penguins lost and seven gained weight during foraging trips. The mean weight change was −111 g. Maximum weight loss was 520 g and maximum weight gained 260 g. Five of the Rockhoppers that lost weight were observed feeding chicks, and had obviously been foraging. Since adult penguins are capable of undergoing prolonged fasts, it may be that they do not always feed for themselves but may collect food only for their chicks during some foraging trips, as suggested by Adams (1987).

Both Macaroni and Rockhopper Penguins feed predominantly on euphausiids and juvenile shrimp *Nauticaris marionis* (Brown and Klages 1987). These are abundant in the immediate vicinity of Marion Island (Boden and Parker 1986). A Rockhopper Penguin that had traveled less than 8 km from its colony was observed feeding crustaceans to its chick and also had several crustaceans caught in the hose clamps attaching the meter to its feathers. Fish species found in the diets of Macaroni and

Rockhopper Penguins were all oceanic myctophids with a broad sub-Antarctic and Antarctic distribution, as is true of the cephalopods consumed (Brown and Klages 1987).

Macaroni and Rockhopper Penguins have broadly similar diets and very similar chick feeding rates, traveling speeds and probably foraging ranges. There is, as yet, no information on the depths to which they can dive, but several penguins of similar size appear to have similar diving capabilities (Adams and Brown 1983, Lishman and Croxall 1983, Wilson and Bain 1984a). Furthermore, the similarity of the prey of Macaroni and Rockhopper Penguins make it unlikely that they forage at different depths.

The principal factor segregating the two species appears to be the timing of the breeding cycle. Macaronis begin breeding 3–4 wks before Rockhoppers and, consequently, chicks hatch earlier. Initially, Macaroni Penguins feed their chicks almost entirely crustaceans. The feeding intervals are short and the birds probably feed relatively close to their breeding sites. As the chicks age they are fed less frequently and the diet includes a large proportion of pelagic fish and cephalopods with relatively few crustaceans. Consequently, at a time when the Rockhopper chicks are hatching and are being fed frequent meals of crustaceans, the Macaroni Penguins are foraging farther afield on slightly different prey. Nevertheless, there is a period of several weeks when both species are feeding large chicks at similar intervals on similar diets. As there is probably an overlap in foraging range during this period, ecological segregation of the two species is incomplete.

ACKNOWLEDGMENTS

This research was conducted under the auspices of the South African Scientific Committee for Antarctic Research. Financial and logistical support was provided by the South African Departments of Transport and Environment Affairs. I thank M.-P. Wilson and R. P. Wilson for assistance and advice with the speed meters and J. Hanekom of the Nuclear Development Corporation, Southern Universities Nuclear Research Institute, for preparing the radioactive beads. P. Bestbier of the South African Bureau of Standard allowed access to a densitometer and R. P. Prŷs-Jones commented on the manuscript.

LITERATURE CITED

ADAMS, N. J. 1987. Foraging range and chick feeding rates of King Penguins *Aptenodytes patagonicus* at Marion Island during summer. J. Zool. (Lond.): in press.

———, AND C. R. BROWN. 1983. Diving depths of the Gentoo Penguin *Pygoscelis papua*. Condor 85:503–504.

———, AND M.-P. WILSON. 1987. Foraging parameters of Gentoo Penguins *Pygoscelis papua* at Marion Island. Polar Biol.: in press.

BODEN, B. P., AND L. D. PARKER. 1986. The plankton of the Prince Edward Islands. Polar Biol. 5:81–93.

BROWN, C. R., AND N. T. KLAGES. 1987. Seasonal and annual variation in diets of Macaroni and Southern Rockhopper Penguins at sub-antarctic Marion Island. J. Zool. (Lond.): in press.

CLARK, B. D., AND W. BEMIS. 1979. Kinematics of swimming of penguins at the Detroit Zoo. J. Zool. (Lond.) 188:411–428.

CROXALL, J. P., AND P. A. PRINCE. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biol. J. Linn. Soc. 14:103–131.

HORNE, R. S. C. 1985. Diet of Royal and Rockhopper Penguins at Macquarie Island. Emu 85:150–156.

KOOYMAN, G. L. 1975. The physiology of diving in penguins. Pp. 115–137, *in* B. Stonehouse, ed. The biology of penguins. Macmillan, London.

———, J. O. BILLUPS, AND W. D. FARWELL. 1983. Two recently developed recorders for monitoring diving activities of marine birds and mammals. Pp. 197–214, *in* A. G. MacDonald and I. G. Priede, eds. Experimental biology at sea. Academic Press, New York.

———, C. M. DRABEK, R. ELSNER, AND W. B. CAMPBELL. 1971. Diving behavior of the Emperor Penguin (*Aptenodytes forsteri*). Auk 88:775–795.

LISHMAN, G. S., AND J. P. CROXALL. 1983. Diving depths of the Chinstrap Penguin *Pygoscelis antarctica*. Br. Antarct. Surv. Bull. 61:21–25.

TRIVELPIECE, W. Z., J. L. BENGSTON, S. G. TRIVELPIECE, AND N. J. VOLKMAN. Foraging behavior of Gentoo and Chinstrap Penguins as determined by new radiotelemetry techniques. Auk: in press.

WARHAM, J. 1963. The Rockhopper Penguin *Eudyptes chrysocome* at Macquarie Island. Auk 80:229–256.

WILLIAMS, A. J. 1982. Chick-feeding rates of Macaroni and Rockhopper Penguins at Marion Island. Ostrich 53:129–134.

———, AND P. A. LAYCOCK. 1981. Euphausiids in the diet of some Subantarctic *Eudyptes* penguins. S. Afr. J. Antarct. Res. 10/11:27–28.

———, AND W. R. SIEGFRIED. 1980. Foraging ranges of krill-eating penguins. Polar Rec. 125:159–175.

———, ———, A. E. BURGER, AND A. BERRUTI. 1979. The Prince Edward Islands: a sanctuary for seabirds in the Southern Ocean. Biol. Conserv. 15:59–71.

WILSON, R. P., AND C. A. R. BAIN. 1984a. An inexpensive depth gauge for penguins. J. Wildl. Manage. 48:1077–1084.

———, AND ———. 1984b. An inexpensive speed meter for penguins at sea. J. Wildl. Manage. 48:1360–1364.

———, W. S. GRANT, AND D. C. DUFFY. 1986. Measurement affects foraging performance in African Penguins. Ecology 67:1091–1093.

———, K. A. NAGY, AND B. S. OBST. Foraging mode comparison for three Antarctic penguins (*Phygoscelis* spp.) nesting sympatrically. Polar Biol.: in press.

Received 26 Mar. 1986; accepted 14 Nov. 1986.