

HUMBOLDT PENGUINS *SPHENISCUS HUMBOLDTI* CHANGE THEIR FORAGING BEHAVIOUR FOLLOWING BREEDING FAILURE

SABRINA S. TAYLOR^{1,2}, MARTY L. LEONARD¹, DARYL J. BONESS³ & PATRICIA MAJLUF⁴

¹*Department of Biology, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada
(taysa083@student.otago.ac.nz)*

²*Present address: Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand*

³*Conservation and Research Centre, National Zoological Park, Smithsonian Institution, Washington DC, 20008, USA*

⁴*Spondylus: Asociación para la Conservación del Mar Peruano, Paul de Beaudiez 520, Lima 27, Peru*

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SUMMARY

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At Punta San Juan, Peru, we examined the foraging behaviour of three Humboldt Penguins *Spheniscus humboldti* following breeding failure, and we compared that behaviour with the behaviour of 22 breeding birds with chicks. Failed breeders appear to take longer foraging trips, to make deeper and longer dives and to dive less often per hour at sea than breeding birds do. We suggest that failed breeders either take longer foraging trips to reduce the number of trips they make to the colony, which reduces the costs of transit, or they travel to more distant foraging areas, as documented for Chile. Study of non-breeding birds that have successfully fledged young would help to clarify the differences in foraging behaviour between non-breeding and breeding birds.

Key words: Humboldt Penguin, *Spheniscus humboldti*, foraging behaviour, failed breeder

INTRODUCTION

During the chick-rearing period, adult seabirds must transport food to their young at frequent intervals to ensure chick growth and survival. The need to return to the nest at regular intervals often constrains the distance that adults can travel to forage and is frequently associated with loss of mass because the costs of transit are increased (Orians & Pearson 1979, Bryant 1988, Weimerskirch *et al.* 1997). To accommodate the costs of frequent trips, adults often adopt a foraging strategy that balances chick feeding with self-maintenance. They usually achieve that balance by interspersing short trips to feed the young with long trips to feed themselves (Chaurand & Weimerskirch 1994; Weimerskirch *et al.* 1994, 1997; Booth *et al.* 2000; Gray & Hamer 2001). Thus, the presence of chicks is expected to strongly influence adult foraging behaviour, resulting in a pattern that is not necessarily optimal for non-breeding adults.

Presumably, adults without young do not have to compromise self-maintenance with frequent trips to the nest; they would be expected to minimize the energy expenditure associated with travelling from the nest to foraging locations by reducing the number of trips. For instance, Wandering Albatrosses *Diomedea exulans* drastically change their foraging behaviour after breeding. Instead of taking a mix of long and short trips, the adults depart for individual, traditional and distant areas of the ocean where they forage until breeding resumes (Weimerskirch & Wilson 2000). Thus, adults may adapt their foraging pattern to their reproductive state, switching to an optimum pattern for self-maintenance when they are without chicks. Similar state-dependent changes in foraging behaviour have been reported for several seal species, which breed in comparable ecologic conditions (Stewart & DeLong 1993, Boness *et al.* 1994).

For the vast majority of seabirds, information on foraging behaviour is collected during the breeding season, although that season may represent a smaller proportion of their annual cycle (Davis *et al.* 1996, Nicholls *et al.* 2000, Weimerskirch & Wilson 2000). Information on foraging behaviour during the non-breeding period is scant, but is important for understanding how seabirds use ocean resources and for identifying conflicts between fisheries and seabirds throughout the birds' life cycle (Nicholls *et al.* 2000, Weimerskirch & Wilson 2000).

For birds threatened by fisheries, information on foraging behaviour is important for identifying and reducing the causes of incidental catches. Current management plans rely mostly on information gathered during the breeding period. However, if protection is to be effective, it must account for changes in foraging patterns throughout the annual cycle.

The Vulnerable Humboldt Penguin *Spheniscus humboldti* (Ellis *et al.* 1998, BirdLife International 2000) sustains large mortality rates in fishing nets throughout its range (Simeone *et al.* 1998, Wallace *et al.* 1999, Majluf *et al.* 2002; see also Araya *et al.* 1998, Luna 2002). However, information on foraging behaviour in non-breeding Humboldt Penguins is sparse. Studies from Chile using a small number of satellite and radio-tagged birds have shown that non-breeding adults travel farther from the breeding colony than do breeding birds (Culik & Luna-Jorquera 1997a, 1997b; Culik *et al.* 1998; Culik *et al.* 2000; Culik 2001). However, except for one study during El Niño, when adults may change their behaviour in response to changes in prey distribution (Culik *et al.* 2000), no information is available on foraging behaviour *per se* (e.g. dive depth and duration) for non-breeding Humboldt Penguins.

During a larger study of foraging behaviour in breeding Humboldt Penguins, we fitted 27 birds with time–depth recorders (TDRs) during the chick-rearing period. Three of those birds abandoned their nests, giving us the opportunity to examine a subset of non-breeding birds.

Failed breeders and successful breeders spend an similar amount of time in a non-breeding state. Successful breeders typically produce two clutches and then moult, which requires approximately 9–10 months (Zavalaga & Paredes 1997), leaving only two to three months of foraging activity without young. Thus, failed breeders represent a potentially important subset of non-breeding birds that show how foraging behaviour in Humboldt Penguins changes when adults are released from the obligation of transporting prey to chicks.

METHODS

We studied Humboldt Penguins at Punta San Juan, Peru, (15°22'S, 75°12'W) from May to November 1999 (see Taylor *et al.* 2001 and 2002 for details on the study site and instrument deployment, description and data extraction). During the study period, we deployed TDRs (Wildlife Computers, Redmond, Washington, USA) and radio-transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA) on 27 penguins to examine foraging behaviour during the chick-rearing period.

Penguins were captured in crevice (rock) or burrow (excavated in guano) nests for instrument attachment and, where possible, were recaptured after two weeks to remove the instruments. Here we describe the foraging behaviour of two males and one female that abandoned their nests in June and July after instrument attachment and were recaptured ashore after 41, 69 and 96 days, respectively. All birds had chicks at least two weeks old at the time of deployment, and two of the three penguins were a mated pair when the instruments were deployed. All birds were recaptured at their original nest sites. One bird was incubating eggs when it was recaptured; the other two appeared to be inspecting the nest with different partners.

A salt-water switch on the TDRs activated collection of data on dive depth and duration every seven seconds when the birds were at sea. To account for the resolution of the TDRs (0.5 m) and for surface waves that can cause false dive readings, we omitted from the analysis dives of less than 2 m.

Data analysis

Using transmitter checks and visits to the nest, we noted when the penguins abandoned their nests, and we examined foraging behaviour after that point. We describe foraging behaviour using mean and maximum dive depth and duration, length of the foraging trip and foraging effort. A foraging trip was defined as any period at sea that included diving activity. Three measures of foraging effort (Boness *et al.* 1994, Boveng *et al.* 1996; Bowen *et al.* 2001) are presented:

- total vertical distance travelled per hour at sea
- cumulative dive duration per hour spent at sea
- number of dives per hour at sea

To minimize disturbance to the instrumented birds, we usually checked their nests every two weeks to determine whether the nests

were active. For the single bird, we determined that it had abandoned the nest within two days of instrumentation. We were therefore able to determine the beginning of the non-breeding period. The other two penguins abandoned their nest after instrument deployment, but before the first nest check. We could not tell exactly when the nest was abandoned within the two-week period between deployment and the first check. We therefore used the period of time after the first check as the non-breeding period, and we did not compare an individual's foraging behaviour during breeding to its foraging behaviour following desertion. Instead, we compared the foraging behaviour of the three birds that deserted their nests to the foraging behaviour of 22 breeding birds from our main study (Taylor *et al.* 2002).

For the one penguin that was incubating eggs at recapture, it was necessary to calculate when the eggs were laid and to remove from the analysis foraging data during incubation. Foraging behaviour during incubation is not comparable to the foraging behaviour of failed breeders, because incubating Humboldt Penguins return to the nest every two to three days to relieve their mates (Taylor 2000). Failed breeders have no such constraint. We calculated the time to re-nest for six pairs of failed breeders from a surface-nesting colony and then used the minimum time to re-nest (22 days; mean: 34.3 ± 13.5 days) to conservatively approximate the period when the instrumented bird did not have an active nest. Thus, we used the first 22 days of data for this bird and discounted the last 19 days when it may have had an active nest.

We tested for differences between failed breeders and breeding birds using the Mann–Whitney *U*-test. We report means plus or minus one standard deviation and set significance at $\alpha = 0.05$. We considered repeated dives and foraging trips by a single individual to be non-independent, and so we used the mean value for each penguin to calculate group means. To calculate the mean maxima, we used the maximum value for each penguin. Because of the small sample sizes and because male and female foraging behaviour during breeding in Humboldt Penguins does not differ (Taylor *et al.* 2002), we did not consider sex differences.

RESULTS

Some aspects of foraging behaviour in failed breeders appear to differ from those in breeding birds (Table 1). Most importantly, mean and maximum foraging trip duration were both significantly longer in failed breeders than in breeding birds (Table 1). Although one of the three failed breeders had a mean trip duration (27.1 ± 33.5 h) that was comparable to the mean for breeding birds (22.4 ± 6.5 h), the other two failed breeders had average foraging trips of 93.0 ± 68.6 h and 59.8 ± 59.4 h, which greatly exceeded the average reported for breeding birds. No overlap in maximum foraging trip duration was observed between failed breeders and breeding penguins. All three failed breeders had longer maximum foraging trip durations than did any of the breeding penguins.

Mean and maximum dive depth and mean dive duration appear to differ between failed breeders and breeding birds (Table 1). Failed breeders tended to make deeper, longer dives than their breeding counterparts. One measure of foraging effort—dive frequency—also differed between failed breeders and breeding penguins (Table 1). Failed breeders tended to dive less frequently than breeding penguins did.

DISCUSSION

The most obvious difference in foraging behaviour between failed breeders and breeding Humboldt Penguins appears to lie in the duration of foraging trips. At Punta San Juan, the three penguins that abandoned their nests took foraging trips that lasted on average 93.0, 27.1 and 59.8 hours. In contrast, Humboldt Penguins with chicks take characteristic foraging trips (Taylor *et al.* 2002) consisting of overnight trips (mean: 25.8 h) or, more rarely, day trips (mean: 10.4 h). Neither of these trip types last longer than the averages observed for failed breeders.

Maximum foraging trip duration for failed breeders ranged from 126.5 h to 203.4 h and was always greater than that for breeding birds. For breeding penguins, only 5 trips of 155 documented for 22 birds lasted longer than 40 hours. The longest that any trip lasted was 106.7 h. It appears that penguins without chicks change their foraging behaviour by increasing the amount of time that they spend at sea.

There are at least two possible reasons for penguins to increase the time spent at sea following a breeding attempt. Remaining at sea to forage, independent of foraging location, is presumably less costly than regularly returning to the colony, because the energy spent in transit is reduced. These energy savings may be especially important if the penguins have abandoned their nests because of poor body condition. If they are to regain condition and breed again, eliminating unnecessary transit time by increasing the length of their foraging trips may be the most efficient way to gain mass.

Alternatively, penguins may increase their time at sea following breeding because they travel to more distant foraging areas. Alternating between breeding and non-breeding foraging areas appears to be a common strategy in penguins. Breeding Adélie Penguins *Pygoscelis adeliae* typically remain within 272 km of the breeding colony (Davis & Miller 1992); but, during the winter when they are not breeding, the birds migrate up to 1467 km from

the colony (Davis *et al.* 1996). In Chile, studies examining foraging behaviour in Humboldt Penguins showed that non-breeding birds foraged more distantly than breeding birds did. In Chile during the 1997/98 El Niño, satellite-tagged Humboldt Penguins with chicks ($n = 5$) remained within 100 km of the breeding colony; but, after abandoning their nests, they travelled up to 895 km away in search of food (Culik *et al.* 2000). Clearly, El Niño conditions are exceptional, and the distances that penguins travel to find food may be greater than usual. However, in the only other studies to examine foraging behaviour in non-breeding Humboldt Penguins, the birds continued to follow that pattern. Satellite-tagged breeding birds ($n = 2$) remained within 35 km of the breeding colony (Culik & Luna-Jorquera 1997a, Culik *et al.* 1998). Satellite-tagged non-breeders usually remained within 90 km of the colony ($n = 4$), but could travel up to 640 km away [$n = 1$ (Culik & Luna-Jorquera 1997b)]. It seems possible that Humboldt Penguins in Peru follow the same pattern as they do in Chile and travel farther from the colony after breeding ends.

There are at least two possible advantages for non-breeding penguins to travel to more distant foraging areas. Distant foraging areas may be beyond the reach of breeding penguins constrained by chick-feeding obligations, and so competition from breeding penguins may be reduced (Birt *et al.* 1987, Weimerskirch & Wilson 2000). Additionally, richer prey patches may be more distant. Because non-breeding birds are not tied to the nest site, they can travel to take advantage of such sites. Satellite tagging of Peruvian Humboldt Penguins would help to resolve whether penguins remain in the same foraging area following nest abandonment or whether they move to different foraging areas.

In Peru, failed breeders appear to make longer, deeper dives than do breeding birds, which may indicate that they are taking different types of prey. Differences in prey items between breeding and non-breeding periods have been observed in other seabirds, such as Heard Island Cormorants *Phalacrocorax [atricaps] nivalis*

TABLE 5

Mean and maximum dive parameters (with standard deviation) for failed breeders (present study) and breeding birds (Taylor *et al.* 2002)

Parameter		Failed breeders ($n=3$) ^a	Breeding birds ($n=22$) ^a	Mann-Whitney <i>U</i> statistic	<i>P</i> value
Dive depth (m)	Mean	13.9±0.3	10.1±2.4	6.0	0.024
	Maximum	61.8±4.7	43.8±10.9	4.0	0.015
Dive duration (s)	Mean	46.2±1.4	40.5±5.4	6.0	0.024
	Maximum	163.3±14.6	148.6±41.4	22.5	0.378
Foraging trip duration (h)	Mean	60.0±33.0	22.4±6.5	2.0	0.010
	Maximum	161.6±38.9	35.3±17.9	0.0	0.006
Foraging effort	Vertical distance travelled (m/h at sea)	524.8±57.8	493.9±107.2	25.0	0.503
	Cumulative dive time (h/h at sea)	0.243±0.03	0.2790±0.05	49.0	0.181
	Dive frequency (n/h at sea)	18.9±2.2	25.0±5.0	60.0	0.024

^aMean and maximum dive depth and duration, foraging trip duration and foraging effort for the non-breeding and breeding penguin groups were calculated using the mean and maximum for each penguin.

(Green & Williams 1997). Non-breeding cormorants take polychaetes; breeding birds take fish (Green & Williams 1997). For Humboldt Penguins, the slight increase in dive depth observed in failed breeders may indicate that they switch prey when they are not breeding. Alternatively, if Humboldt Penguins move to a different foraging area when they are not breeding, patches of the same prey may simply lie in deeper water.

We also found a significant difference in dive frequency between breeders and failed breeders. However, greater dive depth and duration produce longer recovery times at the surface, reducing dive frequency. Mean dive depth and duration are greater for failed breeders, and so it is not surprising that failed breeders also dive less frequently. No difference was observed between failed breeders and breeding birds in the vertical distance travelled or the cumulative dive time. Humboldt Penguins therefore do not appear to reduce their foraging effort following breeding failure.

Failed breeders may forage differently from penguins that have successfully fledged young and are in a non-breeding state. Not only might failed breeders need to regain mass, they may also have enough time to make another attempt at breeding. Any penguins attempting to re-nest would need to return to the colony occasionally to examine potential nest sites and to court. Penguins that have fledged young may have no reason for returning to the colony and so may remain at sea (e.g. Weimerskirch & Wilson 2000).

In the present study, one penguin re-nested, and both penguins from the pair were recaptured inside their original crevice nest, which suggests that they may have been considering another breeding attempt. If they were returning to the colony to examine nests and to court, their foraging trip duration might be shorter than that expected for a post-breeding bird that has successfully fledged young.

The present study provides additional information on the foraging behaviour of failed breeders, a subset of non-breeding Humboldt Penguins. Although small, our sample indicates notable differences in the length of foraging trips between breeding penguins and failed breeders. The pattern is consistent with previous results from satellite- and radio-tagged Humboldt Penguins (Culik & Luna-Jorquera 1997a, 1997b; Culik *et al.* 1998; Culik *et al.* 2000). Differences in other parameters, including mean and maximum dive depth, mean dive duration and dive frequency, also appear to exist. We suggest that additional study of non-breeding foraging behaviour would clarify the differences between breeding and non-breeding Humboldt Penguins.

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REFERENCES

- ARAYA, B., GARLAND, D., ESPINOZA, G., SANHUESA, A., SIMEONE, A., TEARE, A., ZAVALLEGA, C., LACY, R. & ELLIS, S. (Eds). 2000. Population and habitat viability assessment for the Humboldt Penguin (*Spheniscus humboldti*). Olmüe, Chile 28 September–1 October 1998. Final Report. Apple Valley: IUCN/SSC Conservation Breeding Specialist Group.
- BIRDLIFE INTERNATIONAL 2000. Threatened birds of the world. Cambridge: BirdLife International.
- BIRT, V.L., BIRT, T.P., GOULET, D., CAIRNS, D.K. & MONTEVECCHI, W.A. 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series* 40: 205–208.
- BONESS D.J., BOWEN, W.D. & OFTEDAL, O.T. 1994. Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the Harbor Seal. *Behavioural Ecology and Sociobiology* 34: 95–104.
- BOOTH, A.M., MINOT, E.O., FORDHAM, A.R. & IMBER, M.J. 2000. Coordinated food provisioning in the Little Shearwater *Puffinus assimilis haurakiensis*: a previously undescribed foraging strategy in the Procellariidae. *Ibis* 142: 139–158.
- BOVENG, P.L., WALKER, B.G. & BENGTONSON, J.L. 1996. Variability in Antarctic Fur Seal dive data: implications for TDR studies. *Marine Mammal Science* 12: 543–554.
- BOWEN, W.D., IVERSON, S.J., BONESS, D.J. & OFTEDAL, O.T. 2001. Energetics of lactation in Harbour Seals: effect of body mass on sources and level of energy allocated to offspring. *Functional Ecology* 15: 325–334.
- BRYANT, D.M. 1988. Energy expenditure and body mass changes as measures of reproductive costs in birds. *Functional Ecology* 2: 23–34.
- CHAURAND, T. & WEIMERSKIRCH, H. 1994. The regular alternation of short and long foraging trips in the Blue Petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *Journal of Animal Ecology* 63: 275–282.
- CULIK, B.[M.] 2001. Finding food in the open ocean: foraging strategies in Humboldt Penguins. *Zoology (Jena)* 104: 327–338.
- CULIK, B.M. & LUNA-JORQUERA, G. 1997a. Satellite tracking of Humboldt Penguins (*Spheniscus humboldti*) in northern Chile. *Marine Biology* 128: 547–556.
- CULIK, B.M. & LUNA-JORQUERA, G. 1997b. The Humboldt Penguin *Spheniscus humboldti*: a migratory bird? *Journal für Ornithologie* 138: 325–330.
- CULIK, B.M., HENNICKE, J. & MARTIN, T. 2000. Humboldt Penguins outmanoeuvring El Niño. *Journal of Experimental Biology* 203: 2311–2322.
- DAVIS, L.S. & MILLER, G.D. 1992. Satellite tracking of Adélie Penguins. *Polar Biology* 12: 503–506.
- DAVIS, L.S., BOERSMA, P.D. & COURT, G.S. 1996. Satellite telemetry of the winter migration of Adélie Penguins (*Pygoscelis adeliae*). *Polar Biology* 16: 221–225.
- ELLIS, S., CROXALL, J.P. & COOPER, J. (Eds). 1998. Penguin conservation assessment and management plan. Report from the workshop held 8–9 September 1996, Cape Town, South Africa. Apple Valley: IUCN/SSC Conservation Breeding Specialist Group.
- GRAY, C.M. & HAMER, K.C. 2001. Food-provisioning behaviour of male and female Manx Shearwaters, *Puffinus puffinus*. *Animal Behaviour* 62: 117–121.

- GREEN, K. & WILLIAMS, R. 1997. Biology of the Heard Island Shag *Phalacrocorax nivalis*. 3. Foraging, diet and diving behaviour. *Emu* 97: 76–83.
- LUNA, G.J., HENNICKE, R., WALLACE, R., WOLFAARDT, A., WHITTINGTON, P., ELLIS, S. & McGOVERN, M. (Eds). 2002. *Spheniscus* Penguin conservation workshop. Universidad Católica del Norte, Coquimbo, Chile; 9–10 September 2000. Final Report. Apple Valley: IUCN/SSC Conservation Breeding Specialist Group.
- MAJLUF, P., BABCOCK, E.A., RIVEROS, J.C., ARIAS SCHREIBER, M. & ALDERETE, W. 2002. Catch and bycatch of sea birds and marine mammals in the small-scale fishery of Punta San Juan, Peru. *Conservation Biology* 16: 1333–1343.
- NICHOLLS, D.G., MURRAY, M.D., BUTCHER, E.C. & MOORS, P.J. 2000. Time spent in Exclusive Economic Zones of southern oceans by non-breeding Wandering Albatrosses (*Diomedea* spp.): implications for national responsibilities for conservation. *Emu* 100: 318–323.
- ORIAN, G.H. & PEARSON, N.E. 1979. On the theory of central place foraging. In: Horn, D.J., Stairs, G.R. & Mitchell, R.D. (Eds). *Analysis of ecological systems*. Columbus: Ohio State University Press.
- SIMEONE, A., BERNAL, M. & MEZA, J. 1998. Incidental mortality of Humboldt Penguins *Spheniscus humboldti* in gillnets, central Chile. *Marine Ornithology* 27: 157–161.
- STEWART, B.S. & DELONG, R.L. 1993. Seasonal dispersion and habitat use of foraging Northern Elephant Seals. *Symposium of the Zoological Society of London* 66: 179–194.
- TAYLOR, S.S. 2000. Parental care during incubation and chick-rearing in Humboldt Penguins, *Spheniscus humboldti* [MSc thesis]. Halifax: Dalhousie University.
- TAYLOR, S.S., LEONARD, M.L., BONESS, D.J. & MAJLUF, P. 2001. Foraging trip duration increases for Humboldt Penguins tagged with recording devices. *Journal of Avian Biology* 32: 369–372.
- TAYLOR, S.S., LEONARD, M.L., BONESS, D.J., & MAJLUF, P. 2002. Foraging by Humboldt Penguins (*Spheniscus humboldti*) during the chick-rearing period: general patterns, sex differences and recommendations to reduce incidental catches in fishing nets. *Canadian Journal of Zoology* 80: 700–707.
- WALLACE, R.S., GRZYBOWSKI, K., DIEBOLD, E., MICHEALS, M.G., TEARE, J.A. & WILLIS, M.J. 1999. Movements of Humboldt Penguins from a breeding colony in Chile. *Waterbirds* 22: 441–444.
- WEIMERSKIRCH, H. & WILSON, R.P. 2000. Oceanic respite for Wandering Albatrosses. *Nature* 406: 955–956.
- WEIMERSKIRCH, H., CHASTEL, O., ACKERMANN, L., CHAURAND, T., CUENOT-CHAILLET, F., HINDERMEYER, X. & JUDAS, J. 1994. Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour* 47: 472–476.
- WEIMERSKIRCH, H., CHEREL, Y., CUENOT-CHAILLET, F. & RIDOUX, V. 1997. Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. *Ecology* 78: 2051–2063.
- ZAVALAGA, C.B. & PAREDES, R. 1997. Humboldt Penguins at Punta San Juan, Peru. *Penguin Conservation* 10: 6–8.