Foraging by Humboldt penguins (*Spheniscus humboldti*) during the chick-rearing period: general patterns, sex differences, and recommendations to reduce incidental catches in fishing nets

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**Abstract**: We studied the foraging behaviour of endangered Humboldt penguins (*Spheniscus humboldti*) to examine general foraging patterns, sex differences in foraging behaviour, and the reasons for incidental catches in fishing nets. Humboldt penguins foraged diurnally and typically made short, shallow dives within 30 m of the surface. Males and females made overnight (lasting 25.8 ± 3.4 h; mean ± SD) and day (10.4 ± 2.0 h) trips when they departed the colony to forage. Overnight trips were more common (68.2% of all trips) and were associated with a significantly greater amount of foraging time. Males dived to greater maximum depths than females but did not differ in other diving parameters, including foraging time, foraging effort, and proportions of day and overnight trips made. Adults may maintain their body condition during chick rearing by making a mixture of overnight and day trips. The two foraging periods observed during overnight trips may function to feed both the adults and the chicks, whereas the single period observed during day trips may function to accommodate the rate of provisioning required by the chicks. We suggest that both males and females would be protected from incidental catches in fishing nets if commercial fisheries avoided setting surface nets at night and setting nets between 0 and 30 m depth during the day in areas where penguins forage and transit.

**Introduction**

Species that forage at sea and breed on land may be restricted during the reproductive period because they must transport prey to the young, an obligation that may limit their foraging range and the duration of their foraging trips. In seabirds, a number of reproductive characteristics are attributed to the high costs of foraging and transporting prey...
to the chicks (Ashmole 1971; Mock and Fujioka 1990; Wooler et al. 1992). For instance, low chick-feeding rates, slow chick growth rates, and small brood sizes may all be associated with the high cost of foraging at sea (Lack 1968). This in turn has presumably selected for monogamy and biparental care because a single parent cannot simultaneously rear chicks and feed itself.

Although the capacity of seabirds to successfully raise young ultimately depends on a pair’s joint ability to obtain food, males and females may have distinct parental roles (e.g., egg laying) that result in differences in foraging behaviour and chick provisioning between the sexes. For instance, female guillemots (Uria aalge) feed the young significantly more often at the nest site than males, but it is the male that takes the chicks to sea, where feeding continues (Wanless and Harris 1986). Sex differences in foraging behaviour have been particularly well studied in several species of large seabirds, including albatrosses and penguins, in part because these species can carry recording devices such as satellite tags and time–depth recorders (TDRs). The detailed information obtained for some species has shown significant differences between males and females in foraging depth, foraging area, trip duration, and the prey species used to feed young (Weimerskirch et al. 1997; Clarke et al. 1998).

Identifying differences in foraging behaviour between the sexes may be important for several reasons. First, differences in foraging behaviour may reveal how males and females maintain their body condition during chick rearing, the most energetically costly period for most seabirds (e.g., Weimerskirch et al. 1997). Second, self-maintenance during chick rearing may be linked to life-history traits, including reproductive effort and trade-offs between current and future reproduction. For example, differences in how the sexes maintain their body condition may help us to understand the factors responsible for nest abandonment. Finally, for species at risk, particularly those threatened by fisheries, it is important to have information on foraging behaviour so that effective management strategies can be formulated. To date, the only information on foraging patterns of Humboldt penguins (Spheniscus humboldti) comes from Chile (Wilson et al. 1989; Culik and Luna-Jorquera 1997; Luna-Jorquera and Culik 1999; Culik et al. 2000). Luna-Jorquera and Culik (1999) found that Humboldt penguins forage during the day in shallow water close to their breeding areas. However, they can change their behaviour according to the availability and location of their prey. For instance, during the 1997–1998 El Niño, the penguins increased foraging effort and changed location to find sufficient prey (Culik and Luna-Jorquera 1997; Culik et al. 2000). Geographic differences in foraging behaviour are also feasible if prey are distributed differently; however, there is no information on either Humboldt penguins’ foraging behaviour in Peru or on sex-specific differences.

Observations of foraging behaviour

We studied the foraging behaviour of Humboldt penguins at Punta San Juan from May to November 1999 by deploying Mark 7 TDRs (Wildlife Computers, Redmond, Wash.) on 27 individuals (13 females and 14 males). The TDRs were programmed to record depth every 7 s while the penguin was in contact with salt water and the number of dry readings when the animal was on land. At the time of instrument deployment, penguins were weighed, measured, and banded with stainless-steel flipper bands (Lambournes, West Midlands, England). When possible we recaptured the penguins after approximately 2 weeks (16.8 ± 2.11 days (mean ± SD), range = 10–19 days, n = 23) to remove the instruments and reweigh the penguins. For further details on instrument deployment and description see Taylor et al. (2001a). The protocol for this study was approved by the National Zoological Park Institutional Animal Care and Use Committee, Smithsonian Institution, and the animals were studied following the principles and guidelines of the Canadian Council on Animal Care.

To prepare dive data for analysis, the hexadecimal data files from the TDRs were run through two software programs. The first was a zero-offset correction program (Wildlife Computers) that corrected for potential drift in the calibration of the TDRs’ pressure transducers. The second was a dive-analysis program (Wildlife Computers) that extracted preselected dive parameters (e.g., depth and duration) for dives that exceeded a user-specified depth. We considered a dive to have occurred if the TDR recorded a depth equal to or greater than 2 m. Otherwise we considered the penguin to be at the surface to account for both the resolution of the TDRs (0.5 m) and surface noise from waves spilling over the pressure transducer while the penguin was at the surface. All dive records were examined graphically by plotting depth against time for the entire period of deployment.

We analyzed penguin diving behaviour at three levels: individual dives, diving bouts, and foraging trips. Based on the distribution of dive depths (see Results), we defined dives between 2 and 4 m as shallow dives, which may be indicative of travelling, and dives deeper than 4 m as deep dives, which most likely represent foraging (Wilson et al. 1989; Chappell et al. 1993a; Boness et al. 1994; Robinson and Hindell 1996; Luna-Jorquera and Culik 1999). Dive bouts or periods of foraging activity were considered to have started if there was a minimum of four consecutive dives to at least 4 m depth followed by a series of deeper dives. Dive bouts were considered to have ended if the animal remained at the
surface for a minimum of 30 min or returned to land. Foraging trips were defined as any period spent at sea that included at least one dive bout. A trip ended when the bird returned to land. The total time spent foraging consisted of all dive bouts in a trip but excluded surface time.

Data analysis

For all statistical analyses in this paper we used SYSTAT Version 8.0. We report means plus or minus 1 standard deviation (SD) and set significance at $\alpha = 0.05$. We used parametric tests because the data were normally distributed and independent.

Dive analysis

To examine overall patterns of penguin diving behaviour we combined the dive records of 10 pairs of male and female penguins and added the records of two other individuals for which we had data (2 females) to supplement the sample size. We plotted dive frequency against depth and time of day to examine the distribution of dive depths and daily foraging patterns. We considered repeated dives and foraging trips by a single penguin to be non-independent, so a mean value for the entire dive record was calculated for each measure for each penguin.

We examined potential sex differences in diving by comparing mean and maximum dive depth and duration, mean foraging time, and foraging effort for males and females by means of paired $t$ tests. Foraging effort was measured using the entire dive record for each penguin to be non-independent, so a mean value for the entire dive record was calculated for each measure for each penguin.

Recovery of devices

Although TDRs were deployed on 27 birds, data from all individuals were not available for analysis. One pair was excluded from the trip and bout analysis because the male made a foraging trip approximately four times longer (106.7 h) than the average duration of an overnight trip (25.8 h), which was likely an effect of the instrument. The TDR on one bird failed to work and was not recovered from another, and the remaining three birds abandoned their nests, and so were not feeding chicks. Males weighed 4.48 ± 0.20 kg ($n = 14$) and females weighed 3.82 ± 0.31 kg ($n = 13$).

Overall foraging patterns

Twenty-two Humboldt penguins made a total of 83 463 dives. Penguin dive depths were bimodal in distribution (Fig. 1) and could be meaningfully grouped into our operational categories of shallow dives (2–4 m; $n = 17$ 287) and deep dives (>4 m; $n = 66$ 176). Humboldt penguins’ dives were typically short (40.6 ± 5.3 s; $n = 22$) and shallow (10.1 ± 2.44 m; $n = 22$). When shallow dives were excluded, dive duration and depth increased to 45.6 ± 5.4 s ($n = 22$) and 11.9 ± 2.5 m ($n = 22$). Dives deeper than 30 m were uncommon (1.8% of all dives; Fig. 1), although dives reaching 64.5 m were recorded.

Trip durations were dichotomous (Fig. 2). Many trips were relatively long, lasting 25.8 ± 3.4 h, whereas others were relatively short, lasting 10.4 ± 2.0 h. Long trips extended past 1 calendar day and so we refer to them as overnight trips. Short trips were completed within 1 calendar day and are referred to as day trips. Overnight trips were more common than day trips and represented 68.2% of all foraging trips (105/154 trips). Relatively little diving (7.1% of all dives) occurred during the hours of darkness (19:00 to 04:00; Fig. 3).
Penguins on overnight trips typically had two periods of foraging activity and were at the surface during darkness (Fig. 4). The first period began after the penguin left the colony and ended with darkness. The second period occurred in the morning with daylight and ended when the penguin returned to the colony. Following the first period of foraging activity, penguins typically remained at the sea surface for about 11 h during the night. Penguins on day trips foraged during daylight hours and returned to the colony in the evening or late afternoon.

Departure time significantly affected trip type ($\chi^2 = 32.34$, df = 1, $p < 0.00$). Morning departures resulted in either overnight trips (54) or day trips (48), whereas afternoon departures resulted almost exclusively in overnight trips (51 overnight trips, 1 day trip). Penguins spent significantly more time foraging during overnight trips (11.96 ± 3.03 h) than during day trips (7.44 ± 1.8 h; $t = -5.618$, df = 31.2, $p < 0.00$).

Sex differences
With the exception of maximum dive depth, none of the features of diving and foraging behaviour measured in this study differed significantly between males and females (Table 1). Males did, however, show significantly greater maximum dive depths than females (Table 1). We also tested for a sex difference in the proportions of day and overnight trips made by males and females, using a randomization test with nest as the unit of analysis. Males and females did not differ in the proportions of overnight versus day trips ($n = 9$, $p = 0.89$).

Discussion
Overall patterns
During the chick-rearing period, Humboldt penguins typically foraged during the day by making short, shallow dives usually within 30 m of the surface. Diurnal diving activity is typical for most penguins (Wilson 1985; Williams et al. 1992; Robinson and Hindell 1996; Wilson et al. 1997; Hull 2000), including Humboldt penguins (Luna-Jorquera and Culik 1999; Culik et al. 2000), and presumably occurs because penguins cannot perceive prey under low-light conditions (Wilson et al. 1993). Dive depth is generally related to penguin size and prey distribution (Wilson 1995). Humboldt penguins are medium-sized penguins that chiefly prey upon anchovy (Engraulis ringens; Wilson and Wilson 1990; Williams 1995; Culik and Luna-Jorquera 1997) and most of their dives occur within 30 m of the surface. These dive depths are consistent with depths expected on the basis of the penguins’ size and the distribution of anchovy (Jóhannesson and Vilchez 1980; Whitehead et al. 1988) and agree well with dive data collected from Humboldt penguins in Chile (Luna-Jorquera and Culik 1999; Culik et al. 2000).

Humboldt penguins of both sexes made two kinds of trips: day trips and overnight trips. These trip types may be the mechanism by which seabirds maintain fat reserves while provisioning chicks. During the reproductive period, breeding birds forage both for themselves and for their offspring, and therefore must make a trade-off between self-maintenance and chick provisioning. In several seabirds this trade-off is reflected in different types of foraging trips. Typically, adults make short trips in order to accommodate the provisioning rate required by the chicks. However, adults may lose mass during short trips and require longer times at sea during which they forage for themselves to regain mass (Weimerskirch et al. 1997). The longer overnight foraging trips made by Humboldt penguins, during which greater amounts of foraging occur, may be associated with self-maintenance, since longer trips also have this function in other seabird species (Chaurand and Weimerskirch 1994; Weimerskirch et al. 1994, 1997). During overnight trips, Humboldt penguins may forage for themselves during the first period of foraging activity and for their chicks during the second period of foraging activity. After the first foraging period, penguins are typically at the surface during darkness, where the food eaten the previous evening may be digested. African penguins (Spheniscus demersus) and gentoo penguins (Pygoscelis papua) can digest fish to bones or otoliths within 10–16 h (Wilson et al. 1985; Gales 1987), and studies on penguin digestion have shown that gastric activity is greater during shallow diving and periods spent at the surface (Peters 2002), so it is likely that food ingested by Humboldt penguins during the first foraging period is digested by morning. Day trips may function mostly for offspring provisioning, which may explain why these trips are relatively uncommon compared with overnight trips if food acquired on overnight trips can nourish both the adult and the chicks.

Types of trips made in relation to self-maintenance or chick provisioning have not been studied in penguins, despite observations of short and long trips in Humboldt penguins (Culik and Luna-Jorquera 1997; Luna-Jorquera and Culik 1999), macaroni penguins (Eudyptes chrysolophus; Croxall et al. 1988), Adélie penguins (Pygoscelis adeliae; Kerry et al. 1995), gentoo penguins (Adams and Wilson 1987), and chinstrap penguins (Pygoscelis antarctica; Jansen et al. 1998). The most detailed information on trip types was 

Fig. 3. Frequency distribution of the numbers of dives made at each hour of the day by Humboldt penguins during chick rearing ($n = 22$). Diving occurs approximately five times more frequently between 05:00 and 18:00 than between 19:00 and 04:00.
reported by Jansen et al. (1998) for chinstrap penguins. This species makes both day (4–11 h) and overnight trips (13–14 or 18–22 h). Following day trips, chinstrap penguins return to their nests with Antarctic krill (Euphausia superba) in their stomachs. In contrast, penguins returning from overnight trips return with Antarctic krill and highly digested

Fig. 4. Dive depths versus time of day during an overnight trip by a representative Humboldt penguin. Two periods of foraging activity (12:30–18:16 and 05:32–12:30) occurred during daylight and a period was spent at the surface during darkness (18:16–05:32). Positive depths reflect normal fluctuations in the pressure transducer.

Fig. 5. Dive depths versus time of day during a day trip by a single Humboldt penguin, showing foraging activity between 05:46 and 17:33. Positive depths reflect normal fluctuations in the pressure transducer.
There may be other explanations for different types of foraging trips in penguins. First, the amount of daylight remaining when a penguin leaves the colony to forage may affect the type of trip made (Jansen et al. 1998). Chinstrap penguins appear unwilling to depart from or arrive at the colony during darkness, presumably because high surf may increase the risk of injury. Thus, they either return before darkness or the next morning during daylight (Jansen et al. 1998). In Humboldt penguins, departure time affects the type of trip taken. Although morning departures result in either overnight or day trips, afternoon departures mostly result in overnight trips.

The other possibility is that the distance to the foraging site and the water temperature affect the type of trip taken (Luna-Jorquera and Culik 2000). If the foraging site is more than 9 km away in 12°C water, penguins should make an overnight trip because the cost of thermoregulating overnight at sea is less than the cost of travelling back to the breeding site and returning to sea the next morning. In Peru, the average sea-surface temperature is 15°C (Paredes and Zavalaga 1998). In contrast, little penguins (Eudyptula minor; Bethge et al. 1997), emperor penguins (Aptenodytes forsteri; Wienecke and Robertson 1997), and Adélie penguins (Chappell et al. 1993a, 1993b; Clarke et al. 1998) showed significant differences between males and females in dive depth, dive frequency, dive duration, swimming speed, energy expenditure, trip duration, feeding locality, and (or) diet composition. It is not clear why these patterns vary across species. One possibility is that differences are related to the condition of males and females when they enter the chick-rearing period. For instance, male emperor penguins are solely responsible for incubating the egg and lose body mass as a result. During the brooding stage males take foraging trips that are a week longer, on average, than those of females, presumably to regain body mass (Wienecke and Robertson 1997). Maximum dive depth is the one aspect of foraging behaviour that differed between males and females. Male Humboldt penguins dived to greater maximum depths than females, which may be related to the larger size of the males (Kooyman 1989). If deep diving is associated with the ability to catch different species of fish, then it is possible that males provide offspring with a slightly different diet than females if they bring back different prey from deeper waters. However, we were unable to determine whether there were differences in the prey types provided to the chicks because we did not collect stomach samples from males and females. A greater maximum dive depth may also provide males with an advantage over females during El Niño years. Males may be more able to undertake deep dives and thus survive El Niño events when fish migrate to deeper water (Arntz et al. 1991). This might explain the male-biased sex ratio we observed at our study site following the 1997–1998 El Niño (Taylor et al. 2001b).

### Table 1. Mean differences in dive depth, duration, maximum depth, and maximum duration, foraging time, and foraging effort for male and female Humboldt penguins (Spheniscus humboldti).

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>Males</th>
<th>Females</th>
<th>SD</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of pairs</td>
<td>10</td>
<td>10.5</td>
<td>9.9</td>
<td>1.89</td>
<td>0.35</td>
</tr>
<tr>
<td>Mean dive depth (m)</td>
<td>10</td>
<td>41.7</td>
<td>40.0</td>
<td>6.77</td>
<td>0.45</td>
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<tr>
<td>Max. dive depth (m)</td>
<td>10</td>
<td>47.9</td>
<td>39.6</td>
<td>7.98</td>
<td>0.01</td>
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<tr>
<td>Mean foraging time (h)</td>
<td>9</td>
<td>11.2</td>
<td>10.5</td>
<td>2.74</td>
<td>0.47</td>
</tr>
<tr>
<td>Vertical distance travelled (m/h spent at sea)</td>
<td>10</td>
<td>484.1</td>
<td>495.2</td>
<td>132.73</td>
<td>0.80</td>
</tr>
<tr>
<td>Cumulative dive time (h/h spent at sea)</td>
<td>10</td>
<td>0.273</td>
<td>0.276</td>
<td>0.08</td>
<td>0.89</td>
</tr>
<tr>
<td>Dive frequency (no./h spent at sea)</td>
<td>10</td>
<td>23.7</td>
<td>25.1</td>
<td>6.94</td>
<td>0.53</td>
</tr>
</tbody>
</table>

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fishing gear. Between 1992 and 1994 approximately 646 penguins were caught in fishing nets that had been set at the surface at night to catch a valuable prey species (Seriolella violacea; Majluf et al. 2002). At the time it was clear that the nets were a problem, but it was not clear why the penguins were caught in such high numbers.

The results of our current study suggest two potential causes of incidental catches of penguins at Punta San Juan. Nets set at the surface, particularly at night, pose a serious risk of entanglement for Humboldt penguins because they spend most of the night at the surface on overnight foraging trips, and because it may be difficult for them to see the nets. In areas where fisheries and Humboldt penguins co-occur, we recommend avoiding the use of surface nets, especially at night. To a lesser extent, nets set between 0 and 30 m depth during the day may also catch penguins because they usually forage at these depths during the day. If possible, we suggest that 0–30 m be the recommended depth to avoid during the day in areas where penguins forage and transit. Males may be more vulnerable to nets set at greater depths; however, in most cases there were no apparent sex differences in diving behaviour and these recommendations should protect both sexes from incidental catches in fishing nets.

Acknowledgements

We are grateful to G. Battistini, G. Mori, M. Roca, and N. Ampuero for assistance in the field, D. Boersma for help with TDR deployment, and M. Braun at Wildlife Computers for technical support with the data files. We thank T. Porter, A. King, C. Stuicer, I. McLaren, and W. Montvecocchi, for helpful comments on earlier drafts. It is our pleasure to acknowledge financial assistance from the Oregon Zoo, the Wildlife Conservation Society, the Smithsonian Institution Sisley Fund, the Friends of the National Zoo, the Canadian International Development Agency, the Manomet Center, Dalhouse University Faculty of Graduate Studies, and the Natural Sciences and Engineering Research Council of Canada. In Peru, PROABONOS – Ministry of Agriculture and Shougang Hierro provided vital logistical support. Finally, we are indebted to W. Blanchard for valuable statistical advice and particularly for running the randomization test.

References


