

Spatial and temporal variation in the provisioning behaviour of female rockhopper penguins *Eudyptes chrysocome filholi*

Yann Tremblay and Yves Cherel

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As seabirds are central place foragers during breeding, their provisioning behaviour and their ability to face variable energy demand from the chicks is expected to vary with environmental conditions. The provisioning behaviour of female rockhopper penguins *Eudyptes chrysocome filholi* was recorded over the chick-rearing period at Kerguelen (KER) and Crozet (CRO) archipelagoes (two very distinct marine environments), using time-depth recorders, or VHF transmitters coupled with an automatic recording station. No influences of the method have been found on the average foraging trip durations. Some previously undescribed short and multiple trips within a day were recorded using the automatic recording system. These multiple trips (6.8 h) were mostly performed with < 5 days old chicks, a period during which feeding rates were the highest (1.1 meals per day), at both sites. During the brooding period, both KER and CRO females mainly performed daily trips of increasing duration (2 h longer at CRO) and at decreasing frequency. During the crèche compared to the brooding period, females from KER performed slightly fewer daily trips (0.6 per day) and more (< 3 days) overnight trips, while females from CRO performed very few daily trips (0.1 per day) and more overnight trips, some of them being long trips lasting 5 to 29 days, mostly initiated during the transition between the brooding and the crèche periods. The result fit the hypothesis that long trips permit females to restore and/or maintain their body condition at more distant foraging places. It seemed that chick development during the brooding period and environmental factors during the crèche period conditioned trip duration of females. Due to more long trips at CRO, the female feeding frequency was twice as high at KER than at CRO during the crèche period, while males participated in the feeding duties. Based on differences in female behaviour, we hypothesize that the male's contribution is likely to differ strongly from one site to another, and may buffer the possible decrease in female feeding frequency by feeding the chicks if food is less abundant.

Y. Tremblay (correspondence), Department of Ecology and Evolutionary Biology, Institute of Marine Science, Long Marine Laboratory, 100 Shaffer road, University of California, Santa Cruz, California 95060-5730 USA. E-mail: tremblay@biology.ucsc.edu. Y. Cherel, Centre d'Etude Biologique de Chizé, UPR 1934 du Centre National de la Recherche Scientifique, BP 14, 79360 Villiers en Bois, France.

During breeding, penguin parents must ensure that the chick is adequately brooded and provisioned. This requires variable time and energy investment, since the chicks' needs change as they grow (Brown 1987a). During the brooding stage, one parent must stay on the nest while the other searches for food, whereas both parents can forage simultaneously after thermal emancipation of the chicks. During the crèche stage (thermal

emancipation of the chicks in most penguin species), chicks are bigger and need more energy (Brown 1987a). These parameters are likely to influence parental provisioning behaviour. For example, when *Spheniscus* penguins have small chicks, most foraging trips of the feeding parents last less than 24 hours. When chicks are large, and the food demand high and/or food supply around the colonies is depleted (Birt et al. 1987), parents

may spend 2 or more days at sea to search for food (Wilson and Wilson 1990, Scolaro and Suburo 1994). In penguins (like most birds), this task is shared by both parents, but often unequally, leading to large variation in pair provisioning strategies. In rockhopper penguins *Eudyptes chrysocome*, for example, both parents participate in feeding the chicks during the crèche period only, whereas both Adélie penguin *Pygoscelis adeliae* parents share the chick provisioning at all stages (Williams 1995, Clarke et al. 1998).

The potential to adequately provision the chicks may depend on the distribution and availability of prey within parents' foraging range. Thus, we can expect foraging ground quality to strongly influence seabirds' regulation of provisioning behaviours. Being flightless, penguins' foraging range is constrained by their inability to forage at long distances, especially for the smallest species whose swimming speeds are lower (Brown 1987b, Wilson et al. 1989). As a result, penguins are known to forage closer to the colony than most flying seabirds during breeding (Croxall et al. 1984), a characteristic that is likely to make them more sensitive to variation in local prey availability (Hunt and Schneider 1987). One exception is for the largest *Aptenodytes* species whose chick fasting capacity and larger size allow parents to remain at sea several hundreds of kilometres offshore for several days and weeks (Kooyman et al. 1992, Jouventin et al. 1994, Kooyman and Kooyman 1995, Bost et al. 1997).

Rockhopper penguins (the second smallest penguin species) breed in very different areas, surrounded by subtropical to subantarctic and oceanic, neritic to coastal waters, which provide different food availability and thereby cause different feeding strategies (Williams 1995, Tremblay and Cherel 2000, Tremblay and Cherel 2003). In spite of this, they belong to a genus that is recognised to be highly homogenous in terms of foraging patterns. In *Eudyptes*, only females perform daily trips at sea during the brooding period, while both males and females share the foraging duties afterwards during the crèche period (Warham 1975, Williams 1995).

Rockhopper penguins breeding in different localities have to raise a single similar-size chick from hatching to fledging in about the same time, and thus will experience similar constraints from a chick-wise perspective (i.e. they will have to bring ca. 211 kJd⁻¹ during the first week, 5.5 times more halfway through the growth period, and ca. 59,400 kJ in total, Brown 1987a). However, those in different localities may experience very different constraints depending on the distribution of prey at a given place and time. This in turn, may influence diet, growth rate, and breeding success (Ainley et al. 1998, Bost et al. 1994, Barrett 2002). Geographic variation in the foraging behaviour, diet and chick growth was recently found in rockhopper penguins, presumably in relation to differences in prey availability and in the marine environment around the colonies

(Tremblay and Cherel 2003). For example, mass of stomach contents and chick growth rates were greater, and estimated distances to feeding zones were shorter at the inshore (KER) colony than at the offshore (CRO) colony during the brooding period (Tremblay and Cherel 2003). It is thus expected that females provision chicks at a higher rate at Kerguelen, compared to Crozet.

This paper tests the assumption that: (1) provisioning pattern, and (2) the way in which breeding females adjust their behaviour to chick development are based on regional differences in southern rockhopper penguins. To our knowledge, this is the first study that records longitudinally and automatically the provisioning pattern of the rockhopper penguin over a long period of time.

Materials and methods

Birds, study sites and study period

Fieldwork was carried out in January–February 1998 at Mayes Island (49°28'S 69°56'E), Golfe du Morbihan, Kerguelen Archipelago (KER), and in January–February 1999 at Pointe Basse (46°21'S 51°42'E), Possession Island, Crozet Archipelago (CRO). Kerguelen and Crozet Islands are located within the Polar Frontal Zone, between the subantarctic and Antarctic Fronts (Park and Gamberoni 1997). Birds from KER foraged in shallow and sheltered coastal waters in the Golfe du Morbihan, and those from CRO in more open and deeper (neritic) waters, over the shelf surrounding the archipelago (Tremblay and Cherel 2003). Penguin food availability was not recorded in this work, but the differences in physical features are likely to influence marine biomass and productivity among sites. During the study periods, chlorophyll concentrations were >1.3 and 0.3–0.5 mg/m³ at KER and CRO, respectively (SeaWIFS project: <http://daac.gsfc.nasa.gov/>). Previous studies have shown that zooplankton biomass was higher in inshore than in offshore subantarctic waters (Razouls et al. 1997, Labat et al. 2002). Accordingly, a detailed analysis of diving behaviour of rockhopper penguins at the same places and times showed that females from KER dived shallower, used a smaller proportion of time at sea to access to foraging grounds, and brought a heavier mass of food to their chick (Tremblay and Cherel 2003). We thus expected food availability for penguins to be different between the two sites, in the order KER > CRO. As fieldwork was done in two different years between KER and CRO, it is likely that this regional difference includes a temporal component.

We focused on the provisioning pattern of females only, in order to avoid sex-linked differences in foraging behaviour (Tremblay et al. 1997, Clarke et al. 1998). Timing and duration of foraging trips were recorded

from hatching to 60 days later ($\approx 83\%$ of the chick-rearing season). This two months time was divided into four distinct periods: the pre-hatch period (period 1), brooding period (from hatching to 20 days, period 2), transition period (from 21 to 30 days, period 3) and crèche period (from 31 to 60 days, period 4). During the brooding period, female rockhopper penguins feed their offspring while males fast ashore, guarding the chicks. The duration of period 2 has been reported to vary among localities, lasting about 20 days at Campbell and the Falklands (Warham 1963, Strange 1982), 25 days (range 20–28) at Crozet (Stahl et al. 1985), and 26 days at Macquarie Island (Warham 1963). After the brooding period, chicks are left alone, and both males and females undertake foraging trips at sea (period 4).

General procedure

Timing of foraging trips was recorded using two kinds of devices, time-depth recorders (TDR birds), and VHF transmitters (VHF birds). Devices were attached to the lower back of the birds using quick-set epoxy adhesive or cyanoacrylate glue, and plastic ties (Cherel et al. 1999, Tremblay and Cherel 2000). For each trip at sea, we recorded departure and return time and date, and thus its duration. Two nearby colonies were used for TDR and VHF birds and a third one was used as a control colony, in order to quantify a possible human-induced effect on chick growth. In all colonies, chicks were weighed regularly to estimate their growth rates. Only one member of the nesting pair (the female) was monitored over a long period using VHF transmitters in order to minimise disturbance (Croll et al. 1996).

Time-depth recorders

In this study, we used TDR data to record foraging trip duration, which was calculated as the time elapsed from the beginning of the first recorded dive (departure time) to the end of the last recorded dive (return time) of the foraging trip. As all colonies were situated very close to the shoreline, transit times between the shoreline and the nest were considered to be negligible. Females were selected opportunistically and captured in the beginning of the night, after they had fed their chicks. They were weighed (accuracy ± 25 g), fitted with TDRs, and released at their nest 15–20 min following capture. This timing allowed females to recover from the stress of capture overnight, before returning to sea to feed. TDRs were deployed for about 3 days per bird, and no female was equipped during the crèche period (with chicks older than 29 days), because of an increasing risk of losing the devices throughout this period (Wilson et al. 1997).

Most of the TDRs used were Mark V (Wildlife Computers, Woodinville, Washington, USA). They were 9.5 cm long \times 3.7 cm wide \times 1.5 cm high, and weighed 70 g in air, corresponding to about 3% of the bird's body cross-sectional area and $<3\%$ of its body mass. They were streamlined according to Bannasch et al. 1994), in order to reduce their impact on birds' behaviour (Hull 1997). At CRO, some smaller Mark VII TDRs were also deployed. They were 8 cm long \times 1.9 cm wide \times 1.1 cm high, were streamlined and weighed 26 g in air.

Radio monitoring

Females were captured near hatching, and equipped with miniaturised VHF transmitters for about two months. Presence and absence from the colony were continuously recorded during this time, with an automatic recording station (Weimerskirch and Lys 2000, Fraser et al. 2002). Birds that arrived at the colonies before we left the site were recaptured and the transmitters were removed. The others kept the transmitters until they lost them during their annual moult following reproduction (Williams 1995).

Several models of small, streamlined VHF transmitters were used. They were about 3.5 cm long \times 2.5 cm wide \times 1.0 cm high, and weighed from 9 to 12 g, corresponding to $<2\%$ of the bird's cross-sectional area and $<1\%$ of the bird's body mass. They had an external antenna (11–22 cm) in the continuity of the animal's body, and emitted at about 55 pulses per min. An automatic recording station, including a receiver, a data logger (R4000 and DCCII respectively, ATS, Isanti, Minnesota, USA), and a unidirectional antenna was installed near the colony from a high position. The automatic recording station, powered by 12-V batteries, scanned the various frequencies continuously. Each frequency was scanned for a period of 10 s, if at least one pulse was detected during the first 5 s of the scan. If no pulse was detected during this time, the logger switched to the next frequency after 5 s. This procedure allowed maximizing scanning frequency. Depending on the number of equipped birds present at the colony, each VHF frequency was scanned every 75 s to 200 s. Data were downloaded to a laptop computer about every week before the memory of the recording station was filled.

The information provides a list of frequencies, each representing an individual for a particular time. The number of visits to the colony was calculated from these data. The series of pulses were not continuously recorded, probably due to movements of the birds between rocks of the colony or even to short absences at sea for preening or bathing very close to the colony but out of the monitoring antenna's purview. We thus

defined a foraging trip as being represented by a period of absence from the colony greater than 90 min.

Chick growth rate and hatching date

We individually weighed every 5 ± 1 days 145 and 127 chicks from hatching to a maximum age of 38 days, at KER and CRO, respectively. Ninety seven percent of all the 1428 weighing operations were performed with chicks younger than 30 days. After this age, they were all in crèche, and individuals were not identified. During period 2, the growth of individual chicks was linear ($R^2 = 0.97 \pm 0.03$, $n = 272$). The coefficient of the regression lines thus represented growth rate (i.e. the daily increase in body mass), expressed in grams per day. In some nests, hatching was visually determined, and the mass of chicks at hatching recorded. For the other ones, we estimated graphically the hatching date by the extension (back in time) of chick mass against date until the average mass at hatching was reached (accuracy ± 1 day, Tremblay and Chérel 2003).

Data analysis and statistics

Data were analysed using our own program (Tremblay and Logette unpubl. data), and statistics were performed using SYSTAT 7.0. Means are given \pm SD. Non-parametric statistics were used when there was no way of obtaining a normal distribution with the data. When some individual birds represented more than one record in the data set (for example, several foraging trips by the same bird), a nested-ANOVA was performed, and the F-test of the comparison of groups was constructed with the mean square of birds nested within groups as the error term.

When the same parameters were measured using different devices (Table 1), we compared them for each period in order to investigate possible methodological biases. In all periods, no differences were found between devices (nested-ANOVAs: all $F < 2.85$, all $P > 0.100$). Consequently, we pooled all the data for further analysis,

independently of the recording methods (TDR and VHF).

In order to investigate changes in the frequency of trips over time, we needed records from individual birds equipped for a long time. For that reason, the frequency of foraging trips was calculated for VHF birds only, whereas timing and duration of trips was analysed using all recorded trips.

Results

A total of 662 and 666 foraging trips from 50 and 56 birds were analysed from the pre-hatching to the crèche period at KER and CRO, respectively. The numbers of trips recorded per period, per device and per site are given in Table 1. Throughout the whole study period, 91% and 76% of all trips were performed within the same day at KER and CRO, respectively. Birds generally departed early in the morning, and returned back to land in the afternoon (daily trips). The remaining trips included at least one night and were therefore longer. Diving behaviour during these overnight trips differ from daily trips, in particular, birds spend a smaller proportion of their time diving (Tremblay and Chérel 2003) suggesting that they are functionally different. Daily and overnight trips (overnight trips) were thus analysed separately. In daily trips, birds initiated either one (single trips) or several trips within a day (multiple trips; Fig. 1). In overnight trips, we distinguished between short (< 4 nights at sea as Fig. 4 shows some gap at around 4 nights) and long trips at sea.

Frequency of daily trips

During periods 2, 3 and 4, 83.2 ± 15.4 and $84.3 \pm 13.3\%$ of daily trips were single trips and 16.8 ± 15.4 and $15.7 \pm 13.4\%$ were multiple trips at KER and CRO, respectively (differences between sites were not statistically significant, t-test with arcsine transformed percentages: all $t < 0.02$, all $P > 0.990$). Only 2 out of 12 and 2 out of 16 VHF birds never initiated multiple trips at KER and CRO, respectively. Most multiple trips were

Table 1. Repartition of the number of trips recorded over the four periods of the breeding season according to the recording device used, and the kind of trip (daily vs overnight). Number of birds in parentheses.

	Period 1 (pre-hatch)		Period 2 (brooding)		Period 3 (transition)		Period 4 (crèche)		Total	
	KER	CRO	KER	CRO	KER	CRO	KER	CRO	KER	CRO
VHF transmitter	20 (3)	12 (4)	205 (12)	310 (16)	112 (12)	114 (16)	202 (11)	95 (15)	539 (12)	531 (16)
TDR Mk5	–	–	91 (28)	96 (30)	32 (12)	22 (8)	–	–	123 (38)	118 (34)
TDR Mk7	–	–	–	17 (6)	–	–	–	–	–	17 (6)
Daily trips	14 (3)	12 (4)	287 (40)	371 (52)	130 (24)	84 (19)	173 (11)	37 (10)	604 (50)	504 (55)
Overnight trips	6 (2)	–	9 (5)	52 (20)	14 (10)	52 (18)	29 (7)	58 (15)	58 (12)	162 (26)
Total	20 (3)	12 (4)	296 (40)	423 (52)	144 (24)	136 (38)	202 (11)	95 (15)	662 (50)	666 (56)

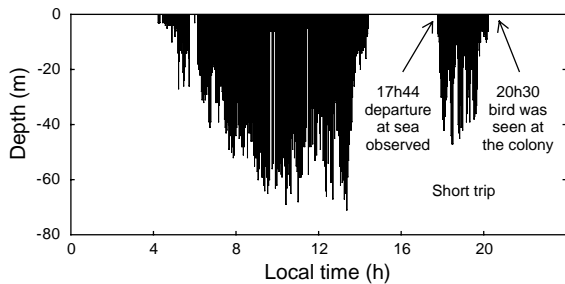


Fig. 1. TDR record of a rockhopper penguin female from Crozet detailing multiple foraging trips initiated within the same day. The second set of bars shows a short trip (see text for details).

performed during period 2, with more than one third before chicks were 5 days old (79.3 and 66.7%, and 13.4 and 12.1% during periods 2 and 4 at KER and CRO, respectively).

The number of daily trips initiated per female and per day (single and multiple trips pooled together) changed accordingly to locality, chick age and the interaction between these 2 factors (Fig. 2A, ANOVA: Locality: $F_1 = 65.53$, $P < 0.001$, Chick age: $F_{12} = 13.97$, $P < 0.001$, Locality \times Chick age: $F_{12} = 2.42$, $P = 0.005$). At both study sites, the number of daily trips decreased during period 2 without significant difference between KER and CRO (about 0.95 and 0.83, respectively, ANOVA: Locality: $F_1 = 3.10$, $P = 0.081$, Chick age: $F_3 = 4.92$, $P = 0.003$, Locality \times Chick age: $F_3 = 0.26$, $P = 0.855$). The number of daily trips decreased dramatically during period 3 at CRO (0.11/bird-day), but not in KER (0.58/bird-day), resulting large regional difference (Fig. 2A period 4, ANOVA: Locality: $F_1 = 74.16$, $P < 0.001$, Chick age: $F_5 = 0.79$, $P = 0.556$, Locality \times Chick age: $F_5 = 2.27$, $P = 0.052$).

Timing and duration of daily trips

Mean duration of multiple trips were not significantly different at both localities (6.5 ± 4.0 , $n = 93$ and 7.2 ± 5.1 h, $n = 70$ at KER and CRO, respectively; nested ANOVA: $F_{1,23} = 0.28$, $P = 0.600$), and were about half the duration of single trips. Overall, single daily trips lasted 13.1 ± 2.9 ($n_{\text{trip}} = 385$, $n_{\text{bird}} = 12$) and 13.5 ± 3.5 h ($n_{\text{trip}} = 304$, $n_{\text{bird}} = 16$) at KER and CRO, respectively (nested-ANOVA: $F_{1,26} = 0.29$, $P = 0.597$). Their duration changed over time with a similar pattern at the two localities (ANOVA: $F_{1,383} = 92.88$, $P < 0.001$, and $F_{1,302} = 46.43$, $P < 0.001$ at KER and CRO, respectively). It increased from period 1 to the beginning of period 4 and decreased thereafter (Fig. 3). Single trips, however, lasted about 2 hours longer at CRO than at KER during most of periods 2 and 3 (Fig. 3, for all

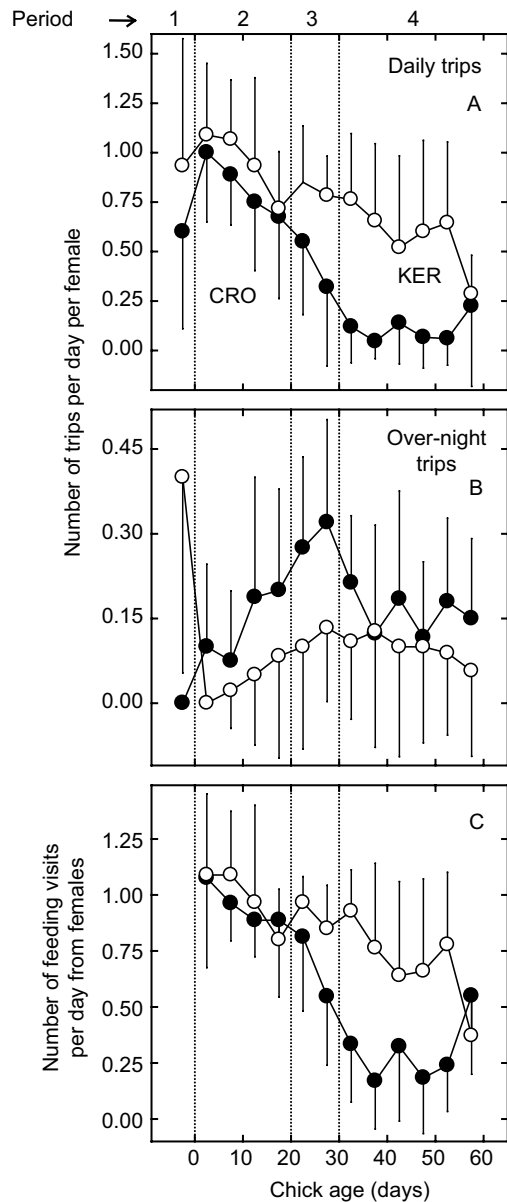


Fig. 2. Number of daily (A), and overnight (B) trips initiated per day and female provisioning rate (C) in relation to chick age at Kerguelen (empty circles) and Crozet (filled circles). Values are means \pm SD.

chick-age classes, nested-ANOVAs: all $F > 5.65$, all $P < 0.05$).

As departure and returning times of a given multiple-trip depends on the other(s) trip(s) performed during the same day, the timing of multiple trips is not independent. Thus, we focused the timing analysis on the most numerous and representative single trips during the chick rearing period. Birds departed to sea at 4.45 ± 1.63 h and 5.25 ± 1.97 h in the morning at KER and

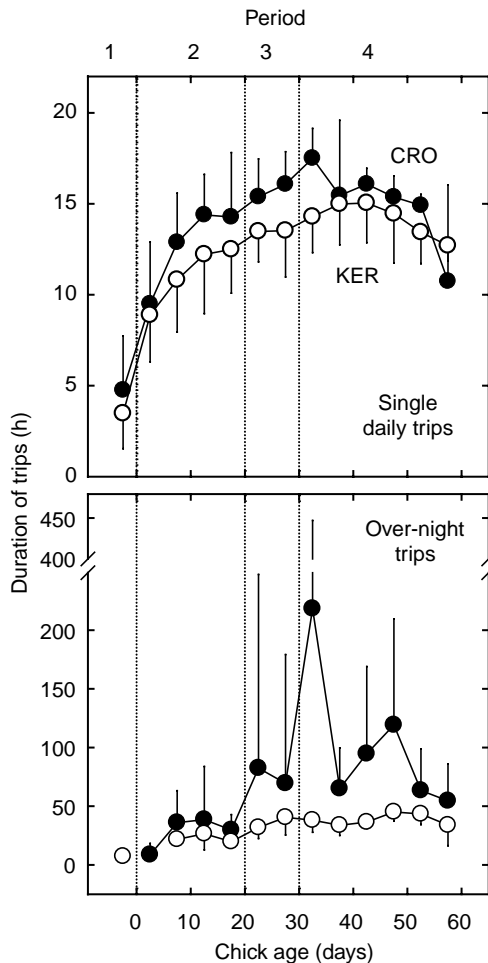


Fig. 3. Duration of single daily trips (top panel) and overnight trips (bottom panel), in relation to chick age at Kerguelen (empty circles) and Crozet (filled circles). Values are means \pm SD.

CRO, respectively (nested-ANOVA: $F_{1,26}=21.91$, $P=0.001$). This was constant during the chick rearing period at both sites (ANOVA: $F_{1,383}=0.94$, $P=0.337$ and $F_{1,302}=1.20$, $P=0.274$ at KER and CRO, respectively). Consequently, changes in trip duration with chick age were due to birds progressively going back to the colony later in the afternoon (ANOVA: $F_{1,383}=129.2$, $P<0.001$ and $F_{1,302}=58.9$, $P<0.001$ at KER and CRO, respectively).

Frequency of overnight trips

The number of overnight trips initiated per day and per female changed according to breeding locality and chick age, and the interaction between these two factors was also significant (Fig. 2B, ANOVA: Locality: $F_1=8.16$, $P=0.005$, Chick age: $F_{12}=2.331$, $P=0.007$, Locality \times

Chick age: $F_{12}=2.04$, $P=0.021$). At both sites, VHF birds initiated an increasing number of overnight trips until the chick was about 30 days old. Then, overnight trip frequency decreased until the end of period 4 (Fig. 2B). Statistically significant differences between localities took place when chicks were 21 to 30 days old (i.e. during the transition period 3, ANOVA: Locality: $F_1=16.10$, $P<0.001$, Chick age: $F_1=0.76$, $P=0.389$, Locality \times Chick age: $F_1=0.02$, $P=0.898$). In general, birds at CRO (0.22/bird-day) initiated about 2.5 times more overnight trips than those at KER (0.09/bird-day). It is worth noting that the picture is complicated by large standard deviations (Fig. 2B), which indicates that the decision to initiate an overnight trip was very different from one female to another at both sites.

Timing and duration of overnight trips

Short-time deployment (3 days) of TDRs precluded the recording of the rarest and longest overnight trips. Most of the data thus came from VHF birds, which all performed overnight trips. At KER, overnight trips never extended over more than 2 nights, while at CRO, 21% of overnight trips included more than 2 nights at sea (Kolmogorov-Smirnov test: max. difference = 0.625, $P=0.002$; Fig. 4). At CRO, the 25 trips that included at least 4 nights at sea were called long trips. All but one female performed at least one long trip, and 96% of long trips were performed after period 2. The mean age of chicks when females initiated their first long trip was 32.0 ± 7.4 days ($n=15$). We could distinguish between 2 kinds of long trips, the medium ones (5 to 9 nights at sea), and the very long ones (21 to 28 nights at sea; Fig. 4).

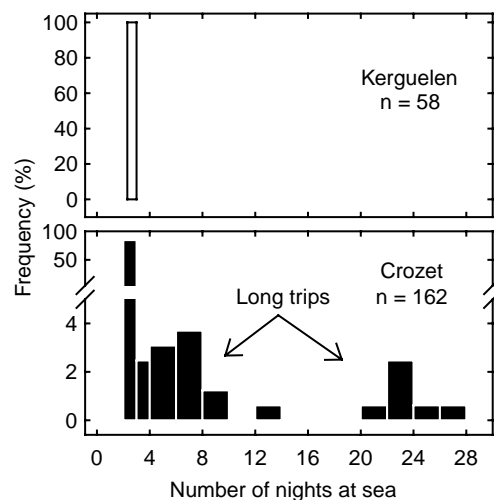


Fig. 4. Frequency distribution of the number of nights spent at sea per overnight trip at Kerguelen and Crozet.

The departure and arrival times of overnight trips were more widespread over the course of the day than those of daily trips, and they were not significantly different between sites. Similarly, duration of overnight trips was not significantly different between sites but changed according to chick age (Fig. 3). Like for daily trips, most of the average trip duration calculated by 5-day intervals tended to be slightly longer at CRO than at KER, very large values and standard deviations at CRO resulted from birds performing long trips (Fig. 3).

Estimated feeding frequency from females

To calculate an estimated feeding rate from VHF birds, we considered, following Barlow and Croxall (2002), that all foraging trips resulted in a feeding event at the return date of the female. During period 4, males also contributed meal provisioning. The feeding rate by female was similar at KER and CRO during period 2 (0.99 ± 0.14 and 0.98 ± 0.08 meal per day at KER and CRO, respectively), and decreased steeply during period 3 at CRO but not at KER (Fig. 2C). Consequently, the feeding rate by females was greater at CRO than KER during the period 4 (0.75 ± 0.21 and 0.40 ± 0.08 meal per day at KER and CRO, respectively; Fig. 2C).

From the records of 5 and 10 females that were continuously monitored during about 50 days, the total number of feeding visits was 45.4 ± 5.3 and 32.9 ± 5.5 at KER and CRO, respectively (t-test, $t = 4.20$, $P = 0.001$). We thus estimated that during the whole chick-rearing period (70 days), chicks from KER received about 64 meals and those from CRO received about 45 meals from the females.

Growth rates of chicks

Growth rate of chicks of female parents carrying transmitters was not significantly different from that of control chicks (44.9 ± 3.8 and 46.5 ± 6.7 g per day, $n = 12$ and 93 , and 41.6 ± 6.2 and 43.6 ± 6.7 g per day, $n = 16$ and 68 , for "VHF" and control chicks at KER and CRO, respectively). Growth rates were significantly different between KER and CRO (46.3 ± 6.4 and 43.2 ± 6.6 g per day, $n = 105$ and 84 , respectively, "VHF" and control chicks having been pooled), with no interaction between the type of devices and the localities (ANOVA: Device: $F_{1,187} = 1.80$, $P = 0.182$, Locality: $F_{1,187} = 5.33$, $P = 0.022$, and Device \times Locality: $F_{1,187} = 0.01$, $P = 0.915$).

There was no relationship between growth rate and both the estimated feeding rate and the total cumulated time at sea by the female during period 2 ($R^2 = 0.50$, $P = 0.049$, $n = 8$, and $R^2 = 0.01$, $P = 0.789$, $n = 16$ for esti-

mated feeding rate, and $R^2 = 0.08$, $P = 0.484$, $n = 8$, and $R^2 = 0.02$, $P = 0.651$, $n = 16$ for cumulated time at sea, at KER and CRO, respectively).

Discussion

Foraging pattern of female rockhopper penguins changed with chick age at both CRO and KER but in different manners between sites. The local foraging environment therefore seems to influence foraging pattern of rockhopper penguins.

Impact of the devices

In this study, foraging trip duration was identical for birds carrying smaller (VHF) and larger (TDR) devices, as were the growth rates of control vs VHF chicks during the brooding period at both CRO and KER. This suggests that devices had the same impact, presumably small, on female penguins at the two sites and that they provide valuable comparative information on the bird's behaviour. The streamlining of all of our devices may have accounted for such a result, since non-streamlined devices are known to increase trip duration in penguins (Wilson et al. 1986, Hull 1997). The occurrence of long trips at CRO cannot be attributed to the influence of the transmitters only, since females from KER (that were also fitted with transmitters) did not exhibit this behaviour.

Comparison with previous data in penguins

The average duration of daily single trips during the brooding period was similar to values reported in females from Amsterdam Island (12h09 and 10h43–11h11 in Chérel et al. 1999 and Tremblay and Chérel 1999, respectively). Thus, this parameter appears very consistent and geographically stable in female rockhopper penguins, suggesting that the regulation of trip duration during the brooding period may be a response to the rapid increase in chick's energy needs during the first week of their life (Brown 1987a) and/or a consequence of locally depleted resources following the first weeks of chick provisioning (Birt et al. 1987).

Foraging trip duration after the brooding period has never been longitudinally recorded for rockhopper penguins at various localities, although indirect measurements were collected by measuring feeding frequency using visual observations (Strange 1982, Stahl et al. 1985) or by the chick-weighing method (Williams 1982). Compared to the automatic scanning, both of these methods record information in a time sparsed manner and both underestimated feeding frequency. For

example, Williams 1982) estimated that chicks received 30 meals from both parents during the whole rearing period at Marion Island. This contrasts with our data, since females alone brought 1.5 to 2.1 times more meals, similar to the value reported for macaroni penguins (Barlow and Croxall 2002a). We suspect that the daily weighing protocol did not allow discrimination between one or two meals between two weighing sessions, thus underestimating the feeding frequency. As evidence, Williams 1982) recorded frequent chick-weight increase of more than 600 g, a value 2 to 3 times the stomach content mass recorded in some recent extensive studies (Tremblay and Cherel 2000, Tremblay and Cherel 2003).

In general, our results confirm that crested penguin (genus *Eudyptes*) females perform mostly daily foraging trips (Warham 1975), with rare overnight trips (Cherel et al. 1999, Barlow and Croxall 2002a, Tremblay and Cherel 2003). Daily trips associated with some overnight trips in varying proportions seem to be also the rule for all other non-*Aptenodytes* penguins, e.g. pygoscelids (Williams and Rothery 1990, Bengtson et al. 1993, Ballard et al. 2001, Watanuki et al. 2002), *Spheniscus* spp. (Scolaro and Suburo 1991, Radl and Culik 1999, Taylor et al. 2002), the yellow-eyed penguin *Megadyptes antipodes* (Moore 1999), and the little penguin *Eudyptula minor* (Gales et al. 1990, Collins et al. 1999).

The shortest trips, especially multiple trips, have not been previously described in rockhopper penguins but some very short trips were previously recorded in the macaroni penguin *Eudyptes chrysolophus* (Barlow and Croxall 2002a) and reported in the yellow-eyed penguin (Moore 1999), using a VHF recording technique. Although the minimum threshold differed for considering an absence as a foraging trip, it is noteworthy that short trips were only recorded using this method. We visually observed two TDR birds from CRO that went to sea for a short trip. A female went to sea early in the morning, came back ashore in the afternoon, and returned to sea for 02h26 where she performed 111 dives >3 m (Fig. 1). During this time, she regularly dived deeper than 30 m. The second female behaved similarly (unpublished data). Thus, short trips were devoted to foraging and were distinguishable from shorter absences (<90 min) devoted to preening and bathing (Y. Tremblay pers. obs.).

To our knowledge, very long trips have not been described before in rockhopper penguins. We do not know the behaviour of VHF birds out of the colony, but we recorded it in 2 females that carried a TDR for 10 and 11 days. Diving data indicated that these females did not land at all during this time; instead, they foraged during the day, resting at the sea surface at night (unpubl. data).

Spatial and temporal variation in provisioning behaviour

During the brooding period (period 2), females from KER and CRO behaved similarly. They made frequent visits to their chicks, mostly performing daily trips. This resulted in feeding the chicks almost once a day, with more food loads for very young chicks. Initially the chick's food intake is limited by its stomach capacity (Williams 1982), food load ranging from <100–142 g to 250–416 g at the beginning and the end of the brooding period, respectively (Williams 1982, Tremblay and Cherel 2003). Thus, it could be advantageous to receive frequent rather than large meals, especially for small chicks. The short trips that we observed were likely to meet this demand from the chicks, and were in accordance with observation from Downes et al. (1959) in the macaroni penguin. During this period, we reported for the first time that duration of daily trips increased with chick age. This temporal change at a medium time-scale can be a response to (1) changes in food quality (Tremblay et al. 1997) and/or availability (Cherel et al. 1999) and/or (2) a response to the increasing energetic needs of the chicks (Brown 1987a, Tremblay and Cherel 2003). As the productivity of the two study sites is expected to be contrasted, higher at KER and lower at CRO (see Tremblay and Cherel 2003), the explanation of this behaviour is probably multi-causal.

Females from KER and CRO reduced their feeding frequency from the brooding period (period 2) to the crèche period (period 4) (Warham 1963, 1975, Stahl et al. 1985). Although female *Eudyptes* penguins lose mass during period 2 (Tremblay and Cherel 2003), they have been reported to maintain stable body mass during period 4 (Croxall 1984, Guinard unpublished). Like in the Adélie penguin (Clarke 2001) and in the macaroni penguin (Barlow and Croxall 2002b), it is possible that longer foraging trips allowed rockhopper females to feed more for self maintenance, but this requires further investigations.

Although females from both sites reduced their provisioning rate, the frequency of the foraging trips dropped considerably at CRO compared to KER, as a result of both a greater number and longer duration of overnight trips. Longer trips have been found to be associated with lower adult body mass at departure in Adélie penguins (Clarke 2001, Watanuki et al. 2002), more distant foraging zones in macaroni penguins (Barlow and Croxall 2002b) and Adélie penguins (Clarke et al. 1998), and with differences in diet in rockhopper and macaroni penguins (Adams and Brown 1989) and in the Adélie penguin (Clarke et al. 1998). Females from KER and CRO weighed about the same mass at the end of the brooding period (Tremblay and Cherel 2003). Thus, it may not be the body mass at departure *per se*, but the body mass relative to the quantity of food close

to the breeding colonies that would shape the provisioning pattern of females when they need to restore and/or to maintain their body condition. During these longer trips, we expect that females fed in more distant zones at CRO (similar to rockhopper and macaroni penguins at Marion Island; Adams and Brown 1989), while at KER females probably remained closer to the colonies, with possibly rare excursions out of the inshore Golfe du Morbihan to forage.

Depending on the female individuals, 0 to 3 long trips were performed, and some went to sea for about 7–8 days, while others ceased chick feeding during half of the crèche stage. This suggests that other parameters such as body condition or experience of females may interfere, conditioning the decisions to initiate or to end a long trip.

At South Georgia, female macaroni penguins also initiated more longer trips during the crèche period (Barlow and Croxall 2002a), but their provisioning rate did not change. Trip duration of South-Georgia birds was longer during period 2 than period 4, a result that contradicts previous results on the same species at the same place (Trathan et al. 1998), and at Marion Island (Adams and Brown 1989). Contradictory results were also found in a comparative study between two distinct colonies in the Adélie penguin (Wienecke et al. 2000). This suggests that the response of penguins to the emancipation of their chick is highly variable and thus, strongly dependent on the environmental situation.

We show that the spatial and temporal comparative method is useful in interpreting provisioning behaviour since none of our conclusions could have been found in separate studies. Provisioning behaviour is likely to vary substantially at medium temporal scales (5 days intervals in this study), thus, comparison between studies or data sets must consider this component.

The paradox of the crèche period at CRO

Spatial variation in the regulation of foraging pattern by females was found to concern mainly the crèche period, and to take place through various proportions of overnight trips. These trips were (for some of them) surprisingly long at CRO, leading to relatively low provisioning rate from the females. Such long trips may have led to breeding failure, since chicks should have starved if not enough provisioned. Paradoxically, none of our field observations support this claim. Data derived from our chick mass survey indicates that 35% of chicks were missing after the first 22 days (period 2, 1.6 chick per day), and only 10% for the next 41 days (period 3 & 4, 0.24 chick per day). No chick was found starving or emaciated. Females that initiated long trips regularly came back and forth afterward, suggesting they were still feeding their chick.

We suggest that males compensated the absence of feeding from females who undertook a long trip. This observation was made in the macaroni penguin, with some males participating more than others in chick provisioning (Barlow and Croxall 2002a). If this true, males' contribution would be facultative and variable according to environmental parameters, as it was already described in several species of passeriforms (Wittenberger 1982, Wolf et al. 1988, Dunn and Robertson 1992, Whittingham and Robertson 1994, Kuitunen et al. 1995). Ultimately, this potential buffering role of males is likely to provide more flexibility in provisioning behaviour. This could extend the panel of foraging plasticity at the scale of the breeding pair, a possible mechanistic explanation for sexual differences in provisioning behaviour. Further scientific investigations are needed on this topic, since our data suggest rather than support this hypothesis.

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