

Observations on the chick-rearing strategy of yellow-eyed penguins (*Megadyptes antipodes*) on Otago Peninsula, New Zealand

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Abstract The chick-rearing strategy of yellow-eyed penguins (*Megadyptes antipodes*) breeding on Otago Peninsula was examined in 12 pairs of adults, between 17 November 1996 and 31 March 1997, from time of hatching of chicks to parental moult. Differences in behaviour of both male and female parents towards one- or two-chick broods were not statistically significant, but behaviour towards all offspring changed significantly over time with respect to breeding phases. Differences observed resulted from a change in feeding procedure. "Food-walks" started significantly earlier in the course of a feeding session as time progressed, while major components (duration and number of individual feeds) decreased significantly. The changes observed are interpreted as resulting from the chicks' growing independence in concert with the parents' decreasing urge to spend time with their offspring outside the still necessary feeding encounters. An evolutionarily stable environment and reliable food source are suggested as the reason for the lack of development of different chick-rearing strategies for different numbers of offspring or for male and female breeders.

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Keywords yellow-eyed penguin; *Megadyptes antipodes*; chick-rearing strategy; one-chick parents; two-chick parents

INTRODUCTION

The yellow-eyed penguin (*Megadyptes antipodes*) breeds along the south-eastern coast of the South Island of New Zealand, on Stewart Island, Codfish Island, and in the Auckland and Campbell Island groups (Richdale 1957). It is one of the largest-bodied penguins breeding in the temperate zone (Stonehouse 1970), and is present year-round in its breeding areas. Both sexes help in rearing the offspring, usually 2 chicks. Sometimes only 1 egg is laid, but more often 1-chick broods will result from an infertile egg or chick death before or after hatching.

Loss of natural breeding habitat and high chick mortality resulting from predation by introduced mammals are believed to have caused a serious decline observed in the South Island population (Darby & Seddon 1990). Today the yellow-eyed penguin is considered to be the rarest of extant penguins (Darby *et al.* 1990).

Since the early 1980s, a variety of conservation measures have been employed (including predator control, farm stock removal, nestboxes, habitat revegetation) with varying success to protect the existing populations. In addition, assessment of the species' reproductive strategy was very important, as these are key factors for both adult survival (birds that will live to breed again) and recruitment of young (surviving chicks that will eventually breed).

The chick-rearing strategy may be considered a mechanism that allows the adult to balance the needs of its offspring against the costs to itself. When this study was conducted, artificial brood reduction (removal of 1 egg from a 2-egg clutch) was discussed as a possible conservation measure for yellow-eyed penguins in years of expected low food availability. It was suggested that the mortality of the adults could be reduced if they were relieved of the burden of rearing 2 chicks (McKinley, quoted in Edge 1996). This study investigated the behavioural differences between one-chick and two-chick parents. Although yellow-eyed penguins do not exhibit any active brood-reduction mechanisms (Seddon & van Heezik 1990), it was hypothesised that parents would opportunistically adjust their behaviour to the number of young reared. For this study, we assumed that (a) 1-chick parents do not need to find as much food for their offspring as 2-chick parents, and (b) that the reduction in food required would be reflected in the return behaviour, with 2-chick parents spending more time at sea and returning later during the day than 1-chick parents.

Biparental care may result in male and female parents contributing differently to the rearing of the offspring (e.g. *Eudyptes* spp. and *Aptenodytes forsteri*, Williams 1995; *Fregata magnificens*, Trivelpiece 1987). Yellow-eyed penguin parents are, however, generally thought to share all chick-rearing duties evenly (Williams 1995), and this study did not expect any gender differences in the contribution of the two parents. However, we did expect to detect changes in parental behaviour towards offspring in the course of time, as the needs of both, parents and offspring, changed.

In this paper we report the results of our investigation of the potential differences in parental investment mentioned, focusing on the time between hatching of the offspring and onset of parental moult after the young have fledged.

STUDY AREA AND METHODS

Observation area

The private reserve of Pipikaretu Beach (4 ha) is part of a 210 ha sheep farm situated on Otago Peninsula (45°51'S, 170°45'E), on the South Island of New Zealand. The reserve consists of a basin enclosed by steep hills on three sides and separated from the beach and ocean by a line of dunes. Its history of conversion to farming means that almost nothing remains of the native forest that originally

covered the whole peninsula. As a result of the sandy soil and previous stock activity, Pipikaretu Beach is dominated by introduced grasses (Poaceae), interspersed with shrubs, including *Hebe elliptica*, *Myoporum laetum*, and *Urtica ferox*, and some trees such as *Griselinia littoralis*, most of which have been planted by the reserve owner. Conservation measures include the provision of A-framed nestboxes, predator control (trapping and shooting), and close monitoring of each bird. All birds are banded. The reserve was established in 1985 when only a few breeding pairs of penguins frequented the area. The number of breeding pairs had risen to 36 (1996/97), and the total number of resident penguins (adults and juveniles) fluctuated around 100 birds.

The main observation area (1.5 ha) for this study was in the northern part of the reserve, where dug-out trenches and observation hides had been built. The system of trenches and hides was constructed to allow guided tours to get close to the penguins without disturbing or frightening the birds, and these hides were used for all observations made in this study.

Banding and marking

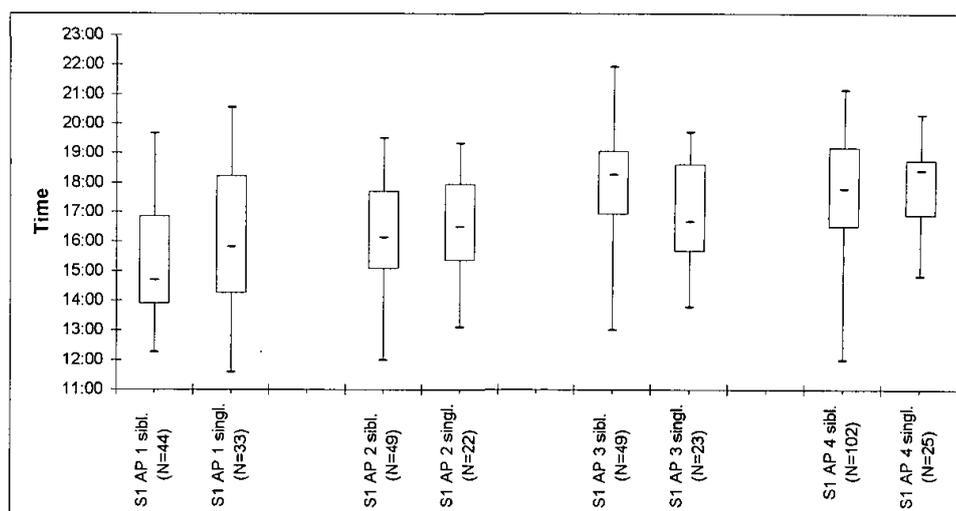
Twelve banded breeding pairs were observed throughout the chick-rearing period. To facilitate identification at a distance, 1 adult of each pair was colour-banded, and 1 sibling of each pair of chicks was colour-marked, using a variety of methods including white water-based paint, 3% hydrogen peroxide, and water- and alcohol-based markers. The sex of the study birds had been determined during previous studies, using either or both the copulatory position (Seddon 1989) and head and beak morphometrics (Darby & Seddon 1990).

Observations

Between 17 November 1996 and 31 March 1997, KS visited the reserve on 108 days, for a total of 424 h 9 min of observation. On 17 November 1996, the chicks of 6 of the 8 sibling-rearing pairs and 2 of the 4 one-chick-rearing pairs had already hatched. All pairs were followed through until after the departure of their respective offspring, and the study finished when the parents started to moult.

Four phases of parental care were identified: (1) guard stage (after hatching, when one or the other adult remains at the nest); (2) transition period (when one adult remains at the nest on some days, but both will be absent on others); (3) post-guard stage (when both adults forage at sea during the day, i.e. from the end of the transition period

Fig. 1 Return times of 2- (sibl.) and 1-chick- (singl.) parents for first feeding sessions (S1) during 4 consecutive age-periods (AP 1 - 4) of their offspring (Nov. 1996 - Mar. 1997). Numbers of returns observed are given in parentheses for each boxplot.



until fledging); and (4) pre-moult period (between fledging of the offspring and onset of parental moult).

After initial observations before the study began, observation times were restricted mainly to between early afternoon (1300) and the onset of darkness (varying from 1830 to 2130), as most parents tended to return during this part of the day. During that time, nests were frequently checked from the observation hides to record which parent was on the nest and which returned at what time. These nest-checks lasted from 1 to 5 min and were made by KS (at least 3 times day⁻¹, 6 days week⁻¹) or by a tour-guide (3-10 times day⁻¹, depending on number of tours conducted, 7 days week⁻¹). Before fledging (when they were c. 80 days old), all chicks were banded with stainless steel flipper bands, weighed, and measured.

For comparison between 2- and 1-chick-rearing pairs, the age of the offspring at the end of the guard stage, the beginning of the post-guard stage, and at fledging was recorded. The length of the transition period between guard and post-guard stage was recorded, as well as the duration of the fattening period between chick independence and the start of moult in the adults. The condition of siblings and single chicks were compared by their weight and by measurements of the head and heel.

To obtain more detailed information on feeding behaviour and check for more subtle male-female differences, 3 pairs rearing sibling chicks were chosen for closer observation. For each feeding session, return time and sex of the feeding adult were noted. In addition, the number of individual feeds each chick received, the duration of individual feeds, the duration of the feeding session, and movements during the feeding session ("food-walk") were recorded on audio-tape to be

transcribed immediately after return from the field. "Food-walk" was used to denote when parents moved away from the chicks, and the chicks followed. Because the movement lacked speed and other characteristics noted by Bustamante *et al.* (1992) for the term "feeding chase", the new term was used. Bouts of continuous observation (range 2-7 h) were carried out 6 days week⁻¹ from 9 January 1997 to 21 February 1997, by which time all 6 chicks had fledged. Conducting a hands-off study in a conservation reserve necessitated the amount of food transferred be estimated rather than measured. The number of individual feeds given to a chick was counted (feeding frequency) and the length of time food was passed from adult to chick was measured using a stop watch (feeding time).

To detect changes through time, the chick-rearing period was divided into 4 age-periods (AP:1-4) of 25 days each (i.e. parental behaviour towards chicks of the same age was compared), and parental return times for first and second feeding sessions were compared separately for each period. The periods were chosen because the end of the 2nd age-period (50 days) corresponded roughly to the start of the post-guard stage, as reported in the literature (Richdale 1957). The end of the fourth period (100 days) was close to the cited average age at fledging (103 days, Richdale 1957). Each of these 2 "natural breaks" in the chick-rearing period was divided in half (resulting in 2 periods of 25 days) to avoid grouping of chicks of too wide an age range. Furthermore, the total period of continuous observation (42 days) was divided into 2 observation intervals of equal length (21 days each), which were then compared. This was possible, because all chicks observed during continuous observation had hatched on the same day.

Table 1 "Chick-rearing schedule" (in days of chicks' age) at 8 two-chick and 4 one-chick nests observed (Nov 1996 - Mar 1997).

	Two-chick nests		One-chick nests		<i>P</i> (<i>t</i> - test)
	Mean	SD	Mean	SD	
End of guard stage	54.09	3.807	51.75	0.957	0.255
Duration of transition period	10.09	4.888	14.25	2.754	0.136
Start of post-guard stage	64.18	7.111	66.00	2.944	0.634
Fledging	109.00	2.449	108.50	4.123	0.774

As several statistical tests were carried out on data gathered from a few individuals only, the authors' observational impressions are presented alongside the test results.

RESULTS

Two- and one-chick-rearing parents

As far as 2-chick nests are concerned, return times shifted towards later in the day from age-period 1 to 3 (Fig. 1). After that there was a slight regression so that during the 4th age-period, 1st feeding sessions occurred, on average, slightly earlier than during the 3rd. In contrast, 1-chick parents' return times showed a constant trend (AP: 1 - 4) towards later returns for first feeding sessions, with the smallest increase in average return time being observed between the age-periods 2 and 3. However, even the most marked difference between 1- and 2-chick-rearing parents, seen during age-period 3, was not significant at the 5% level (Mann-Whitney *U*; AP 1: $n = 77$, $P = 0.810$; AP 2: $n = 71$, $P > 0.5$; AP 3: $n = 72$, $P = 0.0548$; AP 4: $n = 127$, $P > 0.5$). We found no differences between 1- and 2-chick nests in return times for 2nd feeding sessions, which were predominantly recorded during the post-guard stage (i.e. during AP 3 and 4: Mann-Whitney *U*; AP 3: $n = 43$, $P > 0.05$; AP 4: $n = 81$, $P > 0.05$).

The guard stage ended on average slightly later at the 2-chick nests than at 1-chick nests (Table 1). The transition period lasted 7-18 days at 2-chick nests and 11-17 days at 1-chick nests. Two-chick parents entered the post-guard stage slightly earlier than 1-chick parents. Sibling chicks fledged on average 0.5 days later than single chicks. None of the differences found was statistically significant (Student's *t*, $n = 12$, all $P \gg 0.05$, also see Table 1).

On average, parents that reared 2 chicks needed fewer days than 1-chick parents to fatten before moult (means: 20.34, 23 days), but the differences were not significant (Student's *t*, $n = 12$, $P = 0.194$). No statistically significant

difference was found between body masses of siblings and single chicks (mean \pm SD: siblings, $5.30 \text{ kg} \pm 0.5650$, $n = 48$; single chicks, $5.21 \text{ kg} \pm 0.6633$, $n = 19$; Student's *t*, $P = 0.892$) or other morphometrics, such as skull length (mm, mean \pm SD): siblings, 135.69 ± 3.4108 , $n = 35$; single chicks, 136.00 ± 4.4518 , $n = 12$) and heel measurements (mm, mean \pm SD): siblings, 127.63 ± 3.6063 , $n = 35$; single chicks, 127.92 ± 4.3580 , $n = 12$) (skull and heel: 2-way ANOVA: $n = 47$, $P > 0.5$).

Male and female parents

Although females returned consistently earlier than males, differences between 2-chick-rearing male and female parents, in return times for both 1st and 2nd feeding sessions were not quite significant. During the 3rd age-period, after the onset of the post-guard stage, female parents of 4 nests observed were more likely to feed during first feeding sessions than their mates (χ^2 , $df = 1$, $n = 22$, $P = 0.0881$), who were more often observed to be responsible for the 2nd meal of the day (χ^2 , $df = 1$, $n = 12$, $P = 0.0833$). Male-female ratio was 0.47 ($n = 22$) during the 3rd age-period, because females returned about twice as often for the 1st feeding sessions observed. This difference was not nearly as marked during the 4th age-period, during which male-female ratio was 0.8 ($n = 72$).

Regardless of the sex of the parent, if only 1 of 2 siblings was present at a feeding session, it did not get a double share. However, it was fed more often and longer than if its sibling had been present (mean 1 sibling/mean both siblings = 0.67-0.7).

Of 6 parents, only 1 female (#11778, nest 17) showed a significant preference of 1 chick over the other, feeding that chick significantly longer (Mann-Whitney *U*, $n = 22$, $P = 0.0171$) and more often (Mann-Whitney *U*, $n = 22$, $P = 0.0242$). Both chicks of that pair were above average weight, and the "favoured" sibling was the heaviest that season at 6.8 kg.

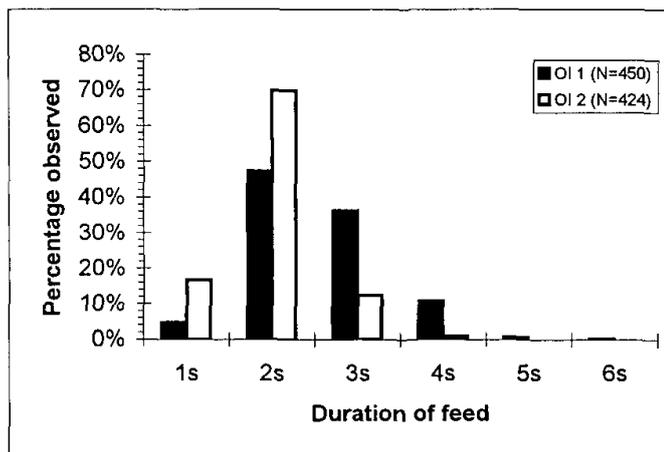


Fig. 2 Duration of feeds given during the 1st (OI 1) and 2nd (OI 2) observation interval by parents rearing 2 chicks (3 pairs, 115 feeding sessions observed). *n* = number of feeds observed.

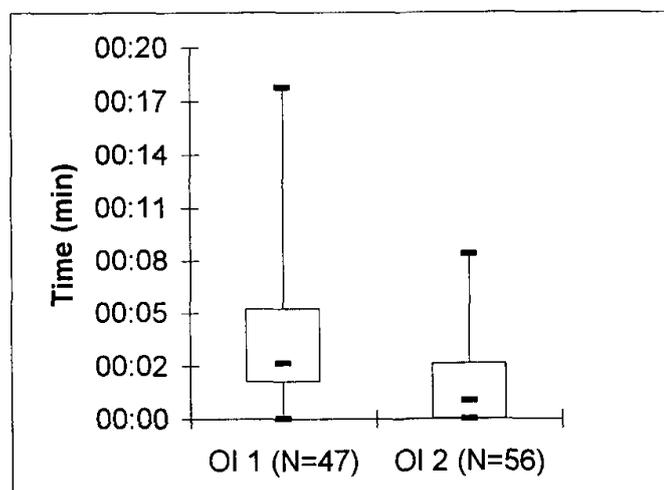


Fig. 3 Time (min) between 1st feed given and start of “food-walk” observed for 3 pairs of 2-chick parents. First (OI 1) and 2nd (OI 2) observation interval are shown separately. Number of sessions observed in parentheses.

Changes over time

For all pairs observed, return times shifted towards later in the day during the course of the chick-rearing period, but the change was continuous for 1-chick parents, whereas 2-chick parents returned earlier during the 4th age-period than during the 3rd.

During the chick stage, both male and female parents decreased the duration and number of the individual feeds given to their offspring (Fig. 2), hence the time during the feeding session that was spent actually passing food. While the duration of the feeding sessions — the time from first to last feed recorded — did not change over time, the time spent moving between the individual feeds (“food-walk”, Fig. 3, 4) increased significantly. Throughout the observation period, male and female

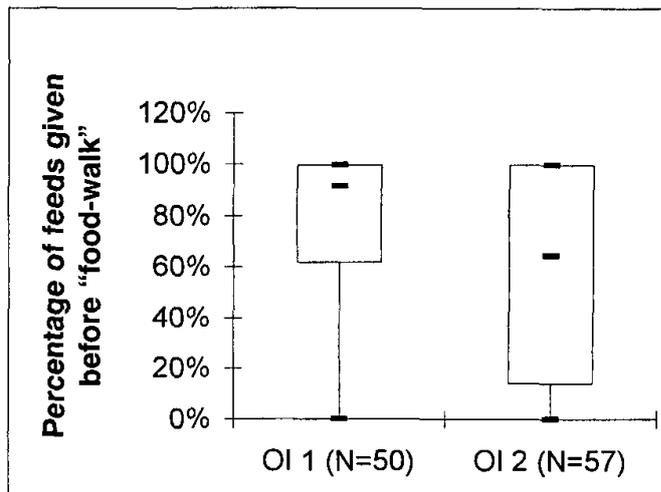


Fig. 4 Feeds given before start of “food-walk” in percent of all feeds given during the feeding session. Observations on 3 pairs of 2-chick parents. First (OI 1) and 2nd (OI 2) observation interval are shown separately. Number of sessions observed in parentheses.

parents did not differ significantly in the time they started the “food-walk” (Mann-Whitney *U*, *n* = 103, *P* = 0.9408) or the number of feeds given while still stationary (Mann-Whitney *U*, *n* = 103, *P* = 0.2900). During the 2nd observation interval both sexes started the “food-walk” significantly earlier in the course of a feeding session (Mann-Whitney *U*, *n* = 103, *P* = 0.0006, also see Fig. 3), and significantly fewer feeds were given before the “food-walk” started (Mann-Whitney *U*, *n* = 103, *P* = 0.0216, also see Fig. 4).

DISCUSSION

We found that chick-rearing strategies of 2- and 1-chick parents did not differ, but all parents changed their behaviour towards their offspring during rearing. Likewise, differences found during the post-guard feeding sessions also occurred through time rather than between male and female parents. We suggest that the changes in parental return behaviour (measured as differences between the 4 age-periods used in the study) exhibited by 2- and 1-chick parents alike were influenced by 2 factors: at first parents foraged increasingly more and longer as the chicks grew more demanding (guard stage and part of the transition period; roughly corresponding to age-periods 1 and 2), with the increase in demand being slightly slower and more gradual at 1-chick nests.

During the post-guard stage (roughly corresponding to age-periods 3 and 4), further changes in the time of parental return resulted from a decreasing inclination to

look after the chicks outside feeding sessions as well as the increasing need to rest without being disturbed by the offspring. As these changes were seen in 2- and 1-chick parents alike, number of offspring does not seem to influence these aspects of the chick-rearing strategy.

Two-chick parents are thought to have brought home more food than 1-chick parents, as otherwise significant weight differences between sibling and single chicks would have been recorded. As 2- and 1-chick parents did not differ in the time of return for feeding sessions, the different stages in the chick-rearing schedule, or the age at fledging of sibling and single chicks, the additional strain seems to be accommodated by the 2-chick parents. The mechanisms employed, however, are not known exactly at present. Yellow-eyed penguin parents are able to successfully fledge up to 3 chicks (van Heezik & Davis 1990), and sibling chicks exhibit a low level of inter-sibling aggression (Schuster, unpubl. data). These facts further indicate that rearing 2 chicks is normally possible without unduly reducing the survival chances of the parents. In other words, the maximum food-gathering capacity of 2 parents is sufficient to sustain both themselves and 2 chicks. One-chick parents would, consequently, forage below their maximum food-gathering capacity. For yellow-eyed penguins then, in general, food-availability does not seem to be a limiting factor in rearing chicks.

Because the duration of the pre-moult period did not differ significantly between 2- and 1-chick parents either, 1-chick parents might forage at a more leisurely rate during that period, and 3 weeks are usually sufficient for healthy 2-chick as well as 1-chick parents to recover from the strain of chick-rearing. It seems as if selection pressure on the evolution of different chick-rearing strategies for 2- and 1-chick parents has been low indeed. Unlike in other seabirds, such as the magnificent frigatebird *Fregata magnificens* (Trivelpiece & Ferraris 1987), and also in the yellow-eyed penguin's closest relatives, the crested penguins (*Eudyptes* spp.) (Williams 1995), different strategies have not been found for male and female parents.

Yellow-eyed penguin males face an ever-increasing shortage of females in the course of their lifetime (Richdale 1957). This could have favoured the long-lasting pair-bond characteristic of yellow-eyed penguins, which in turn would select against different reproductive cycles (which exist in the frigatebird) that might result in different chick-rearing strategies employed by male and female parents.

Differences in the post-guard feeding sessions, observed in the course of time (measured as differences between the 1st and 2nd observation interval) resulted from a change in the feeding procedure. While the duration of the feeding sessions remained unchanged, its major components (duration of individual feeds, number of feeds given per session) decreased significantly, because the "food-walks" started significantly earlier in the course of a feeding session as time progressed.

As long as feeding was basically stationary, individual feeds tended to be longer and to occur in quicker succession. In the course of the "food-walk", however, the time between individual feeds was increased as the chicks had to catch up with the parent. The duration of individual feeds decreased with the parent walking away.

We attribute the changes observed in the course of time to the chicks' growing independence dove-tailing with the parents' decreasing inclination to look after them. It is also probable that a further reason for reduced parent-offspring contact might be the adults' increasing need to look after themselves. Although the amount of food brought home to feed 2 chicks supposedly reaches its asymptote around the end of the guard stage and remains unchanged afterwards — assuming the results recorded for pygoscelid penguins by Lishman (1985) are true for yellow-eyed penguins as well — the parents forage more often than they would if they were only feeding themselves. Any chick-rearing strategy must include mechanisms that ensure the parent feeds the offspring enough to keep it healthy and alive, but at the same time does not over-exploit its own resources. For this, it is very important that the parent stops taking care of the offspring and starts looking after itself at a time that allows them both to survive.

The lack of different chick-rearing strategies for different clutch sizes found in this study is in line with the general lack of brood-reduction mechanisms exhibited by the yellow-eyed penguin (van Heezik & Davis 1990), and confirms the penguins' vulnerability to adverse feeding conditions.

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