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Nest defence by Chinstrap Penguins Pygoscelis antarctica *in relation to offspring number and age*

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We manipulated clutches of Chinstrap Penguins to examine the effects of brood size and offspring age on brood defence levels. Nest defence intensity increased with increasing offspring age. Experimental birds reduced nest defence intensity after losing one egg. These results support predictions derived from life-history theory which assumes changes in nest defence intensity to be related to changes in the reproductive value of the brood.

Animals strive to maximize their lifetime reproductive success. With respect to a single reproductive event, two important factors that may affect this long-term strategy are the value of the current brood and the future reproductive potential of the parent (Williams 1966, Pianka and Parker 1975). A trade-off between current and future reproductive investments is expected in long-lived species (Pugesek 1983, Sargent and Gross 1986).

When animals defend their offspring, they incur risks that may lead to death (Buitron 1983, Walter 1983, Curio and Regelmann 1986). For a long-lived species, a reduction in the number of offspring during a reproductive event should cause a decrease in the intensity of offspring defence, because the value of the current brood is depreciated. Indeed, it has been shown that the intensity of nest defence is positively correlated with offspring number (Montgomery and Weatherhead 1988, Redondo 1989). In addition, it has been suggested that expected future benefits for parents may influence the intensity of nest defence. As nesting progresses, the brood becomes more valuable because the difference between survival probabilities of adults and young decreases, and thus expected future benefits for adults increase (Andersson et al. 1980).

In this paper we present the results of a study of nest defence by Chinstrap Penguins *Pygoscelis antarctica*. Our aim was to examine the effect of brood size as well as brood age on brood defence levels.

Study species and methods

Pygoscelid penguins are long lived species which first reproduce when they are 3–7 years old (Ainley et al. 1983). The Chinstrap Penguin is a colonial nester in which laying is rather synchronized at the colony level (Moreno et al. 1994). Clutch size of this species is usually 2, and eggs are incubated by both sexes in alternate shifts each lasting 5–6 days; the clutch is not replaced if lost, except if the first egg is lost before the second is laid, then that one egg is replaced (Marchant and Higgins 1990).

The field work was conducted at the Vapour Col Chinstrap Penguin colony on Deception Island (63°00′ S, 60°40′ W), South Shetland Islands, in December 1992. We arbitrarily chose four large sub-colonies (>400 nests) located in the centre of the colony. In these breeding groups we individually marked, with wooden sticks, 60 nests containing two eggs, marking every third or fourth nest along transects initiated at the periphery and running along the longest axis of sub-colonies. We included only central nests, which we defined as those that were separated by at least two nests from the periphery of the sub-colony. We randomly allocated 30 nests as "control" and 30 as "experimental." One day after marking the nests, we individually marked incubating birds at these nests with numbered aluminium flipper bands. Two days later, we manipulated all nests by removing one egg. Eggs removed from control nests were immediately returned to their respective nests, but eggs removed from experimental nests were placed under incubating adults in nearby nests and returned to their original nests after the experiment finished.

To quantify nest defence behaviour, the same observer slowly approached each marked nest, put his hand (protected by thick gloves) about 20 cm from the incubating penguin, and remained immobile. Nest defence was the number of pecks received during the next 30 s. Our intention was to expose the incubating bird to a mild threat. Such a threat was considered appropriate for our purpose because Chinstrap Penguins react to the presence of human disturbance in a way that was relevant for testing predictions about variations in nest defence intensity (Viñuela et al. 1995). Nest defence was quantified prior to egg removal, just before the adults were banded (hereafter $time_1$), and again three days after egg removal ($time_2$). If on the last occasion the marked bird was not at the corresponding nest because of having been relieved of incubating duties by its mate, we visited its nest daily until the marked bird was again found incubating, when its nest defence behaviour was recorded. On average, the number of pecks at $time_2$ was recorded a few days before hatching. The mean time (± 1 s.d.) elapsed between $time_1$ and $time_2$ was similar for control and experimental nests (6.80 ± 1.0 days vs. 6.97 ± 1.2 days, respectively, Mann-Whitney U-test, $U = 393$, $p = 0.26$).

A temporal increase in nest defence could be due not to changes in offspring age but to a positive reinforcement as a result of parents having been approached and handled (Knight and Temple 1986). To control for this, we recorded the pecking rates of 50 Chinstrap Penguins that were incubating two eggs in sub-colonies not previously entered by us, and compared these data with those recorded for penguins in the control group at $time_2$. The data for previously undisturbed birds were recorded immediately after we had finished recording all data in the control group.

Throughout the paper means are presented ± 1 s.d.

Results and discussion

The control and the experimental group contained 19 males and 11 females each (see Amat et al. 1993 for sexing procedure). There were no statistically significant differences in the mean number of pecks between the control and the experimental groups before egg removal (Table 1; $t = 1.56$, $p = 0.125$).

The number of pecks by penguins in the control group increased 1.68 ± 1.56 times from $time_1$ to $time_2$ (calculated for each penguin individually as no. pecks at $time_2$/no. pecks at $time_1$ and then averaged) (Table 1). This increase was significant when tested against the null hypothesis of no increase (Student's paired t-test, $t = 2.39$, $p = 0.024$). Among individuals in this group, responses were consistent between $time_1$ and $time_2$ ($r = 0.68$, $p < 0.001$). The temporal increase in the number of pecks was not due to a positive reinforcement, as the mean number of pecks of control birds at $time_2$ and that of previously undisturbed birds (27.0 ± 14.0) were similar (Student's t-test, $t = 0.32$, $p = 0.748$).

We also found a temporal increase in the number of pecks in the experimental group (Table 1). In this case the average number of pecks was 1.31 ± 0.53 times greater at $time_2$ than at $time_1$, and although lower than in the control group was also significant when tested against the null hypothesis of no increase (Student's paired t-test, $t = 3.00$, $p = 0.005$). Therefore, these results support the prediction that nest defence intensity increases with increasing offspring age.

Table 1. Mean number of pecks (± 1 s.d.) directed by incubating Chinstrap Penguins at an observer during 30 s, before egg manipulation ($time_1$, normal clutch size not reduced) and after egg manipulation ($time_2$, normal clutch size of 2 reduced to 1) in control (egg removed replaced immediately after manipulation, $n = 30$) and experimental (egg removed not replaced, $n = 30$) groups.

	Number of pecks	
Group	$Time_1$	$Time_2$
Control	20.1 ± 9.5	26.1 ± 9.4
Experimental	16.6 ± 7.6	20.6 ± 10.1

We also tested whether the intensity of nest defence was lower in the experimental than in the control group, as a result of birds in the first group having lost one egg, by comparing differences in pecking rates between the two groups in two ways. First, we compared the mean number of pecks between control and experimental birds at time$_2$, and found a significant result (Table 1; Student's t-test, $t = 2.25$, $p = 0.028$). Second, we tested the rate of change for the experimental birds against the null hypothesis of $H_0 = 1.68$ (the same rate of increase as in the control group), and also found a significant result (Student's t-test, $t = 3.81$, $p < 0.001$). Therefore, these results indicate that, when the effect of the temporal increase is controlled, experimental birds actually reduced the number of pecks after losing one egg.

In conclusion, Chinstrap Penguins defended their nests less vigorously when brood size was reduced. This may be because the reproductive value of the current brood decreased, and by reducing investment accordingly, an individual could increase its lifetime prospects. Wallin (1987) found some evidence supporting the last possibility for Tawny Owl *Strix aluco* females. In a previous observational study on Chinstrap Penguins, Viñuela et al. (1995) found that brood size did not affect nest defence intensity. However, in most experimental studies in which brood sizes have been manipulated, both in birds and fishes, results are in accordance with theoretical predictions (e.g., Carlisle 1985, Ridgway 1989, Thornhill 1989, Lavery and Keenleyside 1990, Wiklund 1990, this study).

Moreover, our data also indicate that nest defence intensity increased with increasing offspring age, again suggesting that the value of the current reproductive effort is important. Presumably, this may be due to an age-related increase in the probability of current offspring surviving to reproduce (Andersson et al. 1980).

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