

# Correlations between body size, defensive behaviour and reproductive success in male Little Blue Penguins *Eudyptula minor*: implications for female choice

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Field studies exploring relationships among body size, defensive behaviour (including vocalizations) and reproductive success in male Little Blue Penguins *Eudyptula minor* were conducted to identify behavioural and physical attributes that might provide females or opponents with information on male quality. Head length provided a simple estimator of body size in both sexes. Nests defended by large males produced eggs and chicks earlier in the breeding season, and contained chicks that grew more quickly than chicks in nests defended by small males. In contrast, female body size did not affect any of the reproductive parameters we measured. The pitch of male defensive calls varied significantly with male size, so females (or opponents) could potentially gauge male size by assessing the calls. Large males were also more likely to respond vocally to simulated nest intrusions. As a result, by 'keeping company' with prospective partners early in the breeding season, females can obtain information about males that would allow them to select better partners and improve their own reproductive potential.

## INTRODUCTION

Theoretical models of sexual selection have focused on the evolution of female mate choice (Andersson 1994). In particular, the relationship between male body size and female preference has been most thoroughly investigated, because male body size can show strong positive correlations with reproductive success in a wide range of species (e.g. Ewing 1961, Borgia 1981, Kraak *et al.* 1999). Large males are more successful during male–male competitions (e.g. Arak 1983, Rowland 1989), court more frequently (e.g. Partridge *et al.* 1987, Abell *et al.* 1999) and acquire food more efficiently (Ryan 1980, Wiklund & Kaitala 1995) possibly making them superior parents (e.g. Downhower & Brown 1980, Côte & Hunte 1989). Thus, body size should be an important component of female mate choice.

Davis and Speirs (1990) suggested that female Adélie Penguins *Pygoscelis adeliae* may prefer larger mates. Penguins are sexually dimorphic in body size, with males being slightly larger than females (Agnew & Kerry 1995, Williams 1995). Larger than average

male Adélie Penguins were found to breed earlier than smaller ones, suggesting that large males were preferred by females (Davis & Speirs 1990). Penguins normally have three prebreeding stages: courtship, a prelaying exodus and a prelaying stage. In Adélie Penguins, males then fast for around 10 days immediately following egg-laying, to incubate the eggs while females replenish their fat reserves at sea. Davis and Speirs (1990) argue that the main advantage of selecting large males is that 'fat birds can fast longer', thus reducing the chances of nest desertion and the costs of reneating. However, in many penguins, the post-laying fast is only 1–2 days long (e.g. Gentoo Penguins *Pygoscelis papua*, Trivelpiece *et al.* 1983, Jackass Penguins *Spheniscus demersus*, Williams & Cooper 1984); temperate and tropical penguins also tend to have shorter incubation shifts than Adélie Penguins (Williams 1995). As a result, 'fast endurance' may not always be the key factor promoting sexual dimorphism or a female preference for large males. On the other hand, size could contribute to the success of penguins in a number of other ways (e.g. male–male competition, feeding ability). However, the ways in which male size might influence the reproductive success of female penguins have not yet been explored in any detail.

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The burrow-dwelling Little Blue Penguin *Eudyptula minor* is an excellent subject for investigating links between male attributes and female reproductive success for several reasons: (1) Early in the breeding season, unmated females 'keep company' with different males in burrows (Waas 1991a), allowing them to obtain accurate information on mate size and other characteristics. (2) Because the males play a lead role in instigating most courtship activities including copulation (Waas 1988), they may have a major influence on the timing of reproduction. (3) Once paired, the males have a very short incubation fast (2 days, Stahel & Gales 1987; 3–4 days, Chiaradia & Kerry 1999), so the risk of nest desertion is unlikely to be the main factor promoting a female preference for large males. (4) Males are more aggressive than females, and have evolved a wide range of well-defined defensive activities to protect the breeding burrow (Waas 1991b), so the male's role in nest defence can be quantified easily.

Here we examine whether the size of male Little Blue Penguins influences nest defence, the timing of reproduction and the growth rates of their chicks. It could be expected that, if sexual dimorphism in penguins is 'driven' by a female preference for large males, it should be male size, not female size, that accounts for most size-success correlations (although female size might increase as an artefact of selection for large size in males). To examine these ideas, we quantified the contribution that male and female size made to the measures of reproductive success that we recorded.

Our results indicate that the size of males, but not of females, was correlated with defensive activities, the timing of breeding and the reproductive success of Little Blue Penguins. Thus, we provide evidence that female Little Blue Penguins can improve their own reproductive potential by selecting larger males as breeding partners.

## METHODS

### Study area and period

The study was conducted on a population of Little Blue Penguins on Tiritiri Matangi Island (36°36'S, 174°53'E), 4 km off Auckland, New Zealand, during the 1999 breeding season (August–December). At night, we walked along the shoreline and main pathways around the island and found nests by listening for sexual and aggressive calls (see Waas 1988, 1990, for descriptions of calls). The Little Blue Penguins

nested mainly in grasslands, where soil depth allows burrowing, and amongst boulders on the rocky shores around the island.

### Measurements

Forty-one breeding pairs, spaced sporadically along approximately 1 km of shoreline, were investigated. To assess body size, we measured bill length, bill depth and head length with digital calipers (following Jones 1978). Head length was measured from the tip of the bill to the back of the skull. Flipper and foot sizes were measured by tracing the outspread appendage on paper and later measuring them to the nearest 1 mm. Flipper size was estimated by measuring from the elbow to the tip of the outstretched flipper. Foot size was estimated by measuring the distance between the base of the first digit and the tip of the claw of the third digit. Because body weights were extremely variable (i.e. they could vary dramatically before and after feeding trips) during the breeding season, weight was not used to estimate body size.

For each pair's nest, the date of egg laying, chick hatching, chick deaths and chick fledging were recorded (nest contents were checked every day). Chicks from each pair's nest were placed in a cloth bag of known mass and weighed every 5 days with a 500-g or 1.5-kg *Pesola* scale from hatching to fledging. If chicks were not located for 10 days in succession, they were assumed to have died. All observed chick deaths occurred within 18 days of hatching. Only chicks reaching 50 days of age were considered to have fledged (Williams 1995).

The recordings that were used for nest defence experiments (see below) were made with a Digital Audio Tape-corder (DAT, model TCD-D7, Sony Corporation) and an AKG shotgun microphone (head, model C460B; body, model CK68-ULS). During the pairing period, five good low to medium bray calls were recorded from five different males that were not otherwise used in the study. After removing a male and female from their nest, the male was released into the nest. In this context, most males produced a low or medium bray call. Once satisfactory recordings of the male were obtained, the female was also released into the nest.

### Sex determination

We used Gales' (1988) formula for determining the sex of Little Blue Penguins by bill measurements. The formula sexes the adults with 94% accuracy

(Gales 1988). We studied only breeding pairs in nest burrows.

### Body size

A Principal Component Analysis (PCA) was used to identify the best parameter (chosen from head length, bill length, bill depth, foot size and flipper size) to use in body size estimates. The parameter explaining most variation in Principal Component 1 (PC1) was selected for analyses (see Manly 1986 for a description of PCA).

### Design of nest defence experiment

Little Blue Penguins call most frequently after dusk and before sunrise (Waas 1988). To examine the relationship between a given male's response to intruders and its body size, we conducted the following experiment. During the daytime, we scouted for nests that contained only a single male. These nests were then visited again during the night. All playback experiments at the 41 nests that we sampled were carried out on calm evenings between 18:00 and 20:00 h, and between 05:00 and 07:00 h. A speaker (Sony, model SRS-77G) was used with a cassette player (Aiwa, model HS-SP550) for playback (the DAT recordings described above were transferred to cassette tapes using an Aiwa cassette recorder, model HS-JX970). The speaker was placed approximately 1 m in front of the nest burrow entrance; the bray call of a single male was then broadcast at a level equivalent to the amplitude of a displaying bird. Each bray call had three consecutive exhalation–inhalation phrases (see Waas 1990). After playing the bray call of the simulated male intruder, we remained still and recorded any vocal responses for 30 s (any sounds were recorded to DAT). After the 30-s silent period, we played back the same bray call again and then listened for another 30 s. In total, three playback–silence sets were presented to each subject. After waiting a further 30 s, we moved a penguin model composed of blue clay moulded into the shape of a penguin's head to within 30 cm of the burrow occupant to simulate the approach of a stranger; the model remained there for 30 s. Any responses to the model were then recorded. Following the presentations, we rechecked the identity of the bird (to ensure that only the single male was present). We conducted a total of 111 experiments on the 41 males through the breeding season (each male was tested 1–6 times during the breeding

season, but consecutive tests on a given male were always at least 2 days apart). By rotating which of the five intruder calls we used with each subject, we limited habituation to simulated intruders. We calculated the percentage of experiments in which each penguin performed each of three activities (remained silent, vocalized or hissed) in response to playback or the model presentation. To determine whether there was any relationship between male size and the response to the playback/model, we used a linear regression analysis.

Female Little Blue Penguins show little in the way of defensive behaviour unless accompanied by their mate (Waas 1991a), so it was not possible to quantify their defensive behaviour independently.

### Growl measurements

We examined the calls that males produced in response to playback. 'Growl' is the most common vocalization used by Little Blue Penguins, in both defensive and sexual contexts. This low-pitched sound, produced as the bird exhales, is used both before and after pairs engage in mutual displays (Waas 1988). We analysed the growls of 26 male subjects by measuring: (1) the peak frequency (Hz), (2) the highest frequency (Hz), (3) call duration (s) and (4) the number of syllables per second. Growl responses were analysed by producing sonagrams with Canary 1.2.4 software on a Macintosh computer. A one-way ANOVA was conducted to obtain an *F* ratio for each call feature. By comparing the *F* ratios, we identified the call features that showed the greatest inter- vs. intra-individual variation (Campbell 1989). After that, we looked at the relationship between the call features and male body size by using a linear regression analysis.

### The relationship between body size and reproductive parameters

Associations between the parameter that best estimated body size, and the reproductive parameters we measured (egg-laying date, chick hatching date, chick growth rate and chick fledging mass and age), were examined by using a regression analysis. The chick growth pattern approximated a linear function against development time between the ages of 1 and 15 days ( $n = 25$ ,  $r > 0.95$ ,  $P < 0.05$  for all chicks), so individual growth rates were estimated by using a linear regression between these ages. Hatching and fledging success were each independently classified on a scale of 1–3 (1: no hatching/no fledging chick, 2: one hatching/

**Table 1.** Principal component analysis of five morphometric characters of males and females, and a sexual dimorphism index. The percentage of explained variance is also shown ( $n = 74$ ).

Variable	PC1	PC2	Dimorphism (male/female)
Head length	-0.527	-0.122	1.09
Bill length	-0.484	-0.143	1.08
Bill depth	-0.384	-0.668	1.14
Foot size	-0.432	0.32	1.04
Flipper size	-0.392	0.645	1.06
Percent of total variance	53.2	18.1	

one fledging chick, 3: two hatching/two fledging chicks); success and the mean body size of parents (both males and females) were then compared. With respect to the breeding scores, the influence of mean body size or reproductive success was examined by using a one-way ANOVA.

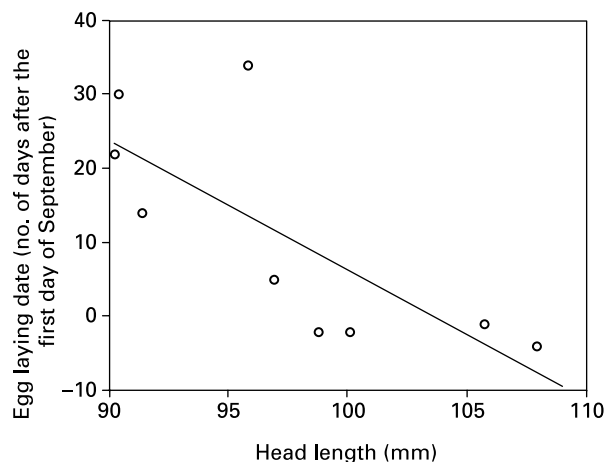
## RESULTS

### Body size

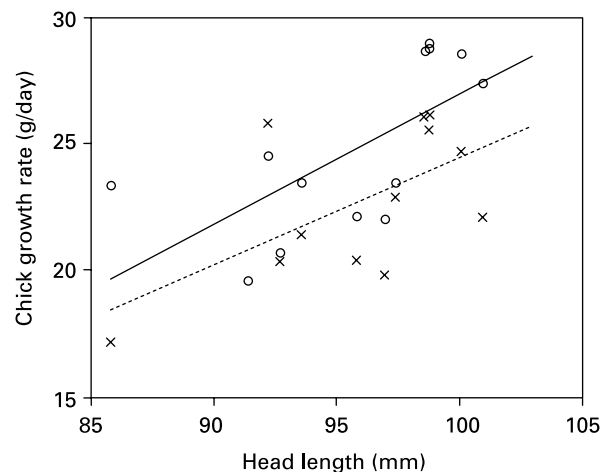
The results of our PCA of body size measures for Little Blue Penguins on Tiritiri Matangi Island are shown in Table 1. The variation in body size accounted for over 53% of the variance (Table 1). Head length was the most important PC1 parameter, and was therefore used as a quick and simple estimator of body size for both males and females. We went on to examine correlations between head length, reproductive parameters and responses during the nest defence experiments. In general, Little Blue Penguins show sexual dimorphism in a number of features, and males are slightly larger than females (Alexander & Nicholls 1918, Nicholls 1918, Richdale 1940, Reilly & Balmford 1975, Jones 1978). In all five morphometric characters measured, males were found to be larger than females (Table 1). There was no significant correlation between males and their partners in terms of the head length ( $r_{37} = 0.17$ ,  $P = 0.28$ ) or PC1 score ( $r_{35} = 0.04$ ,  $P = 0.83$ ).

### Breeding parameters

The relationship between body size (estimated by head length) and reproductive parameters was examined separately for males and females. The first eggs fathered by large males appeared significantly earlier in the breeding season than those of smaller males (Fig. 1;  $r_7 = 0.72$ ,  $P < 0.05$ ). The first chicks of



**Figure 1.** The timing of 1st egg laying, in relation to male head length. The date of 1 September corresponds to the zero value on the y-axis.



**Figure 2.** Chick growth rate (g/day) in relation to male head length. The growth rates of first chicks are shown by circles while those of second chicks are shown by crosses. The solid line shows the regression line of the first chick's growth.

larger males also hatched significantly earlier than those of smaller males ( $r_{18} = 0.46$ ,  $P < 0.05$ ). In birds that had two chicks, both the first and the second chicks of larger males grew at a faster rate than those of smaller males (Fig. 2; first chick,  $r_{11} = 0.66$ ,  $P < 0.05$ ; second chick,  $r_{10} = 0.61$ ,  $P < 0.05$ ), although male size did not influence the mean fledgling mass (first chick,  $r_8 = 0.10$ ,  $P = 0.78$ ; second chick,  $r_8 = 0.22$ ,  $P = 0.54$ ) or the mean fledging age (first chick,  $r_8 = 0.36$ ,  $P = 0.31$ ; second chick,  $r_8 = 0.56$ ,  $P = 0.10$ ). There were no significant differences in the mean body sizes of males in terms of the three levels of hatching or fledging success identified

( $F_{2,33} = 0.36$ ,  $P = 0.70$  and  $F_{2,33} = 0.27$ ,  $P = 0.76$ , respectively).

There were no significant correlations between female body size (estimated by head length) and any reproductive parameter (first egg-laying date,  $r_7 = 0.19$ ,  $P = 0.94$ ; first chick hatching date,  $r_{18} = 0.01$ ,  $P = 0.96$ ; chick fledging age, first chick,  $r_8 = 0.12$ ,  $P = 0.73$ , and second chick,  $r_8 = 0.19$ ,  $P = 0.59$ ; chick growth rate, first chick,  $r_{11} = 0.15$ ,  $P = 0.62$ , and second chick,  $r_{10} = 0.10$ ,  $P = 0.76$ ; chick fledging mass, first chick,  $r_8 = 0.24$ ,  $P = 0.51$ , and second chick,  $r_8 = 0.05$ ,  $P = 0.89$ ; hatching success,  $F_{2,33} = 2.24$ ,  $P = 0.12$ ; fledging success,  $F_{2,33} = 2.31$ ,  $P = 0.12$ ).

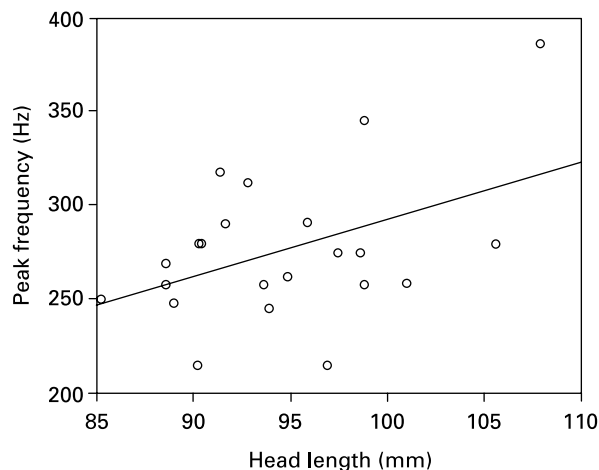
### Vocalizations

When playback was presented to males at their nests, they either remained silent or vocalized (growled or brayed). Large males were no more likely than smaller males to vocalize in response to playback ( $r_{36} = 0.04$ ,  $P = 0.81$ ). Response data for each male were also analysed separately with respect to the stage of the breeding cycle when the tests were conducted (incubation, guard and post-guard stage). In the post-guard stage (2 weeks after hatching), large males were more likely to call in response to playback than smaller males ( $r_{12} = 0.70$ ,  $P < 0.01$ ), although there were no significant differences between size and response to playback during incubation ( $r_{30} = 0.05$ ,  $P = 0.77$ ) or the guard stage ( $r_{19} = 0.16$ ,  $P = 0.50$ ).

When a model was moved towards their burrow, males either remained silent, vocalized (growled or brayed) or hissed (a display where the performer lunges forward and expels a short burst of air; Waas 1990). There was no significant difference in response to the model stimulus between large and small males ( $r_{36} = 0.04$ ,  $P = 0.80$ ). There were also no significant differences between large and small males in response to the model with respect to the stage of the breeding cycle (incubation,  $r_{30} = 0.05$ ,  $P = 0.80$ ; guard,  $r_{20} = 0.11$ ,  $P = 0.64$ ; post-guard,  $r_{14} = 0.20$ ,  $P = 0.46$ ).

Growls included frequencies up to 4620 Hz. The mean peak frequency was 148.6 Hz (range 10–290 Hz). An ANOVA conducted across the males sampled indicated that the only significant differences between individuals were in peak frequency ( $F_{6,34} = 4.09$ ,  $P < 0.01$ ) and the number of syllables per second ( $F_{5,30} = 2.63$ ,  $P < 0.05$ ). Differences between individuals in call duration ( $F_{6,37} = 0.86$ ,  $P = 0.53$ ) and highest frequency ( $F_{6,37} = 2.21$ ,  $P = 0.06$ ) were not significant.

Large males growled at higher peak frequencies (Hz) than smaller males (Fig. 3;  $r_{20} = 0.44$ ,  $P < 0.05$ ).



**Figure 3.** The relationship between peak frequency of growl and head length.

Differences between large and small males were not apparent in the number of syllables per second ( $r_{16} = 0.07$ ,  $P = 0.78$ ).

We also analysed all the relationships mentioned above by using PC1 scores. All the trends in the relationship between male PC1 scores and reproductive parameters, responses to playback (and models) and vocalizations were the same as those identified between male head length and each parameter. There were significant differences in egg-laying date ( $r_7 = 0.73$ ,  $P < 0.05$ ), in response to playback in the post-guard stage ( $r_{11} = 0.61$ ,  $P < 0.05$ ) and in peak frequency ( $r_{19} = 0.67$ ,  $P < 0.001$ ) between larger and smaller males. No significant relationships between female PC1 scores and reproductive parameters could be detected.

### DISCUSSION

Our results show that, in Little Blue Penguins, large males bred earlier than smaller ones and that chicks of larger males grew more rapidly than those of smaller males. A female's body size, however, did not affect her reproductive success. Large males also used higher-pitched aggressive calls and were more likely to vocalize in response to an intruder's call, but only during the post-guard stage. This vocal information could be used by opponents as well as females to gauge male attributes.

### Nest defence behaviour

The agonistic behaviour of Little Blue Penguins has been investigated in detail by Waas (1988, 1990,

1991a, 1991b). He reported that several aggressive displays, including calls, are used when penguins are confronted by strangers, especially when both the male and the female are present in the burrow. A lone bird in the nest, which might have difficulty deterring an intruder, tended to remain silent and avoid advertising the presence of a burrow (Waas 1991a).

There was no significant difference in response to playback between large and small males. However, when we examined the response with respect to each breeding stage (incubation, chick-guard and post-guard), large males were found to have responded more often than small males in the post-guard stage. Aggressive displays may reveal information on the performer's willingness to escalate conflict during aggressive encounters (Waas 1991a). Large males in the post-guard stage appeared to be more willing to defend or protect their offspring than small males, presumably because the value of chicks peaks during the post-guard stage (just before fledging).

No differences between large and small males were found in response to a penguin model. There can be serious costs associated with using aggressive displays (Waas 1991a). In particular, a physical response to a potential stranger has higher risks or costs than responding vocally from within the burrow. We expected larger males to be more willing to bear the costs of escalating conflicts, but this was not the case. Perhaps there is a significant 'positional' advantage associated with occupying a burrow that leads both large and small males to adopt a 'wait and see' strategy. In our experiment, the model stimulus was presented to each subject for 30 s and then withdrawn. In this context, the intruder may have been seen by both large and small males as backing down, preventing further escalation (Waas 1991a).

The growls of Little Blue Penguins are low-pitched pulsed sounds produced as the bird exhales. Individuals differed little in both the variation in the highest frequency and the length of calls they produced, so these features may not be useful for revealing individual-specific information. In contrast, the peak frequency and the number of syllables per second varied considerably between individuals (see also Jouventin 1982). However, there were no significant correlations between the number of syllables per second of the males' calls and their body size. In playback experiments conducted by Jouventin (1982), the removal of the highest and lowest frequencies of calls had little effect on a Little Blue Penguin's response. The *F* ratios generated by our ANOVAs showed that the greatest inter- vs. intra-individual

variation was in the peak frequencies. Thus peak frequencies might be expected to be useful in distinguishing between males.

The peak frequency of the male defensive 'growl' was positively correlated with male body size. When the PCI score was used as a body size index instead of head length, the relationship became much stronger ( $r = 0.67$ ,  $P < 0.001$ ). Therefore, various body features that might have been better measured by the PCI score (e.g. lung size, chest size) appeared more strongly associated with call features. 'Growl' is the most common aggressive vocalization used by Little Blue Penguins. Their calls are graded (from growl to low, medium and finally full brays; Waas 1990). The pitch of the calls (both within and between the four 'levels') increases with the intensity of the response. Thus, large males may have had higher pitched growls because they were responding more strongly to the standardized stimulus, perhaps indicating a greater willingness to escalate conflicts. We suggest that large males producing higher pitched growls may be preferred by females because they may be better, or more willing, defenders of the nest-site.

### Timing of reproduction

On Tiritiri Matangi Island, Little Blue Penguins lay one clutch per year (Jones 1978). Large males fathered their first eggs and first chicks significantly earlier in the breeding season than did small males. This suggests that large males may have mated earlier than small males, assuming the pairing dates can be backdated from known egg-laying or hatching dates using a mean incubation period of 35 days (Reilly & Balmford 1975). Female Adélie Penguins may choose males on the basis of characteristics that correlate with body size (Davis & Speirs 1990). Large male Adélie Penguins were thought to breed first because of a female preference for large males. Assuming that early egg-laying and hatching dates are valid indicators of the mate preferences of females (Catchpole 1980, Searcy 1984, Davis & Speirs 1990), our findings suggest that mate choice by female Little Blue Penguins could be influenced by male body size. Another reason why females may prefer large males is that the growth rates of the chicks may be improved.

### Parental care

The growth rate of the chicks of large males was higher than that of small males. Little Blue Penguin

parents take turns to feed and guard their chicks on alternate nights from immediately after hatching (the guard stage; Hursthouse 1939). Adult weight is at a minimum during the 2- to 3-week guard stage that follows hatching (Chiaradia & Kerry 1999), suggesting that adults may find it difficult to obtain enough food when they have to begin providing for both their chicks and themselves (a goal that can sometimes be achieved by feeding closer to the colony during the guard stage; Weavers 1992). Many birds cannot cope with the sudden increase in demand, especially if food availability is a problem, so the mortality rate of chicks is highest during the early guard stage (Renner 1998). Thus, the parent's feeding ability during the guard stage is an extremely important factor in determining reproductive success. In our study, chicks of large males grew significantly faster between the ages of 1 and 15 days (the guard stage) than those of small males; this may simply be a consequence of hatching earlier, if food is more plentiful early in the season. Alternatively, larger males might be better foragers or providers; females that select larger males may themselves be better providers. Because there were no significant relationships between female body size and chick growth, it may be male body size that most influences chick growth, and females should use information on male size to obtain the best mates. However, there were no significant differences between large and small males in the fledging age or mass of chicks (although, on average, chicks of large males fledged earlier and heavier). This might simply reflect a lack of statistical power.

Age has been known to affect breeding success in Little Blue Penguins (Dann & Cullen 1990) and probably affects the timing of pair reunions (which will, in turn, have implications for the success and timing of breeding). In our study, without knowing the age of our males, it is not possible to comment on the possibility that our relationships simply reflect differences in success of young (small) birds (e.g. 2–3 years old) and older (more experienced) birds. However, from the female's perspective this distinction may be immaterial – by selecting a large male, she improves her own reproductive success, regardless of whether male size or age is responsible for the effect.

## CONCLUSIONS

Females mated with large male Little Blue Penguins produced eggs and chicks earlier in the breeding

season. This may be because large males courted more, had a superior ability to obtain resources, or were more successful during male–male competition. Also, large males may mate earlier than small males because females prefer them and select them first. This preference may occur because chicks of large males grow faster than those of small males. Large males were more likely to respond to an intruder to protect their offspring, at least during the post-guard stage when the value of chicks would be expected to peak. In contrast, there were no significant correlations between female body size and any reproductive parameter. Female Little Blue Penguins can improve their own reproductive potential by selecting larger males for mates. However, we would expect there to be a 'ceiling' on selection for larger males, assuming that costs associated with large size (e.g. heat stress, loss of manoeuvrability) will eventually outweigh the benefits. Females may select males of an optimum size, not necessarily just the largest males.

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## REFERENCES

- Abell, A.J., Cole, B.J., Reyes, R. & Wiernasz, D.C. 1999. Sexual selection on body size and shape in the western harvester ant, *Pogonomyrmex occidentalis* Cresson. *Evolution* **53**: 535–545.
- Agnew, D.J. & Kerry, K.R. 1995. Sexual dimorphism in penguins. In Dann, P., Norman, F.I. & Reilly, P. (eds) *The Penguins: Ecology and Management*: 299–318. Sydney: Surrey Beatty & Sons.
- Alexander, W.B. & Nicholls, B. 1918. A study of Australian specimens of the Little Penguin (*Eudyptula minor*, Foster). *Emu* **18**: 50–57.
- Andersson, M.B. 1994. *Sexual Selection*. Princeton: Princeton University Press.
- Arak, A. 1983. Sex differences in choosiness: Male-male competition and mate choice in anuran amphibians. In Bateson, P. (ed.) *Mate Choice*: 181–210. Cambridge: Cambridge University Press.
- Borgia, G. 1981. Mate selection in the fly *Scatophaga stercoraria*: female choice in a male-controlled system. *Anim. Behav.* **29**: 71–80.

- Campbell, R.C.** 1989. *Statistics for Biologists*. Cambridge: Cambridge University Press.
- Catchpole, C.K.** 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour* **74**: 149–166.
- Chiaradia, A.F. & Kerry, K.R.** 1999. Daily nest attendance and breeding performance in the Little Penguin *Eudyptula minor* at Phillip Island, Australia. *Mar. Ornithol.* **27**: 13–20.
- Côte, I.M. & Hunte, W.** 1989. Male and female mate choice in the redlip blenny: why bigger is better. *Anim. Behav.* **38**: 78–88.
- Dann, P. & Cullen, J.M.** 1990. Survival, patterns of reproduction and lifetime reproductive output of Little Penguins *Eudyptula minor* on Phillip Island, Victoria, Australia. In Davis, L.S. and Darby, J.T. (eds) *Penguin Biology*: 63–84. San Diego: Academic Press.
- Davis, L.S. & Speirs, E.A.H.** 1990. Mate choice in penguins. In Davis, L.S. & Darby, J.T. (eds) *Penguin Biology*: 377–397. San Diego: Academic Press.
- Downhower, J.F. & Brown, L.** 1980. Mate preferences of female Mottled Sculpins, *Cottus bairdi*. *Anim. Behav.* **28**: 728–734.
- Ewing, A.W.** 1961. Body size and courtship behaviour in *Drosophila melanogaster*. *Anim. Behav.* **9**: 93–99.
- Gales, R.** 1988. Sexing adult Blue Penguins by external measurements. *Notornis* **35**: 71–75.
- Hursthouse, E.W.** 1939. Some observations on the breeding habits of the Little Penguin. *Emu* **39**: 15–17.
- Jones, G.** 1978. *The little blue penguin* (*Eudyptula minor*) on *Tiritiri Matangi Island*. MSc thesis, University of Auckland, New Zealand.
- Jouventin, P.** 1982. *Visual and Vocal Signals in Penguins, Their Evolution and Adaptive Characters*. Berlin: Verlag Paul Parey.
- Kraak, S.B.M., Bakker, T.C.M. & Mundwiler, B.** 1999. Sexual selection in sticklebacks in the field: correlates of reproductive, mating, and paternal success. *Behav. Ecol.* **10**: 696–706.
- Manly, B.F.J.** 1986. *Multivariate Statistical Methods. A PRIMER*. London: Chapman & Hall.
- Nicholls, B.** 1918. An introduction to the study of the penguins of the Nobbies, Phillip Island, Western Port, Victoria. *Emu* **18**: 118–144.
- Partridge, L., Ewing, A. & Chandler, A.** 1987. Male size and mating success in *Drosophila melanogaster*: the roles of male and female behaviour. *Anim. Behav.* **35**: 555–562.
- Reilly, P.N. & Balmford, P.** 1975. A breeding study of the Little Penguin *Eudyptula minor* in Australia. In Stonehouse, B. (ed.) *The Biology of Penguins*: 161–187. London: Macmillan.
- Renner, M.** 1998. *Survival of little penguin chicks*. MSc thesis, University of Otago, New Zealand.
- Richdale, L.E.** 1940. Random notes on the genus *Eudyptula* on the Otago Peninsula, New Zealand. *Emu* **40**: 180–216.
- Rowland, W.J.** 1989. The effects of body-size, aggression and nuptial coloration on competition for territories in male Threespine Sticklebacks, *Gasterosteus aculeatus*. *Anim. Behav.* **37**: 282–289.
- Ryan, M.J.** 1980. Female mate choice in a neotropical frog. *Science* **209**: 523–525.
- Searcy, W.A.** 1984. Song repertoire size and female preferences in Song Sparrows. *Behav. Ecol. Sociobiol.* **14**: 281–286.
- Stahel, C. & Gales, R.** 1987. *Little Penguin: Fairy Penguins in Australia*. Kensington, New South Wales: New South Wales University Press.
- Trivelpiece, W.Z., Trivelpiece, S.G., Volkman, N.J. & Ware, S.H.** 1983. Breeding and feeding ecology of pygoscelid penguins. *Antarctic J. United States* **18**: 209–210.
- Waas, J.R.** 1988. Acoustic displays facilitate courtship in Little Blue Penguins, *Eudyptula minor*. *Anim. Behav.* **36**: 366–371.
- Waas, J.R.** 1990. Intraspecific variation in social repertoires: evidence from cave- and burrow-dwelling Little Blue Penguins. *Behaviour* **115**: 63–98.
- Waas, J.R.** 1991a. Do Little Blue Penguins signal their intentions during aggressive interactions with strangers? *Anim. Behav.* **41**: 375–382.
- Waas, J.R.** 1991b. The risks and benefits of signalling aggressive motivation: a study of cave-dwelling Little Blue Penguins. *Behav. Ecol. Sociobiol.* **29**: 139–146.
- Weavers, B.W.** 1992. Seasonal foraging ranges and travels at sea of Little Penguins *Eudyptula minor*, determined by radiotracking. *Emu* **91**: 302–317.
- Wiklund, C. & Kaitala, A.** 1995. Sexual selection for large male size in a polyandrous butterfly: the effect of body size on male versus female reproductive success in *Pieris napi*. *Behav. Ecol.* **6**: 6–13.
- Williams, T.D.** 1995. *The Penguins: Spheniscidae*. Oxford: Oxford University Press.
- Williams, A.J. & Cooper, J.** 1984. Aspects of the breeding biology of the Jackass Penguin, *Spheniscus demersus*. *Proceedings of the Fifth Pan-African Ornithological Conference*: 841–853. Johannesburg: Southern African Ornithological Society.

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