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Location of Colonies in Royal Penguins *Eudyptes schlegeli*: Potential Costs and Consequences for Breeding Success

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The factors affecting breeding success in seabirds has been the topic of debate for many decades (Lack 1954). One important variable is location of nesting sites within colonies (Tenaza 1971; Oekle 1975; Ainley et al. 1983). Another is colony size, with birds in small colonies the least successful (e.g. in some penguin species, Robertson 1986). However, little attention has been paid to the location of a penguin colony (aside from some Antarctic colonies, such as Emperor Penguins *Aptenodytes forsteri*, Robertson 1994), its distance from the water and consequent extra energetic cost to breeding penguins. At Macquarie Island, Royal Penguin *Eudyptes schlegeli* colonies are found at a variety of altitudes from sea level, to sites approximately 200m above sea level (e.g. at Caroline Cove). The added energetic burden of colonies located away from the beach is yet to be assessed.

Taking into account the number of times that an individual penguin needs to return to its nest over a breeding season, the distance and altitude of a colony from the water could substantially increase the total energetic cost of breeding, and possibly affect the breeding success of individuals. It was with this question in mind that we monitored the time taken for Royal Penguins to travel to an inland colony. From the shortest and longest time taken by Royal Penguins to reach the colony, we attempted to assess some of the factors which might affect the variation in time taken. These data were used to calculate a hypothetical energetic cost to the penguins due to the location of this colony and to assess whether location might impact on breeding success.

Methods

The study was carried out at the upper Sandy Bay colony, on the eastern side of Macquarie Island (54°33′57″S; 158°54′57″E). The colony is 1.43 km inland and

Table 1 The number and sex of Royal Penguins used for estimation of the time to reach the colony.

Reproductive stage	Sex	Number marked	Number timed
Pre-laying	Male	20	11
Incubation	Female	15	15
Guard	Female	15	11
Crèche (up)	Female	8	7
	Male	7	7
Crèche (down)	Female	10	8
Total		75	59

at an altitude of 108-123 m. Royal Penguins reach the colony via Finch Creek, which divides into three tributaries near the colony and provided three points of access to the colony.

Measurements of travel time were made at four key stages in the 1994–95 breeding season (prior to egg laying, incubation, guard and crèche). The experiment during each stage was run on a single day. During each period, ten to 20 (Table 1) breeding birds were captured on returning from the sea, weighed, bill measurements taken for determination of sex (Warham 1975; CLH unpubl. data); a number was spray-painted on the breast and the bird was then released. Breeding birds were identified by behaviour, which differs from non-breeders when travelling to the colony (CLH unpubl. data), and the existence of a prominent brood patch. The time when the birds left the beach for the colony was noted from a hide on the beach at the entrance to Finch Creek. A second observer positioned in the colony at a point that provided visibility to the three entrance points, noted the time that animals arrived. In each case the experiment was run until the bulk of the individuals had been resighted, which was approximately four hours. During crèche stage, birds moving down from the colony to the beach were also timed to give an indication of whether there was an extra time component in moving up, compared to down, the creek.

Three of the four trials involved a single sex; the pre-laying stage consisted of males and the incubation and guard stages consisted of females (Table 1). The sexes used during the trials were a reflection of the movements of birds at the time the trial was conducted. For example, males and females move to the colony at different times during the pre-laying and incubation stages, and females move only during guard stage.
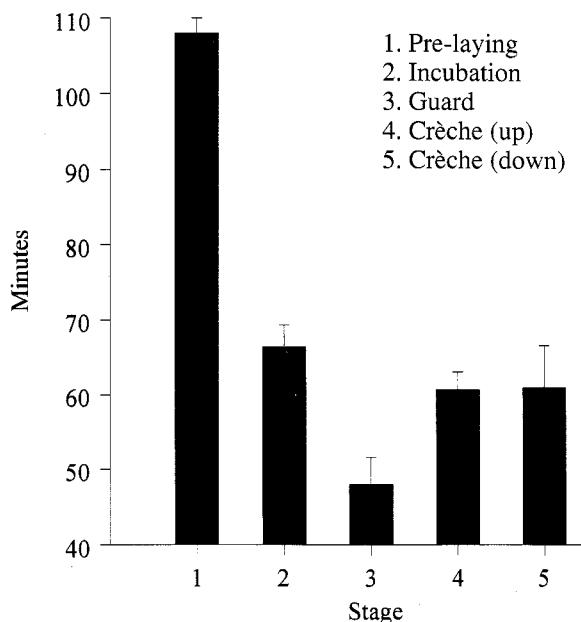

Figure 1 Time (minutes) taken for Royal Penguins to walk to the colony.

Therefore, it was not possible to assess sexual differences during most stages.

Results and discussion

The average times taken for individual Royal Penguins to move up to the Sandy Bay colony are illustrated in Figure 1, which shows that the time taken was significantly longer ($P < 0.05$) during the pre-laying (108.0 min) than any other stage of the breeding season (One-way Analysis of Variance and Tukey Test, $P < 0.05$). The time taken during the guard stage (48.0 min) was significantly shorter than during the incubation stage (up: 60.7 min; down: 61.0 min). There were no significant differences in the time taken during other stages in the breeding season, nor between females (58.57, $s.d.$ = 8.87 min) and males (62.86 ± 8.75 min) to walk up the creek during the crèche stage.

Not all individuals marked during the experiment were observed to reach the colony. This occurred because some birds stayed on the beach, or did not reach the colony within the duration of the experiment, presumably stopping for more than a brief rest along Finch Creek. These birds were most likely failed breeders;

both non- and failed breeders continued to move up the creek during all stages of the breeding season.

The significant difference in time taken during the pre-laying stage compared to all other stages perhaps reflects a lower stimulus for males to return to the colony due to the absence of females, eggs or young. While there was a need for the males to guard their territories during the pre-laying stage, nest site tenacity was perhaps less. Birds were occasionally observed moving from the nest site to later return and re-claim their site from intruders (CLH pers. obs.). Some birds might not have set up territories yet.

Interestingly, it was during the guard stage that birds moved the fastest up the creek. This is the time that chicks are newly hatched, and most vulnerable to starvation as it is the period of maximum growth (Gentoo Penguins *Pygoscelis papua*, Bost & Jouventin 1990). Once eggs are laid the same degree of motivation to return to the colony perhaps existed across the breeding season. There was, however, a slight (although not significant) trend for birds to move faster during the crèche than the incubation stage.

Potential costs of travelling to the upper Sandy Bay colony

During the 1993–94 and 1994–95 breeding season an average Royal Penguin moved up and down Finch Creek at least once during the pre-laying stage, at least once during the incubation stage, at least ten times during guard stage, and at least ten times during the crèche stage (CLH unpubl. data). These estimates exclude short duration trips to the beach for bathing (e.g. not foraging trips) that were occasionally observed. Using the shortest travel time (that during guard stage) and the average number of trips Royal Penguins completed during a breeding season, an average individual could spend 2112 minutes (35.2 hours) walking to and from the colony over a breeding season.

Swimming has been recognised as being energetically cheaper than walking in penguins. When walking, Little Penguins *Eudyptula minor* consume 1.0 l O_2 (kg.km)$^{-1}$ (which is described as being higher than that of other birds) and 50% more expensive than swimming (Baudinette & Gill 1985). Hui (1988) calculated that walking in Humboldt Penguins *Spheniscus humboldti* is 35% more expensive than for a similarly-sized Adelie Penguin *Pygoscelis adeliae* swimming at the same speed. There are no data available on the cost of walking in Royal Penguins. However, it is assumed, that the cost is high because all penguins are regarded

as morphologically adapted to the aquatic environment, so that their locomotion on land is compromised (Pinshow et al. 1977; Baudinette & Gill 1985).

Because there are no data on the costs of walking in Royal Penguins, data from the Adelie Penguin, which is of a similar size, have been used. There are currently energetic estimates of swimming for Adelie Penguins, in both swim canals and from the sea, that found consumption to be 9.0 Jkg^{-1}m^{-1} and 4.9 Jkg^{-1}m^{-1} respectively (Culik & Wilson 1991; Culik & Wilson 1994). Using the more conservative estimate of 4.9 Jkg^{-1}m^{-1}, which is Adelie Penguins swimming at a preferred speed, we can extrapolate the 35% increase in energy consumption when walking to bring the cost to 6.615 Jkg^{-1}m^{-1}, or 47 297.25 J per trip to the colony (calculated for a 5 kg bird [Marchant & Higgins 1990] and the distance to the colony of 1.43 km). This, multiplied by 44 trips to and from the colony, results in an estimated energetic cost of 2081.1 kJ to travel to this colony over a breeding season. The travel times up and down the creek are not significantly different (stages 4 and 5 in Fig. 1), so the assumption has been made that the cost is similar (although travel up the creek would most likely cost more due to the altitude climb).

Brown (1989) calculated that the average (averaged across the sexes) energy expenditure for a Macaroni Penguin *E. chrysolophus* (closely related and of similar size to the Royal Penguin) over the breeding season was 139.75 kJ x 10^9. The estimated extra cost of 2081.1 kJ for birds to travel to the upper Sandy Bay colony represents a potential increase in energy requirements of 0.006%. Food consumption for a Macaroni Penguin at Marion and Prince Edward Islands is 3.37 tonnes, over the seven month breeding season (Brown 1989). An additional cost of 0.006% of energy over the breeding season would approximate to 20.24 kg of food (or 460 g per trip). With approximately 10 000 birds in the upper Sandy Bay colony, this could represent over 202.4 tonnes of food per season. These calculations are based on the minimum and considered to be conservative estimates. Another potential cost may not be in energetic terms, but in the time involved in travelling to the colony, which is time not spent foraging or attending the nest. Whether there is sufficient flexibility in the breeding biology of this species to accommodate this is yet to be ascertained.

All these calculations are extrapolations from work on other species and are only provided to give an indication of potential costs. Whether this estimated added food requirement is significant in terms of breeding

success or survivorship in adults is yet to be tested and would require comparative demographic and energetic data. Our results, however, indicate that the cost may not be great for an individual bird, and hence may not impact on breeding success. The most profound effect that colony location could have on breeding success may be when food is in short supply and so may impact only in ENSO (El Nino Southern Oscillation) years (e.g. Whitehead et al. 1990) or on inexperienced breeders, less efficient at foraging.

Due to the variability in travel time across the breeding season, assessment of this hypothesis would have to be at various times during breeding. A non-significant effect would indicate that there is sufficient 'slack' in the energetic expenditure of breeding in a species to accommodate this cost, or the benefits of the colony outweigh these costs.

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