

Predation risk and nest-site selection in the Inca tern

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Abstract: Most tern species (Sternidae) are typically open-ground breeders; the Inca tern (*Larosterna inca*), however, breeds in crevices. This paper reports the first analysis of nest-site characteristics, predation rates, and breeding success in this species. We tested for evidence of natural selection on nest-site preferences in a colony subjected to high rates of predation by the peregrine falcon (*Falco peregrinus*). Characteristics of occupied sites differed from those of non-occupied sites. Terns selected sites with longer chambers, a greater number of cavities, and more overhead and lateral cover that were located close to the cliff edge. Predation was the main cause of breeding failure, and successful sites differed from unsuccessful sites, which is evidence for ongoing natural selection. Chicks at sites in larger crevices and more cavities remained at the site longer and were less likely to be depredated by peregrine falcons. Probably in response to the presence of predators, adults flew towards the colony in flocks, which “dissolved” at the cliff edge. Sites located far from the edge were more likely to be depredated and adults breeding there fed their chicks less frequently and, consequently, reared lighter chicks. The concordance between site preference and predation pressure on nest-site selection suggests that the use of non-preferred sites imposed a cost in the form of increased nest predation.

Résumé : La plupart des espèces de sternes (Sternidae) se reproduisent en terrain ouvert, mais la sterne Inca (*Larosterna inca*) se reproduit dans des crevasses. On trouvera ici une première analyse des caractéristiques du site de nidification, de la prédation et du succès de la reproduction chez cette espèce. Nous avons cherché des indices de l'influence de la sélection naturelle sur le choix des sites de nidification au sein d'une colonie exposée à des risques élevés de prédation par le faucon pèlerin (*Falco peregrinus*). Les sites occupés par les nids diffèrent des sites vacants. Les sternes choisissent de préférence les sites à crevasses profondes, comportant un grand nombre de cavités et une couverture de protection latérale et supérieure plus importante, situés en bordure des falaises. La prédation est la principale cause d'échec de la reproduction et les sites où la nidification est réussie diffèrent de ceux où la nidification est ratée, ce qui reflète l'action de la sélection naturelle. Les poussins dans les crevasses plus grandes où les cavités sont plus nombreuses restent plus longtemps aux sites et sont moins susceptibles d'être décimés par les faucons. Probablement en réaction à la présence des prédateurs, les sternes adultes se déplacent vers la colonie en bandes qui se dispersent en bordure de la falaise. Les nids installés loin de la bordure de la falaise sont plus susceptibles d'être pillés et les adultes dans ces nids nourrissent leurs poussins moins fréquemment et, par conséquent, ceux-ci sont plus légers. La concordance entre les préférences de sites et les pressions de la prédation sur le choix du site de nidification semble indiquer que l'utilisation de sites autres que les sites préférés entraîne des coûts qui se traduisent par une prédation plus importante des nids.

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Introduction

Predation has a strong influence on the ecology and behaviour of prey species; they are therefore likely to show adaptive strategies such as appropriate habitat choice or behavioural responses in order to reduce predation risk (Caraco et al. 1980; Orians and Wittenberger 1991). Bird nests are typically not distributed randomly among potential breeding sites and it is generally accepted that nonrandom distribution patterns are the result of natural selection (Cody 1985). Factors affecting breeding success can vary within habitats, and

variation in fitness resulting from habitat differences is expected to influence the evolution of habitat selection (Partridge 1978; Orians and Wittenberger 1991). It has been argued that predation is the most selective force affecting nesting success (Martin 1995). The process of natural selection can occur when there are habitat differences between depredated and non-depredated sites and thus over evolutionary time this may modify which habitats are used for nesting (Martin 1998). Nevertheless, short-term selective pressures, such as predation, can oscillate unpredictably, so nest-site selection may reflect long-term optima that are neutral or maladaptive in the short term (Clark and Shutler 1999). Thus, a crucial step in studies of nest-site selection is to identify the differences between selected and non-selected sites and also between successful and unsuccessful sites.

Predation on eggs and chicks directly affects nesting success, and adaptations in the choice of nest sites to reduce the risk of nest predation commonly occur (e.g. Martin and Roper 1988; Gilchrist and Gaston 1997; Stokes and Boersma 1998). Traditionally, studies on nest-site adaptation have focussed on the concordance between selection and predation

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patterns. Nevertheless, the risk of predation on adults can also affect bird behaviour and thus indirectly affect breeding success (Cody 1985). According to life-history theory, investment by organisms in current reproduction should be balanced against the chances of reproducing in the future (Roff 1992; Stearns, 1992). In long-lived species, selection should strongly favour individuals with behaviour that reduces mortality during the breeding season (Williams 1966; Sæther et al. 1993; Mauck and Grubb 1995). In seabirds, adults change their behaviour in response to predation risk (Harris 1980; Watanuki 1986; Harfenist and Ydenberg 1995). Thus, when the predation risk varies among habitats, the provisioning pattern of birds breeding in high-risk habitats may differ from that of birds breeding in low-risk areas, thereby affecting nesting success (Harfenist and Ydenberg 1995). Therefore, nest sites with characteristics that reduce the predation risk for both adults and chicks should be selected.

The Inca tern (*Larosterna inca*) breeds in crevices on talus slopes and cliffs. Inca terns are medium-sized seabirds that are endemic to the Peruvian and Chilean coasts (Guillen 1988). They feed in large flocks on anchovies (*Engraulis ringens*) in the Humboldt Current system (Murphy 1936) and under stable conditions rear two broods per year. They are monogamous, and pair formation occurs afresh every season in the communal areas. Both sexes incubate the eggs and contribute to chick provisioning (Moynihan 1962; Velando et al. 2001). The nesting population is estimated at 50 000 pairs (del Hoyo et al. 1996), a strong decline having been noted from 1900 to the 1990s (Coker 1919; Murphy 1936; Hutchinson 1950; Zavalaga 1997). This population decline can be attributed to habitat destruction caused by the guano industry and to egg and chick consumption by guano workers (Zavalaga 1997).

This paper reports the first analysis of nest-site characteristics, predation rates, and breeding success in this species. We studied the physical characteristics of nest sites used by Inca terns on Isla La Vieja in the Reserva Nacional de Paracas, Perú, and then tested for evidence of natural selection on nest-site preferences in a colony subjected to high rates of predation by the peregrine falcon (*Falco peregrinus*). Specifically, we tested whether (i) occupied crevices differed from unoccupied crevices, which would be evidence for long-term selection; (ii) reproductively successful sites differed from unsuccessful sites, which would be evidence for ongoing natural selection; (iii) Inca terns vary their parental investment according to the degree of predation risk at nest sites.

Methods

Breeding parameters and observations

This study was carried out on Isla La Vieja (14°17'S, 76°11'W) between October and December 1999. Inca terns build their nests in crevices in guano slopes along the coast of the island and lay one or, more frequently, two eggs. Before the laying period, in a study plot we marked every crevice ($N = 179$) that terns could use to nest in. We decided that a crevice was usable when it could contain an incubating bird. A site was considered occupied when an Inca tern laid eggs in it. For each nest with eggs we recorded the number of hatched eggs and the number of fledged chicks (defined

as the number of chicks surviving to 30 days of age). Asymptotic chick body mass was measured (to the nearest gram) at 25–30 days of age using a spring balance.

During the chick-rearing period, when the chicks were 25–30 days old, we observed the study plot in 1-h blocks. We carried out 40 h of observation on 27 nests from a blind. We studied chick and adult feeding behaviour. We converted behavioural categories into frequencies by dividing the number of instances of each behaviour by the number of observation hours at each nest site. Presence was recorded as the number of hours during which at least 1 adult was present on the nest divided by the number of observation hours at each nest site.

Nest-site characteristics

The nest sites in the study area were located in natural holes and crevices in the ground that varied from shallow depressions to deep cavities. Two site dimensions were measured: *entrance area*, measured to the nearest square centimetre, and *chamber length*, measured to the nearest centimetre. The following physical characteristics were recorded as well: *walls*: the number of lateral walls (from 2 to 4) surrounding and isolating the nest; *roof*: an index of the amount of cover over the nest (from 1 for a nest almost totally exposed to 4 for a totally covered nest); *accessibility*: the difficulty the tern had in entering the chamber (from 1, accessible in a straight line, to 4, a labyrinth with more than two bends); *cavities*: many of the chambers had small cavities and different compartments (from 0, only one cavity, to 5, six cavities); *visibility*: the extent to which the surroundings could be observed from the nest (from 0, no visibility, to 4, full visibility). In addition, two other variables related to site location were measured: *nearest neighbour*: the linear distance between the site and the closest occupied nest site (m); *distance to the edge*: the linear distance to the cliff edge (m).

Statistical analyses

Because most of the variables were not normally distributed (Shapiro–Wilk test), we first carried out univariate non-parametric analysis of the data (Mann–Whitney test). To investigate the most influential site characteristics on site selection and reproductive success we performed generalized linear models (GLM; Wedderburn 1974; McCullagh and Nelder 1989). We tested for multicollinearity among the descriptor variables using a principal component analysis. The first component explains a small proportion of data variation (25%), implying that the original variables were orthogonal (Jackson 1993). Hence, we used the original variables in the GLMs. Nevertheless, some correlation coefficients between the site characteristics were significant ($P < 0.05$), although most explained less than 20% of the variance, except chamber length and the number of cavities, which were strongly related (see Table 2).

To avoid pseudo-replication, we regarded the nest site as the unit for statistical analysis. The link function and error distribution in the GLMs were applied taking into account the presumed error distribution of the data and selecting those that minimized the deviance in the model (McCullagh and Nelder 1989; Crawley 1993; Herrera 2000). The ratio of residual deviance to residual degrees of freedom after the variables were fitted in the model was close to 1, indicating

Table 1. Physical characteristics (mean ± SE) of sites not selected and selected by Inca terns (*Larosterna inca*) on Isla La Vieja, and of reproductively successful and unsuccessful sites.

	Nest site				Reproductive success			
	Selected (N = 96)	Not selected (N = 83)	Mann–Whitney test		Successful (N = 39)	Unsuccessful (N = 30)	Mann–Whitney test	
			Z	P			Z	P
Walls	3.02 ± 0.04	2.72 ± 0.06	3.77	<0.001	3.03 ± 0.07	2.97 ± 0.10	0.50	0.617
Roof	3.93 ± 0.03	3.55 ± 0.07	5.09	<0.001	3.92 ± 0.04	3.90 ± 0.06	0.33	0.738
Number of cavities	2.93 ± 0.13	0.91 ± 0.10	9.04	<0.001	3.23 ± 0.21	2.30 ± 0.23	2.57	0.008
Visibility	1.99 ± 0.11	1.86 ± 0.10	1.02	0.299	2.05 ± 0.16	1.87 ± 0.23	0.23	0.820
Accessibility	2.90 ± 0.10	2.91 ± 0.11	0.06	0.953	3.10 ± 0.15	2.97 ± 0.21	0.17	0.867
Entrance area (m ²)	0.038 ± 0.003	0.049 ± 0.006	0.07	0.941	0.37 ± 0.04	0.41 ± 0.07	0.04	0.971
Chamber length (m)	0.76 ± 0.04	0.42 ± 0.03	8.42	<0.001	0.81 ± 0.07	0.61 ± 0.04	2.38	0.017
Distance to the edge (m)	17.10 ± 1.42	19.30 ± 1.68	1.02	0.306	13.30 ± 1.94	21.90 ± 3.07	2.16	0.031
Nearest neighbour (m)	2.93 ± 0.31	3.86 ± 0.38	1.84	0.066	3.16 ± 0.59	3.03 ± 0.48	0.13	0.899

Note: Values that are significantly different are shown in boldface type.

Table 2. Spearman’s rank correlations between the physical characteristics of studied sites on Isla La Vieja (N = 179).

	Walls	Roof	Entrance area	Visibility	Cavities	Distance to the edge
Roof	0.438***	—	—	—	—	—
Visibility	—	—	0.222**	—	—	—
Accessibility	—	—	0.217**	0.357**	—	—
Number of cavities	0.413***	0.479***	—	−0.200**	—	—
Chamber length	0.338***	0.432***	—	—	0.689***	—
Nearest neighbour	—	—	—	—	—	0.344***

Note: Only significant correlations are shown; **, P < 0.01; ***, P < 0.001.

that the data were not overdispersed (Dean 1992; Smith and Heitjan 1993). We fitted each explanatory variable to the observed data following a modification of a traditional forward stepwise procedure. Each variable was tested for significance in turn. The variable contributing to the largest significant change in deviance from the null model was then selected and fitted. Once a variable was fitted to the model we tested if the addition of a second variable significantly improved the model. It has been proposed that stepwise procedures are not necessarily able to select the most influential variable from a subset of variables (James and McCulloch 1990). We use a modification of a stepwise procedure to test alternative models that were obtained when the second or third most significant variable was included at each step instead of the first most significant one. This branching procedure could eventually produce a set of different models, but in most instances converged into a single model or a set of models from which similar causal relationships could be inferred. Quadratic relationships and the interaction between response variables were tested. Statistical significance was established at P < 0.05.

Results

Nest-site characteristics and selection

Inca terns on Isla La Vieja used 96 crevices out of the 179 sites marked before breeding began. Site characteristics varied significantly between selected and nonselected sites. Selected sites had more lateral walls, a larger roof area, more cavities, and a longer chamber than nonselected sites (Table 1). Moreover, these variables were significantly inter-

Table 3. Stepwise generalized linear models of selection and reproductive success of nest sites of Inca terns on Isla La Vieja, assuming a binomial distribution of errors and a logistic link.

	Nest-site selection		Reproductive success	
	Step ^a	Change in deviance ^b	Step ^a	Change in deviance ^c
Number of cavities	1	99.138***	1	8.561**
Chamber length	2	7.020*	3	4.432*
Distance to the edge	3	5.385*	2	5.113*
df		176		65

Note: Variables were included in the model at the 5% level; *, P < 0.05; **, P < 0.01; ***, P < 0.001.

^aThe remaining variables were not significant.

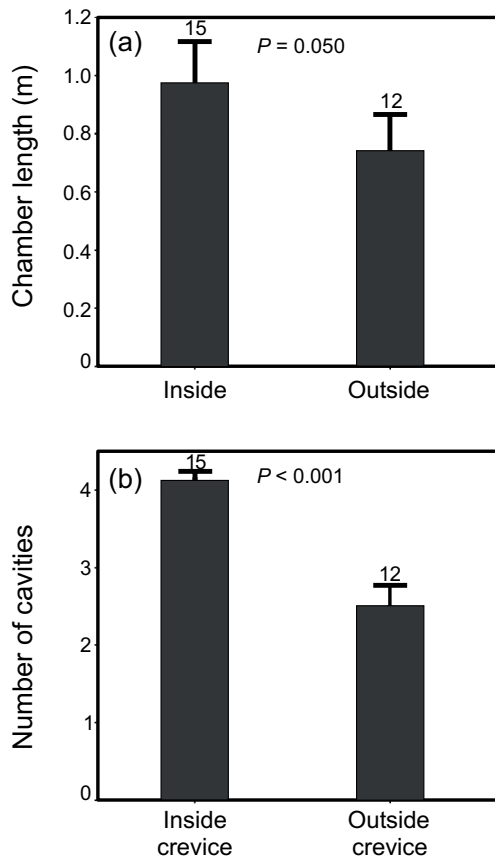
^bDeviance in the null model = 247.202.

^cDeviance in the null model = 94.477.

correlated (Table 2). The GLM fitted with a stepwise procedure included three variables that explained 45% of the deviance: number of cavities, chamber length, and distance to the edge (Table 3).

Of the variables, number of cavities explained most deviance (40%) and was fixed in the model in the first step. Although number of cavities and chamber length were closely correlated (Table 2), chamber length was included in the model in the second step. Thus, these physical characteristics had independent significant effects on the probability of a site being occupied. After the effects of the number of cavities were taken into account, distance to the edge was significant. The model showed that Inca terns selected nest sites closer to the cliff edge with more cavities and a longer

Fig. 1. Relationship between the location of Inca tern (*Larosterna inca*) chicks in relation to the nesting crevice (inside or outside) and chamber length (a) and number of cavities within the crevice (b). Results from Mann–Whitney tests are given (mean \pm SE); numbers above the bars are sample sizes.



chamber. None of the interaction and quadratic terms significantly improved the model. Roof and walls had a significant influence on the selection pattern, although these variables were not significant in the stepwise model, presumably because they were correlated with number of cavities (Table 2), which was included in the first step; the sites with more cavities also tended to have a greater roof and lateral-wall area. Alternative models that included the roof or walls in the first step also included number of cavities. Thus, the effect of the roof and walls is correlated with the effect of number of cavities, although number of cavities also had an independent effect on the probability of occupation. The remaining variables tested were not included in the alternative models.

Predation and reproductive success

Of 127 eggs laid in 69 nests studied (1.83 eggs per pair), 21 failed to hatch. In addition, 50 chicks (47%) died during the chick-rearing period. Thus, 56% of nest sites were successful (fledged at least 1 chick), and mean reproductive success was 0.811 chicks per pair.

During the egg stage, kelp gulls (*Larus dominicanus*) and band-tailed gulls (*Larus belcheri*) were present during our visits. We also saw turkey vultures (*Cathartes aura*) introducing their heads into Inca tern nest sites. No terrestrial

predators such as the Argentine grey fox (*Pseudalopex gris-eus*), common around mainland inland colonies (Murphy 1936; Tovar 1969), were present on Isla La Vieja. Nevertheless, egg losses were only recorded in two nests. During the chick-rearing period, the peregrine falcon was present in the study plot during 60% of 40 h of observation. Seven unsuccessful and one successful falcon attacks on adult terns were recorded. Moreover, peregrine falcons captured 2 chicks outside their nest sites during our observations. Moreover, the depredated carcasses of 6 adults and 10 chicks were found in the study plot during our visits.

Site characteristics and nest success

Site characteristics varied significantly between successful and unsuccessful sites. Successful sites had more cavities and a longer chamber and were located closer to the cliff edge (Table 1). The stepwise branching procedure produced a significant model that included cavities, distance to edge, and chamber length. Thus, these physical characteristics had independent significant effects on the probability of nest-site success (Table 3). The model explained 20% of deviance in the null model. Other alternative models only differed in the order in which the different explanatory variables were included and finally converged on the same model. The quadratic and interaction terms were all nonsignificant. The remaining variables were not included in the models, owing to their nonsignificant effect on mean reproductive success.

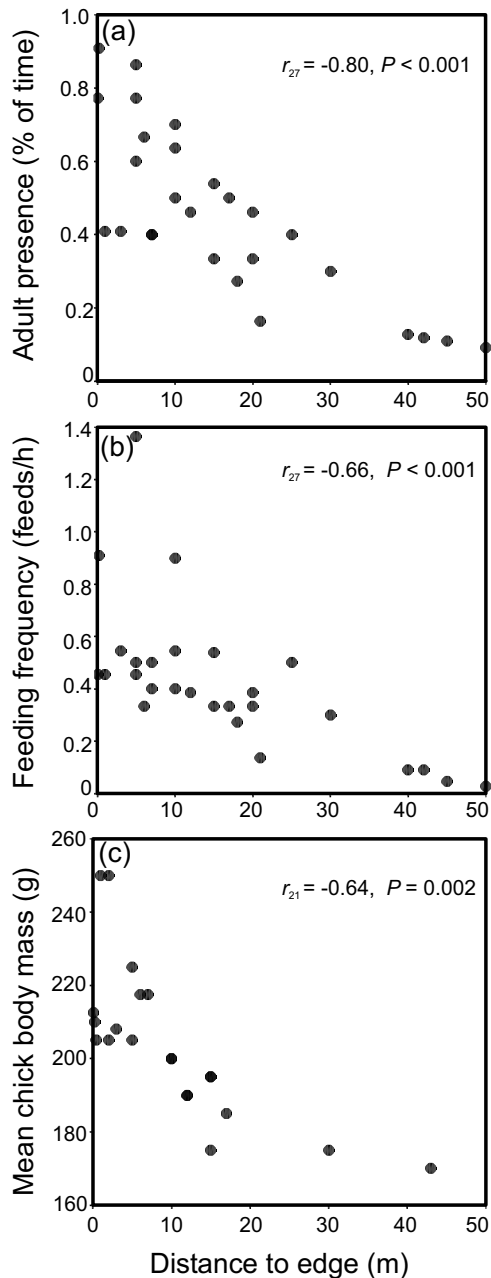
Some chicks left the crevice when the parents were not present, thereby putting themselves at risk from attack by peregrine falcons. Chick presence outside the crevice was related to site characteristics (Fig. 1). Thus, the sites where chicks were recorded outside the crevice had shorter chambers and fewer cavities than sites where chicks remained inside the crevice. No other site characteristics influenced chick movements outside the nest.

Adults returned to the colony in a flock, probably to reduce predation risk. The colony is situated on the slope up the cliff. Once the flock got close to the cliff edge, individuals flew alone over the slope to their nests. The birds nesting close to the cliff edge leave the flock first, as their nest sites are closest to the ocean. Thus, the distance to the cliff edge should be related to the predation risk suffered by the adults. Birds breeding in crevices far from the cliff edge should reduce their nest attendance. We examined this prediction by recording the presence of adults at the nest and the number of feeding visits, as well as chick body mass. Adult presence was significantly higher in nest sites located closer to the cliff edge (Fig. 2a). Moreover, adults fed chicks in nests close to the edge significantly more frequently than those far from the edge (Fig. 2b). This relationship was also significant when the number of feeding visits was corrected for brood size ($r_{27} = 0.66$, $P < 0.001$). Consequently, pairs that bred close to the edge reared heavier chicks (Fig. 2c).

Discussion

On the guano slopes of Isla La Vieja, Inca terns lay their eggs in crevices with a single small entrance. Inca terns bred in half of the crevices marked prior to breeding and were selective in their choice of nest sites, which is evidence for long-term natural selection on nest-site choice (Martin 1998).

Fig. 2. Adult presence (a), adult feeding frequency (b), and mean chick body mass (c) in relation to the distance from the nest site to the cliff edge. Pearson's correlations are given.



The species showed an overall preference for sites with more cavities, a bigger chamber, and greater lateral and overhead cover. The density of nest sites was higher close to the cliff edge.

The variables selected could reflect long-term selection rather than an adaptive response to short-term selection pressures. In fact, some bird studies have shown that nest-site characteristics do not affect success (Best and Stauffer 1980; Holway 1991; Howlett and Stutchbury 1996). However, in our study there was concordance between site preferences and selective pressures on nest-site selection, suggesting that these preferences have been selected to be maintained (Petit and Petit 1996; Martin 1998).

Moreover, our results suggest that predation was a strong selective force operating on site selection by Inca terns, as occurs in many seabird species (e.g. Nettleship 1972; Graves et al. 1986; Gilchrist and Gaston 1997; Stokes and Boersma 1998; Velando and Freire 2001). One important factor affecting the reproductive success of Inca terns on Isla La Vieja was the presence of peregrine falcons: they preyed on chicks and adults and had an indirect effect on breeding success, owing to the behavioural responses of adults to this high predation risk. Thus, since predation risk varied among sites, Inca terns selected those with a lower risk. The sites selected by Inca terns also protected their eggs and chicks against the heat and radiation of the noonday sun, so thermal stress could also have played an important role in the evolution of habitat choice by this species.

Inca terns selected long crevices and laid their eggs far away from the entrance, thereby probably avoiding consumption of the eggs by gulls and vultures and also by terrestrial predators. The Inca tern is a semi-precocial species that lays a large egg (ca. 17% of female body mass; Zavalaga 1997). We found that chicks were left in the crevice by their parents a few days after hatching. As occurs in other tern species, Inca tern chicks were mobile within a few days of hatching. Chicks more often left the nest when it was in a crevice with a shorter chamber and fewer cavities. If predation is an important selective force, chicks should be selected to stay inside the crevice. Nevertheless, early development and precocial behaviour in tern species could be a constraint on chick behaviour and affect the optimal crevice size or structure in this species. Chicks in larger crevices with a greater number of cavities remained on the site and were thus at less risk of being preyed on by aerial predators.

Predation risk can also affect bird behaviour. It has been documented that many bird species form flocks when the predation risk is high (Tinbergen 1951; Hamilton 1971; Caraco et al. 1980). During our study we found a clear change in Inca tern behaviour: they packed tightly together into flocks when a peregrine falcon was in the vicinity of the colony. In other areas of Isla La Vieja (see Velando et al. 2001) located close to sea level and with low peregrine falcon presence, adults arrived at the colony alone, forming flocks only when we visited the nests. In contrast, in the area studied in this paper the terns flew towards the colony in flocks that broke up at the cliff edge. Thus, the sites located far from the edge suffered a higher predation risk, as birds had to fly alone over the inland slopes to their nests.

It is predicted that long-lived birds should reduce their parental investment when the risk of mortality is high (Williams 1966). Inca terns breeding far from the cliff edge, i.e., with a high predation risk, fed their chicks less frequently and were present at the nest less often than those breeding closer to the edge. Consequently, pairs that bred far from the edge reared lighter chicks. Thus, predation risk is associated with site location and seems to change the parental behaviour of adult birds. The results of this study agree with those of other studies on seabirds that reported a reduction of parental investment when the predation risk was high. For example, in response to predator presence, Atlantic puffins (*Fratercula arctica*) decrease the time spent at the colony and their chicks fledged at a lower mass (Harris 1980). Rhinoceros auklet (*Cerorhinca monocerata*) chicks in high-

predation areas fledged earlier than chicks in low-predation areas (Harfenist and Ydenberg 1995). Thus, this study seems to confirm that predation risk represents a cost of reproduction to seabirds and that individuals are able to vary their behaviour according to the predation risk. Nevertheless, despite the correlations between site location and parental investment, it is not clear whether this behaviour is due to behavioural changes in the face of predation risk or to attributes of birds nesting in nonpreferred sites. After the effect of another site characteristic (number of cavities) is taken into account, Inca terns showed a low preference for sites far from the cliff edge. Because birds in good condition are able to hold the preferred sites, the higher parental investment at these sites may simply be the result of the positive correlation between bird condition and site location. Experimental studies are needed to test the role of predation risk on parental behaviour in this species.

Our results show that nesting Inca terns choose habitats that reduce predation risk. In addition to habitat choice, Inca terns also show other types of concealment behaviour that reduce predation risk (see Gaston 1992). They do not defecate anywhere around their nest sites, and crevices are free of external signs of occupation (Murphy 1936; Moynihan 1962; Tovar 1969). Selected nest sites also had more lateral and overhead cover, providing better concealment. Habitat selection by this species can also show long-term responses to terrestrial predators such as the foxes that are very common in other seabird colonies in Peru (Murphy 1936; Tovar 1969; Duffy 1983). In conclusion, the nest-site characteristics preferred by Inca terns on Isla La Vieja reduced predation risk during the breeding period, suggesting a important effect of predation on the evolution of habitat choice in this species.

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