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ORIGINAL ARTICLE

Distance from the forest edge matters in habitat selection of the Blue-footed Booby *Sula nebouxii*

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Abstract The relationships between breeding site location in forest habitat and age, behaviour and reproductive performance of Blue-footed Boobies *Sula nebouxii* were examined in two different plots on the northeast corner of Isla Isabel, Mexico. Birds nesting closer to the forest edge, where nest density is highest, laid their clutches earlier and fledged more chicks. In plot A, proximity to the forest edge was associated with more wakefulness and wing drooping in chicks and more interactions with other species in female breeders. In plot B, ages of breeders increased closer to the forest edge. The patterns of nest density, laying date and age distribution suggest that, on the northeast corner of Isla Isabel, the boobies prefer to nest close to the forest edge, possibly because the benefits, including easy landing and take-off, are greater than the costs associated with inclement weather, high density of conspecifics and allospecifics, and negative social interactions.

Keywords Behaviour · Habitat selection · Nest location · *Sula nebouxii*

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Introduction

Suitability of habitat depends on biotic factors such as densities of conspecifics, predators and parasites, and abiotic factors such as microclimate and topology (Cody 1985; Sutherland 1996). The best quality habitats, associated with the highest breeding success, are often the first to be occupied by good quality breeders and are densely inhabited (Fretwell 1969). Conspecific density has both positive and negative effects on habitat suitability, influencing level of competition, degree of protection against predators and opportunity for mating. At high density, individuals may suffer more from increased conspecific interference, aggression, parasite load and pathogens. Colonial organisms are thought to obtain net benefits despite incurring such costs (Stokes and Dee Boersma 2000).

Habitat location within a colony influences energy expenditure and breeding success (Tenaza 1971; Kim and Monaghan 2005a, b). Habitat quality in terms of microclimate, accessibility to resources such as food and mates, predation risk and conspecific density are often heterogeneous within a colony. A favourable microclimate can reduce energy expenditure of breeders and offspring. Individual quality, habitat location and conspecific density can interactively influence breeding success in colonial birds. Age, experience and physiological condition of breeders are often associated with timing of breeding within the season (Langston et al. 1990), territory defence (Pearson et al. 2005) and chick provisioning (Ratcliffe et al. 1998; Tveraa et al. 1998), and consequently influence breeding success. Nesting centrally within the colony can reduce risk of predation on eggs and chicks (Tenaza 1971; Wiklund 1982; CôTé 2000), and nesting at low density can reduce social stress and cannibalism of chicks (Burger 1980; Brouwer and Spaans 1994; Forero et al. 2002).

In this study, we examined the effects of breeding site location within the colony on reproduction of the Blue-footed Booby *Sula nebouxii* on Isla Isabel in Mexico. Whereas the colony centre is often preferred in seabird colonies in unforested habitat, the preferences of Blue-footed Boobies, which often nest among and near trees and manoeuvre poorly in the air, are likely to be influenced by forest structure. In the northeast corner of the island, temporal and spatial distributions of breeding sites in the colony seemed to suggest that areas close to the forest edge are preferentially selected by breeders. Boobies returning from foraging trips to breeding sites on or close to the forest edge walk just a few metres after landing, but breeding sites further from the forest edge (within the forest) require landing by the forest edge then walking as far as 150 m through the colony, unless there is a gap in the tree canopy near the nest site, and getting past hostile territory holders. Taking off requires a long walk to the forest edge even when there is a gap in the canopy. However, boobies nesting close to the forest edge, where nest density appears higher, seem to suffer more frequent territorial disputes with conspecifics and more frequent predatory harassment by Heerman's Gulls *Larus heermanni*, as well as greater thermal stress.

We analysed reproductive performance and nesting density in two study plots perpendicular to the forest edge in the northeastern corner of the island, plots A and B. We related distance from the forest edge (1) in both plots, with laying date, breeding density, breeder age and breeding success, and (2) in plot A only, with behaviours of breeders and chicks that reflect social stress by conspecifics, disturbance by allospecifics and thermal stress. Finally, we related distance from the forest edge to breeding success.

Methods

Study area and species

We worked from late February to July 2006 on Isla Isabel, a volcanic island (1.3 × 1.7 km) 28 km off the coast of Nayarit (21°52′N, 105°54′W), in the Mexican Pacific. The Blue-footed Boobies nest on horizontal ground in a forest of *Crataeva tapia* and on the adjacent beach and grassland. Since 1989, the reproductive biology of the boobies has been systematically monitored every year in a 20,800-m^2 study area of the colony, where most fledglings have been marked with numbered metal rings (Drummond et al. 2003).

Blue-footed Boobies defend breeding territories throughout the breeding season (Nelson 1978). The male and female jointly select a breeding site within a territory originally defended by the male (Stamps et al. 2002) and jointly care for clutch and brood during roughly 5.5 months, until their offspring become independent after the age of 4 months (Nelson 1978; Torres and Drummond 1999a). One or two, sometimes three, eggs are laid, and usually one or two, exceptionally three, chicks fledge (Drummond et al. 1986). In males and females, breeding success peaks at age 8–10 years (Velando et al. 2006).

The two study plots, A and B, are approximately 35 m apart and cover a total of 11,541 m^2; they are forested and extend inland from the northeastern shore of the island (Fig. 1). At the forest edge, an onshore breeze and downward sloping terrain make take-off easy at most times of day for the heavy-bodied boobies. However, territories on and close to the forest edge have little or no tree shade and are visually exposed to Heerman's Gulls, whereas those in the forest benefit from cover and patches of shade. Plot A measures 116 × 51 m, and tree density there increased from east to west. Plot B measures 120 × 25 m, and is adjacent to grassland where grasses (Graminae, Poaceae and Cyperaceae) were 0.5–2.10 m high in the 2006 breeding season (Fig. 1). Rings allowed us to identify ages of 79% of males and 80% of females breeding in the two plots.

General field procedures

Contents of all nests in the study plots were recorded every few days from shortly after the start of hatching in February until the last chick fledged (reached age 70 days) in July (methods in Drummond et al. 2003). A total of 243 pairs bred in plot A and 198 pairs in plot B. Each breeder's ring number was confirmed by independent readings on 3 days. Dates of laying were recorded when they occurred during the survey period or estimated from hatching dates or length of chick's ulnas and culmens at first encounter

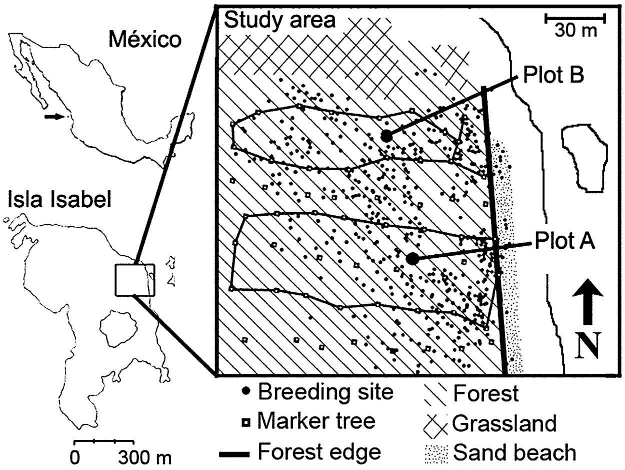

Fig. 1 Breeding site distribution of Blue-footed Boobies *Sula nebouxii* and vegetation pattern in study plots A and B on Isla Isabel

(see also Torres and Drummond 1999b). Laying dates were counted from 30 November 2005 = day 1. Breeding success was the number of chicks fledged per breeding pair.

Measurements of breeding site distribution

Plots A and B comprised 18 approximate rectangles of roughly 20 × 20 m defined by permanent marker trees at their corners, which were mapped at the start of the population study. Each breeding site was mapped by measuring the distance (nearest 10 cm) and direction of its centre from the ground-level estimated centre of the closest marker tree's trunk (Osorio-Beristain and Drummond 1993; Kim et al. 2007). Breeding site locations were expressed in two linear coordinates originating at the marker tree in one corner of the study area.

We calculated the perpendicular distance between each breeding site and the forest edge running parallel to the shore (Fig. 1). As an index of breeding density around each site, we measured distance to the centre of the nearest breeding site in early April, when most breeders had a clutch or brood.

Behavioural observation

To investigate the relationship between breeding location and behaviour, one researcher (A.C. Montes-Medina) monitored the behaviour of parents and chicks at 51 breeding sites in plot A with a brood of two chicks that were 21–70 days old. At each breeding site, observation was made on a single day from 0700 to 1100 hours and from 1500 to 1700 hours, a total of 5 h. The observer sat quietly and unobtrusively 8–12 m away from one or two focal breeding sites. To distinguish senior and junior siblings, we applied a dot of paint to chicks' heads and rumps the day before the observations (Drummond et al. 1986). Chicks older than 1 week are not preyed upon and, in the course of numerous behavioural studies of chicks (Drummond 2001), no behavioural or other effects of paint dots have been suspected.

Sleeping, preening and two thermoregulatory behaviours (panting and wing drooping) were recorded during observation periods using scan sampling at 2-min intervals. Preening and thermoregulatory behaviours were expressed as percentages of the total time adults and chicks were awake (number of nests = 51; mean time awake ± SE: males, 140.98 ± 11.54 min; females, 131.68 ± 11.54 min; senior chicks, 259.10 ± 5.35 min; junior chicks, 248.94 ± 5.87 min). Absolute frequencies of agonistic interactions (alarms and aggression against either conspecific or allospecific individuals) were recorded. A booby was sleeping when its eyes were closed and its head rested on its back (adults and some chicks) or any substrate (chicks). Alarm was recorded when a male whistled or a female grunted at a conspecific or allospecific individual, aggression when parents or chicks performed wing-flailing, jabbing or yes headshaking (Nelson 1978). We recorded the absolute number of conspecifics or allospecifics that passed within 3 m of each breeding site, without distinguishing among individuals.

Statistical analyses

We used parametric tests when data distributions met their assumptions and nonparametric tests otherwise. All tests were two-tailed and we report mean ± SE. Relationships between distance to the forest edge and behaviours were examined using Spearman rank correlation or Pearson correlation. Since the analyses of six different behaviours test a common null hypothesis using the same individuals, we performed a sequential Bonferroni procedure (Holm 1979) to control type I error.

To test effects of distance from the forest edge, laying date and plot on breeding success (number of chicks fledged), we used generalised linear models (GLMs) with a Poisson error distribution and log link. To test effects of distance from the forest edge and plot on laying date and distance to the nearest neighbour, we used GLMs with a Gamma error distribution and reciprocal link. Initially, all explanatory variables and two-way interactions were fitted in a maximal model, and then non-significant interactions and main terms were dropped sequentially to simplify the model. We used deviance tests to compare the simplified minimal adequate model with the model including a non-significant term or with the model excluding a significant term, to assess the statistical significance of each term (Crawley 2005). Analyses were carried out using SPSS v.11.0 and R v.2.3.1 (R Development Core Team 2006).

Results

Breeding site distribution

Both distance from forest edge and plot explained variation in laying date (GLM: distance from the forest edge: deviance$_{1,439} = 0.0003$, $P < 0.001$; plot: deviance$_{1,439} = 0.0003$, $P < 0.001$). Overall, birds in plot A laid their first eggs 20 days earlier than those in plot B (plot A: days 42.4 ± 2.1, $n = 243$; plot B: days 61.9 ± 2.7, $n = 198$). In both plots, the closer to the forest edge a site was, the earlier its laying date (Fig. 2a). The interaction, plot × distance from the forest edge, was not significant (GLM: deviance$_{1,439} = 0.000002$, $P = 0.06$).

There was a significant interacting effect of plot × distance from the forest edge on breeding density (distance to the nearest neighbour) (GLM: deviance$_{1,439} = 7.36$,

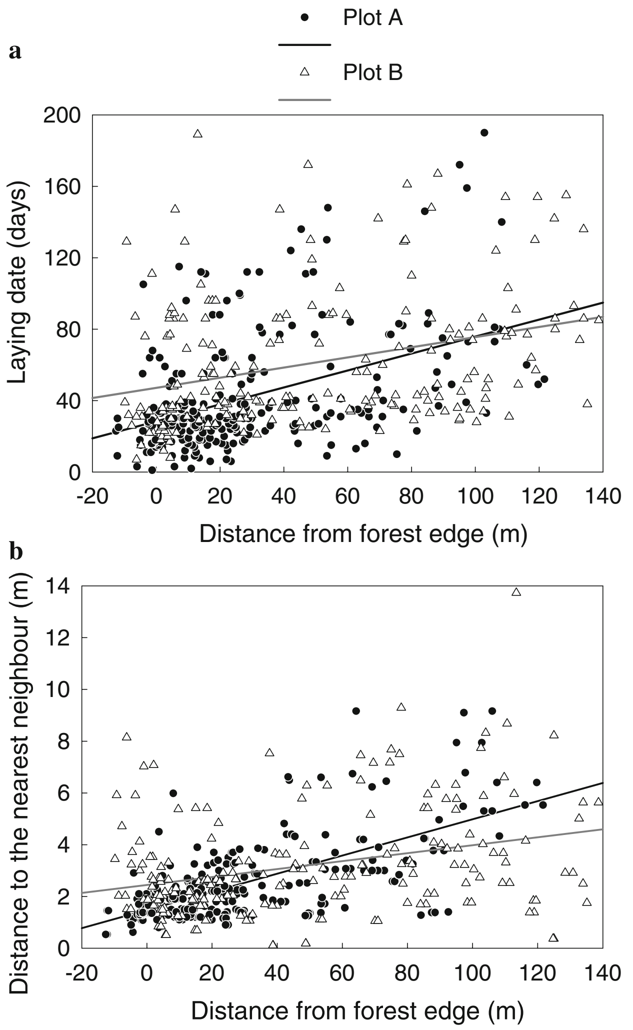

Fig. 2 Relationships **a** between laying date (30 November 2005 = 1) and distance from the forest edge; **b** between distance to the nearest neighbour and distance from the forest edge of all breeding sites in plot A ($n = 243$) and plot B ($n = 198$)

$P < 0.001$). When analysed separately for each plot, the effect of distance from the forest edge on breeding density was significant in both plots (Fig. 2b; GLM: plot A: deviance$_{1,242} = 97.24$, $P < 0.001$; plot B: deviance$_{1,196} = 25.36$, $P < 0.001$). In both plots, breeding sites close to the forest edge were closer to conspecific nests than those further from the forest edge, suggesting that breeding density diminished away from the forest edge (Fig. 2b).

Breeder age and breeding distribution

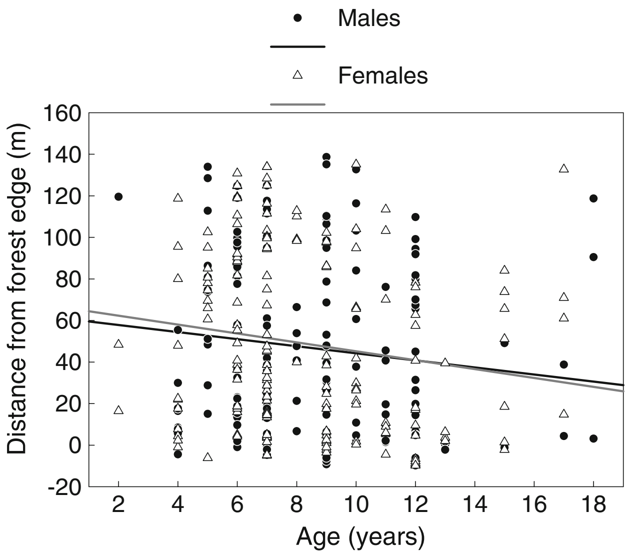

Fig. 3 Relationship between distance from the forest edge and breeder age (years) in plot B (mean breeding age ± SE: males: 8.5 ± 0.2 years, $n = 171$; females: 8.3 ± 0.2 years, $n = 167$)

In plot A, there was no significant correlation between distance from the forest edge and age of either males or females (Spearman correlation rank: males: $r_s = 0.01$, $n = 177$, $P = 0.86$; females: $r_s = 0.05$, $n = 175$, $P = 0.49$). In plot B, there was a significant negative correlation between distance from the forest edge and age of both sexes (Spearman rank correlation: males: $r_s = -0.171$, $n = 171$, $P < 0.05$; females: $r_s = -0.217$, $n = 167$, $P < 0.01$), suggesting that older breeders nested closer to the forest edge (Fig. 3).

Relationship between breeding site location and behaviour

Distance from the forest edge (in plot A) was significantly correlated with percentage of time asleep in senior and junior chicks, but not in adults (Table 1). After sequential Bonferroni adjustment, this association was significant only in junior chicks (Table 1). Junior chicks closer to the forest edge spent less time sleeping (Fig. 4). Females closer to the forest edge spent more of their time awake preening than those further from the forest edge (although this was not significant after sequential Bonferroni adjustment), but this pattern was not significant in males or chicks (Table 1).

There was no correlation between distance from the forest edge and percentage of time awake panting by any family member (Table 1). Both senior and junior chicks closer to the forest edge spent more time awake performing wing drooping than those further from the forest edge (Fig. 4), but this relationship was not significant in adults (Table 1). After sequential Bonferroni adjustment, the negative association between distance from the forest edge and wing drooping was significant only in senior chicks (Table 1).

Distance from the forest edge was significantly correlated with the number of conspecific and allospecific individuals passing within 3 m of a site (GLM:

Table 1 Percentage of time (means ± SE) spent sleeping, preening, panting and wing drooping and the frequency per hour (means ± SE) of conspecific and allospecific interactions (alert and aggression) in males, females, senior chicks and junior chicks of Blue-footed Boobies *Sula nebouxii*

	Subject	*n*	% Time/frequency	Correlation with distance from forest edge	Sequential Bonferroni
Sleeping (%)	Males	47	4.86 ± 1.32	$r = 0.04, P = 0.79$	
	Females	46	2.64 ± 0.56	$r_s = 0.07, P = 0.63$	
	Senior chicks	51	13.63 ± 1.78	$r = 0.34, P = 0.015$	>0.01
	Junior chicks	51	17.02 ± 1.96	$r = 0.37, P = 0.008$	$=0.008$
Preening (%)	Males	25	18.84 ± 2.59	$r = -0.20, P = 0.35$	
	Females	23	15.27 ± 2.88	$r = -0.42, P = 0.045$	>0.01
	Senior chicks	28	26.20 ± 1.89	$r = -0.13, P = 0.50$	
	Junior chicks	28	23.64 ± 1.90	$r = -0.30, P = 0.12$	
Panting (%)	Males	47	22.22 ± 3.49	$r = -0.02, P = 0.90$	
	Females	46	25.06 ± 3.50	$r_s = -0.23, P = 0.12$	
	Senior chicks	51	23.29 ± 1.95	$r = -0.06, P = 0.67$	
	Junior chicks	51	22.55 ± 2.23	$r = -0.21, P = 0.15$	
Wing drooping (%)	Males	47	0.82 ± 0.54	$r = -0.11, P = 0.46$	
	Females	46	1.65 ± 0.74	$r_s = 0.10, P = 0.51$	
	Senior chicks	51	7.04 ± 1.07	$r_s = -0.56, P < 0.001$	<0.008
	Junior chicks	51	8.82 ± 1.26	$r_s = -0.28, P = 0.044$	>0.01
Alert and aggression against conspecifics	Males	47	5.02 ± 1.03	$r = -0.21, P = 0.16$	
	Females	46	5.21 ± 0.76	$r = -0.21, P = 0.17$	
	Senior chicks	51	1.85 ± 0.38	$r = 0.19, P = 0.16$	
	Junior chicks	51	1.53 ± 0.34	$r = -0.27\ P = 0.054$	
Alert and aggression against allospecifics	Males	47	0.83 ± 0.19	$r = -0.36, P = 0.012$	>0.008
	Females	46	1.00 ± 0.27	$r = -0.45, P = 0.002$	<0.008
	Senior chicks	51	0.23 ± 0.10	$r = 0.17, P = 0.23$	
	Junior chicks	51	0.18 ± 0.04	$r = -0.09, P = 0.49$	

Correlations are between distance from the forest edge and the behaviours in males, females, senior chicks and junior chicks (r_s = Spearman rank correlation, r = Pearson correlation). Significant results are adjusted using sequential Bonferroni procedure in each subject

deviance$_{1,30} = 299.05$, $P < 0.001$), but not with agonistic interactions with conspecifics (alarm and aggression) by any family member (Table 1). Males and females nesting closer to the forest edge had significantly more frequent agonistic interactions with other species such as Heermann's Gulls, Mexican Spinytail Iguanas *Ctenosaura pectinata*, Groove-billed Anis *Crotophaga sulcirostris* and Mexican Whiptail Lizards *Aspidoscelis costata* (Fig. 4). However, the association was significant only in females after Bonferroni adjustment (Table 1).

Relationship between breeding site location and breeding success

Variation in breeding success was explained by laying date, distance from the forest edge and plot (Table 2). Birds in plot A fledged more chicks on average than those in plot B (mean ± SE: plot A: 1.45 ± 0.06 chicks, $n = 243$; plot B: 1.40 ± 0.07 chicks, $n = 198$). Early breeders fledged more chicks than late breeders. The closer to the forest edge a bird nested, the more chicks it fledged, but interestingly, this relationship seems to appear only in the plot A (Fig. 5), although the interaction, distance from the forest edge × plot, was not significant (Table 2).

Discussion

Assuming that breeding density indicates relative attractiveness of nesting habitat, plot A seemed more attractive than plot B, and in both plots the forest edge was more attractive than the forest interior. In the more attractive locations, boobies nested earlier and more densely and fledged more chicks. In plot A (the plot where behaviour was observed), proximity to the forest edge was associated with more wakefulness and wing drooping in chicks, more parental interactions with other species and more preening by females. In plot B (only), ages of males and females increased closer to the forest edge.

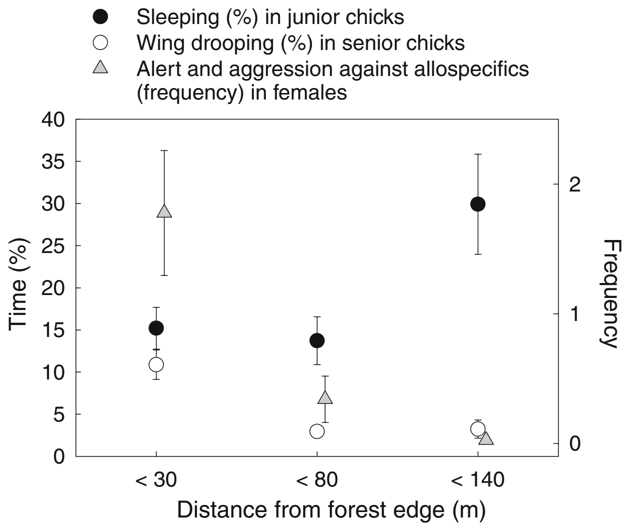

Fig. 4 Mean ± SE percentage of time spent sleeping in junior chicks, percentage of time spent wing drooping in senior chicks and frequency per hour of allopatric interactions (alert and aggression) in females according to the distance from the forest edge, categorised into three groups (<30 m, <80 m and <140 m)

Table 2 Summary of a GLM with a Poisson error distribution and a log link examining the effects of laying date, distance from the forest edge and plot on breeding success (number of chicks fledged)

Variable	Deviance	*df*	P
Laying date	132.26	1,439	<0.001
Distance from the tree line	14.432	1,439	<0.001
Plot	4.291	1,439	<0.05
Laying date × distance from the forest edge	7.662	1,439	<0.05
Laying date × plot	0.320	1,439	0.572
Distance from the forest edge × plot	0.395	1,439	0.530
Laying date × distance from the forest edge × plot	0.723	1,439	0.395

Distance from the forest edge and breeding distribution

Higher breeding density and earlier onset of reproduction in the shoreline area along the forest edge indicate a possible preference for nesting there. Proximity of older birds to the forest edge in plot B also supports this idea, although this pattern was not observed in the other plot. Probably, in some contexts, effects of other factors prevail over effects of age. In migratory birds, experienced and older individuals often arrive early in the breeding season, mate early and have a high reproductive success (Davis 1976; Hill 1988; Perdeck and Cave 1992; Møller 1994; Lozano et al. 1996; Espie et al. 2000; Ezard et al. 2007). Young birds may be forced into suboptimal breeding sites by more competitive breeders (Tenaza 1971; Kokko et al. 2004; Kim et al. 2007), or possibly only competitive birds can pay the costs of early arrival (Kokko 1999).

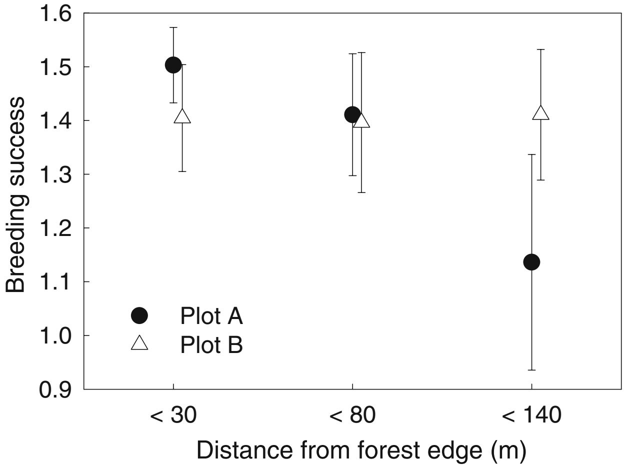

Fig. 5 Mean ± SE breeding success (number of chicks fledged) in plots A and B according to distance from the forest edge, categorised into three groups (<30 m, <80 m and <140 m)

At nests close to the forest edge, boobies can readily take off and land without having to walk overland and interact with hostile conspecifics, and in a forested area, this access advantage may be critical. In addition, males with a territory close to the forest edge, where density is the highest and boobies pass by on route to the forest interior, may encounter more females and enjoy higher mating success (cf. "hidden lek" hypothesis in Wagner 1993; Wagner et al. 2000).

Association between breeding site location and behaviour

Heterogeneity in the study area in physical habitat, breeding density and social stress could produce the observed associations between behaviours of breeders and chicks and distance to the forest edge. It is likely that junior chicks close to the forest edge in the high density area spent less time sleeping due to frequent disturbance by conspecific passers-by, iguanas and gulls, although this effect did not appear in adults. Diminished sleep of chicks close to the forest edge could inflict costs in terms of energy expenditure, restoration of physiological functions and predation risk (Meddis 1975).

For many tropical seabirds with open nests, heat is stressful for chicks and adults (Bartholomew and Dawson 1954; Howell and Bartholomew 1962) and thermal conditions at breeding sites may affect chick development, growth and survival (Salzman 1982). Panting and wing drooping allow birds to release excess body heat. Senior chicks at breeding sites close to the forest edge probably drooped their wings more persistently in response to intense solar radiation throughout morning and midday. A number of studies have suggested that vegetation can provide chicks with important protection against unfavourable microclimate (Salzman 1982; Kim and Monaghan 2005a, b).

Female breeders close to the forest edge faced increased agonistic interactions with allospecifics, mainly because Heermann's Gulls are most common there, apparently attracted by opportunities to steal the food that boobies regurgitate for their chicks. At the forest edge, it is likely that better visual access facilitates detection of feeding events and dropped food by gulls.

Relationship between breeding site location and breeding success

Breeding success tends to vary with nest location within avian colonies (Ryder and Ryder 1981; Perdeck and Cave 1992; Pärt 2001; Geslin et al. 2004). On the forested northeast corner of Isla Isabel, disturbance, kleptoparasitism by gulls, lack of shade and the alleged high ectoparasite density may negatively influence the reproduction of birds that nest close to the forest edge. However, the closer to the forest edge a bird nested, the more chicks it fledged. For boobies nesting in forest habitat, the main advantage of nesting along the forest edge may well lie in nest access. This benefit of nesting close to the forest edge may outweigh the costs of inclement weather, high density of conspecifics and allospecifics and negative social interactions, and consequently result in better breeding success there.

Zusammenfassung

Die Entfernung zum Waldrand spielt eine Rolle bei der Habitatselektion des Blaufußtölpels *Sula nebouxii*

Die Beziehungen zwischen Brutplatz in Waldhabitat und Alter, Verhalten und reproduktiver Performanz von Blaufußtölpeln wurden in zwei verschiedenen Arealen in der nordöstlichen Ecke der Isla Isabel, Mexiko, untersucht. Vögel, die näher am Waldrand brüteten, wo die Nestdichte am höchsten ist, begannen früher mit dem Legen und brachten mehr Küken zum Ausfliegen. In Areal A war die Nähe zum Waldrand mit stärkerer Wachsamkeit und herabhängenden Flügeln bei Küken und häufigeren Interaktionen mit anderen Arten bei weiblichen Brutvögeln assoziiert. In Areal B nahm das Alter der Brutvögel mit der Nähe zum Waldrand zu. Die Muster von Nestdichte, Legedatum und Altersverteilung lassen darauf schließen, dass die Tölpel in der nordöstlichen Ecke der Isla Isabel vorzugsweise nah am Waldrand brüten, möglicherweise da die Vorteile, einschließlich einfachen Landens und Startens, größer sind als die Kosten, die mit rauem Wetter, einer hohen Dichte von Artgenossen sowie Individuen fremder Arten und negativen sozialen Interaktionen verbunden sind.

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