



## Habitat structure and colony structure constrain extrapair paternity in a colonial bird



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Individual variation in sexual fidelity and extrapair paternity (EPP) is widely attributed to environmental heterogeneity, but the only variables known to be influential are food abundance and density of conspecific breeders (potential extrapair partners). Habitat structure is thought to impact EPP but is rarely measured and, when considered, is usually confounded with food abundance and predation pressure. To sidestep these confounds, we tested whether EPP is associated with habitat structure variables and with local conspecific density in a species whose nesting habitat is not used for feeding and lacks predators. In a blue-footed booby, *Sula nebouxii*, colony, the probability of EPP in a female's nest was highest in parts of the study plot where there were few obstacles to locomotion, and was quadratically related to local density of sexually active males, even though local males did not sire the EP chicks. The probability of a male breeder siring EP (extrapair) chicks elsewhere was quadratically related to local density of sexually active males around his nest. From these patterns we infer that both sexes may foray for EP interactions, that males and females nesting at intermediate density are most likely to be accessed by forayers, and that obstacles in the vicinity of a female's nest constrain access of foraging males. To our knowledge, this is the first demonstration that individual variation in EPP is associated with habitat structure in the absence of confounding variation in food availability, predation pressure or breeder quality, and the first evidence that EPP opportunities of female and male breeders are reduced by high density of conspecific breeders above a particular threshold.

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Infidelity and extrapair paternity (EPP) characterize most avian mating systems and vary considerably among individuals, populations and species (reviews in: Birkhead & Møller, 1992, 1996; Gowaty, 2006). Over several decades researchers have expended considerable effort to explain this variation in terms of population density, nesting synchrony, and the age and secondary sexual characteristics of males (reviewed in Griffith, Owens, & Thuman, 2002), while devoting much less effort to ecological variables such as habitat structure, food availability (Hoi-Leitner, Hoi, Romero-Pujante, & Valera, 1999; Václav, Hoi, & Blomqvist, 2003), weather (Bouwman & Komdeur, 2006) and predation pressure. Habitat structure is widely expected to affect opportunities for

extrapair (EP) interactions (Westneat & Stewart, 2003), for example by constraining the extraterritorial foraging by which males and females of some species gain access to potential EP partners or by obstructing visual monitoring and guarding of partners (Sundberg, 1994). For instance, it is suspected that female great grey shrikes, *Lanius excubitor*, perform their EP copulations in secluded parts of their territories to escape detection (Tryjanowski, Antczak, & Hromada, 2007) and that female yellow-breasted chats, *Icteria virens*, have fewer EP chicks in open habitat because their mates can more easily guard them there (Mays & Ritchison, 2004). However, reported associations between habitat quality and EPP are likely due, not to habitat structure per se, but to associated food availability (e.g. Charmantier & Blondel, 2003; Rubenstein, 2007) or predation threat. Surprisingly, impacts of habitat structure on EPP, independent of effects of food availability and predation, have gone largely unstudied.

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To address this omission, we studied a colony of birds that nest densely in a complex habitat in which the residents do not forage and in which predators are absent, allowing us to test for associations between EPP and habitat structure in the absence of typical confounds. Blue-footed boobies, *Sula nebouxi*, nest on the forested margins of the study island, on horizontal or gently sloping ground that is heterogeneous for substrate quality and for presence of obstacles to locomotion and visual monitoring of conspecifics. Adults feed entirely at sea and, as is typical for boobies (Nelson, 1978), are not subject to any predation on land. In a part of the colony with a north–south gradient for obstacle density and an east–west gradient for proximity to the shore, we tested whether probability of EPP at each nest was associated with its location on those two axes and with substrate quality, obstacle abundance and conspecific visibility around the nest. In addition, we tested whether these habitat structure variables around a male's nest affect his probability of siring EP chicks elsewhere.

We also tested for an effect of density of sexually active male breeders around each nest on EPP at the nest and on the male's probability of siring chicks elsewhere, because the boobies' fierce territorial defence constrains locomotion of colony neighbours and passers-by and potentially limits access to EP partners or the scope of EP interactions. In avian species, local conspecific abundance can increase the probability of EPP by increasing the rate of encounters with potential EP partners (Griffith et al., 2002; Stewart, Westneat, & Ritchison, 2010), but it is not known whether dense nesting in terrestrial avian colonies can impede extrapair (EP) interactions.

Importantly, female boobies are larger than males, and extensive observation of EP behaviour in the study colony has shown that copulation is always preceded by reciprocal courtship and never by any behaviour resembling coercion (see *Study Colony and Habitat*; Westneat & Stewart, 2003). This enabled us to interpret observed patterns of paternity as an outcome of male willingness and female choice.

## METHODS

### *Study Colony and Habitat*

On the northeast shore of Isla Isabel, Mexico (21°52'N, 105°54'W), blue-footed boobies nest colonially in and at the edges of a forest of garlic pear (*Crataeva tapia*) and papelillo trees (*Euphorbia schlechtendalli*). They feed exclusively by plunge-diving for fish, and adults have no predators on their nesting grounds. The forest floor of the island is studded with embedded boulders and littered with patches of tall grass and remains of dead and sprouting trees, mostly felled by hurricane Rosa in 1994. There, these large birds walk, hop and flutter awkwardly, slipping and snagging on boulders and fallen branches, occasionally even tearing the webs of their feet. Some die snagged on branches while attempting to land through gaps in the tree canopy. In the 8450 m<sup>2</sup> study plot (part of a wider long-term study area in which 90% of breeders are banded), nests can be as close as 1 m to each other but density is heterogeneous. Territories, which are larger at low densities, are defended 24 h per day; males and females threaten and attack neighbours and intruders, particularly during the period of courtship and copulation when boundaries are being expanded and contested (Nelson, 1978). Nevertheless, most boobies nesting in the forest interior walk to and from the shore for take-off and landing for their foraging trips, bypassing and tussling with territory holders along the way.

Direct observation of relatively dense neighbourhoods in two seasons revealed that 53–61% of males and 33–53% of females copulated with habitual EP partners, usually neighbours, on or beside one of their territories before laying eggs. Sexual conflict

over EPP was indicated by a 35-fold increase in the rate of female EP copulations in the absence of their partners, an increase in within-pair courtship by males after observing their partner's EP courtship and destruction of the first-laid egg by males that were prevented from monitoring their female partner (i.e. removed from the territory for 10–12 h) during the female's assumed fertile period (Osorio-Beristain & Drummond, 1998, 2001; Pérez-Staples & Drummond, 2005; Pérez-Staples, Osorio-Beristain, Rodríguez, & Drummond, 2013).

Female boobies can control EP copulation. They are larger, 32% heavier and sensibly stronger (during handling) than males; copulation can only occur if the female stands still to allow the male to perch on her back; all observed EP copulations were preceded by reciprocal courtship, usually spread over days or weeks; and we have never seen EP males showing aggression to females or their partners (Osorio-Beristain & Drummond, 1998; Pérez-Staples & Drummond, 2005).

### *Blood Sampling*

In 2011, we marked and mapped all nests in the 20 800 m<sup>2</sup> long-term study area, and recorded breeder identities and nest contents every 3 or 6 days (details in Drummond, Torres, & Krishnan, 2003). In the study plot for this project, a 8450 m<sup>2</sup> subsection, we took blood samples between February and May from the families of all 478 nests in which any chick survived to at least age 10 days (72.3% of total nests in that section). In 424 sampled families, we obtained blood from both putative parents and all of their nestlings; in 54 families, broods were incompletely sampled because of early death of one or two chicks, but these families were retained in our analyses.

For sampling, we hand-captured adults on dark nights between 2100 and 0500 hours and removed chicks from their nests at ages 10–40 days between 0800 and 1200 hours or between 1400 and 1800 hours. We withdrew 75 µl of blood from the brachial vein and immediately mixed it with 1 ml of storage buffer (1.0 M Tris: 0.5 M EDTA: 5.0 M NaCl: 10% SDS). Manipulation took less than 10 min and bleeding stopped before release at the site of capture. Released adults promptly settled into their original neighbourhoods, and released chicks were readily attended by their putative parents. The Secretaria del Medio Ambiente y Recursos Naturales (SEMARNAT) provided the permit (SGPA/DGVS/08333/10) to collect blood samples.

### *Parentage*

We extracted DNA with illustra blood genomicPrep Mini Spin Kits from GE Healthcare (Buckinghamshire, U.K.). To analyse paternity we used 10 blue-footed booby microsatellite loci that ranged from three to 22 alleles per locus (Faircloth, Ramos, Drummond, & Gowaty, 2009). We performed all PCR amplifications under the conditions specified by Faircloth et al. (2009) and used GeneMapper version 3.7 (Applied Biosystems, Foster City, CA, U.S.A.) to analyse results. To evaluate genotypic linkage disequilibrium and deviations from Hardy–Weinberg equilibrium with Bonferroni corrections, we used GenePop v.4.0.1 (Raymond & Rousset, 1995). We conducted allele frequency estimations and parentage analyses with a likelihood-based approach in CERVUS 2.0 (Marshall, Slate, Kruuk, & Pemberton, 1998).

The sample was reduced from 478 to 453 focal families by excluding 25 families where either the female or male was genotyped in fewer than 6 of the 10 microsatellite loci; 13 chicks were excluded for the same reason. We performed 10 000 tests and assumed that 90% of sampled males and females (the percentage of individuals in the study area that bear our bands) originated from

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