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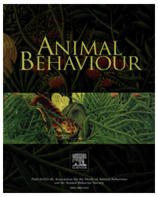

Habitat structure and colony structure constrain extrapair paternity in a colonial bird

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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 foraying 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.

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 foraying 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 nebouxii*, 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^2 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^2 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^2 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 Secretarıa 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

Isla Isabel's population of about 4000 breeders. Relaxed and strict assignment levels were set at values of 80 and 95%, respectively. To assign paternity of EPP chicks, we first assigned maternity by using the putative mother as the candidate parent. If zero or one mismatch was found between the nestling and its putative mother, we assigned maternity. For nestlings that mismatched their putative mother by more than one locus, maternity was scored as unknown for subsequent paternity analysis. For nestlings for which putative mothers were not sampled ($N = 36$), we examined maternity using all sampled females as candidate mothers. If no candidate mother was assigned maternity with strict confidence, maternity was left unknown for paternity analysis. We then checked paternity using the identified male breeder at the nest as the candidate father. When no mismatches occurred within the trio, paternity and maternity were assigned to the two putative parents. We reran CERVUS when mismatches occurred, using the assigned mother and all males with at least six genotyped loci as candidate fathers. If we could still not assign paternity with confidence, we examined parentage using all males and females as candidates. We found 55 EPP chicks in 48 broods and successfully assigned paternity to 17 chicks.

Local Nest Density

We measured local nest density as the number of nests with sexually active males within 10 m of each female's nest. Pairs were included if their male's assumed period of sexual activity (between the 16th day before and the 30th day after their females laid, based on the observed range of EP fertilizations by paired males; see Results) overlapped the female's potential fertile period (her laying period plus 29 days, the average prelaying period: Osorio-Beristain & Drummond, 1998). Local density for analysis of a male breeder's probability of siring chicks at other nests included all nests within 10 m of the male whose males' assumed period of sexual activity overlapped his. We used a radius of 10 m since boobies interact most often with individuals nesting within this distance (Drummond, Torres, Juarez, & Kim, 2010; Montes-Medina, Drummond, & Kim, 2009; Osorio-Beristain & Drummond, 1993).

The local density of sexually active males around nests of females and potential male sires was significantly correlated with densities of local breeders in all reproductive stages (Pearson correlation: females: $r_{421} = 0.94$, $P < 0.001$; males: $r_{421} = 0.97$, $P < 0.001$). However, significance values and changes in deviance in nested generalized linear models indicated that the density of sexually active males was a better predictor for female EP paternity and male EP paternity gain than was density of local breeders in all stages.

Habitat Structure

After the breeding season, we measured density of obstacles to locomotion, substrate quality and visibility of standing boobies to each other at 152 focal nest sites: at 100 randomly selected sites and at all sites with EP chicks or EP sires. By error, we omitted eight sites of EP chicks and two sites of EP sires where breeder ages were unknown, leaving samples of 38 and 14 sites, respectively. In a 5 m radius around each site, we counted the objects that could obstruct walking boobies (standing and fallen tree trunks >15 cm in diameter and rocks protruding >30 cm from the substrate), visually estimated the percentage of substrate covered by grass and by rocks, and computed a visibility index by posing a 40 cm high stick (representing a standing booby) 5 m away at eight standard, evenly spaced compass bearings, scoring the proportion of the stick (100%, 50%, 0%) that an observer at the site could see from a height of 35 cm (booby eye-height), and summing the eight scores. A 5 m radius permitted sensitive discrimination among sites; visibility decreased with distance and, at 10 m, most bearings scored 0% visibility.

Analysis

To analyse the probability of a female breeder having an EP chick in her nest and the probability of a male breeder siring a chick at another nest, we used generalized linear models (GLMs) with binomial distribution and logit link function. Full models included local nest density, laying date and spatial coordinates (X and Y) within the sampling area as explanatory variables, plus quadratic terms and interactions of interest (see Results, Table 1). Laying date was expressed as a proportional rank that ranged from zero to one, using all 1360 nests in the study area in 2011. The sample was reduced from 453 to 423 focal families by exclusion of 25 nests located less than 10 m from the edge of the sampling area (whose local nest density could not be fairly calculated), three nests lacking spatial coordinates and two nests with unknown laying dates. At one excluded nest the male breeder sired an EP chick elsewhere, and two of the excluded nests had EP chicks. Excluded nests were included in the analyses as neighbours of focal nests, except when their spatial coordinates or laying date were unknown.

Two additional GLMs tested whether any of the four habitat structure variables (obstacles, grass cover, rock cover and visibility) predicted the probability that females at focal nests would have EP chicks in their broods or that males at focal nests would sire chicks elsewhere. Variance inflation factors (VIFs) for all explanatory variables were less than 2, indicating acceptable levels of multicollinearity (Zuur, Ieno, & Elphick, 2010; Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

We simplified full models with deletion tests, removing nonsignificant interactions, quadratic factors and linear factors sequentially (Crawley, 2007). Each term was individually removed to evaluate its significance and change in deviance, then reintroduced to the model. After evaluating every term, we permanently removed the nonsignificant term that accounted for the least change in deviance and repeated the process until only significant terms remained. We used deletion tests to obtain the P values associated with each term in the final model. Statistics were performed in R statistical software v.2.12.2 (R Development Core Team, 2008). Means ± SD are reported throughout the manuscript.

RESULTS

Females with EP Chicks

Forty-eight (10.6%) of the 453 genotyped families had one or two EP chicks (41 had one EP chick and seven had two EP chicks), and 46 (10.9%) of our reduced sample of 423 focal females had at

Table 1

Generalized linear model of the relationship between probability of an extrapair (EP) chick in a nest and its location (X coordinate) and local nest density ($N = 423$ nests)

Variables in final model	B	SE(β)	Deviance[a]	P[a]
X coordinate	0.016	0.005	10.01	<0.001
Density	0.162	0.103	2.76	0.096
Density^2	−0.004	0.002	3.74	0.052

Full model: (EPP ~ X coordinate + Y coordinate + laying date + density + (density)^2 + (X coordinate)^2 + (Y coordinate)^2 + X coordinate $*$ Y coordinate + density $*$ laying date + laying date $*$ Y coordinate + laying date $*$ X coordinate + X coordinate $*$ density + Y coordinate $*$ density + (X coordinate)^2 $*$ (Y coordinate)^2, family = binomial).

[a] We obtained statistical significance and changes in deviance from comparison tests between nested models.

least one EP chick (39 with one EP chick and seven with two EP chicks). The probability of a brood including an EP chick was related to location in the sampling area, habitat structure and local nest density, but not to laying date (Table 1).

The relationship between EPP and spatial location of nests was significant for the X coordinate (GLM: $P < 0.001$) but not the Y coordinate (GLM: $P = 0.76$) or their interaction (GLM: $P = 0.12$): probability of EPP decreased southward in the sampled area regardless of a nest's distance from the shoreline, and there were no EPP chicks in the southernmost 22 m band (Fig. 1).

Analysis of habitat structure revealed only one (marginally) significant association: probability of EPP increased as the density of obstacles to locomotion within 5 m of a female's nest decreased (GLM: deviance = 3.79, $N = 138$, $P = 0.051$). Density of obstacles decreased in the same direction that probability of EPP increased: northward (Fig. 2). Probability of EPP was not related to substrate quality (GLM: grass coverage: $P = 0.30$; rock coverage: $P = 0.66$), visibility (GLM: $P = 0.58$), or any interaction between habitat structure variables.

The observed associations between EPP and both location and obstacle density could potentially be driven by associations between breeder quality and those environmental variables. To test for this, for all boobies of known reproductive history that bred in the study plot in 2011, we sought correlations between the X coordinate and two indices of their quality: age and previous breeding success. We expressed individuals' previous breeding success as the average of the numbers of fledglings they produced each year (standardized for each year) between birth and 2010. All four Spearman rank correlation coefficients were small and none approached significance (male age: $r_S = 0.043$, $N = 596$, $P = 0.30$; male reproductive success: $r_S = 0.037$, $N = 324$, $P = 0.51$; female age: $r_S = 0.054$, $N = 587$, $P = 0.19$; female reproductive success: $r_S = -0.017$, $N = 295$, $P = 0.78$). In addition, to test whether the probability of EPP was associated with male or female body condition or size, we tested whether those variables were correlated with the X coordinate, using the 333 males and 326 females in the study plot that were weighed and measured in 2011. Condition was expressed as the residuals of a regression of body mass on body size (ulna length). Again, Spearman rank correlation coefficients were small and none approached significance (male body condition: $r_S = 0.076$, $P = 0.16$; male body size: $r_S = 0.067$, $P = 0.22$; female body condition: $r_S = 0.017$, $P = 0.75$; female body size: $r_S = 0.016$, $P = 0.77$).

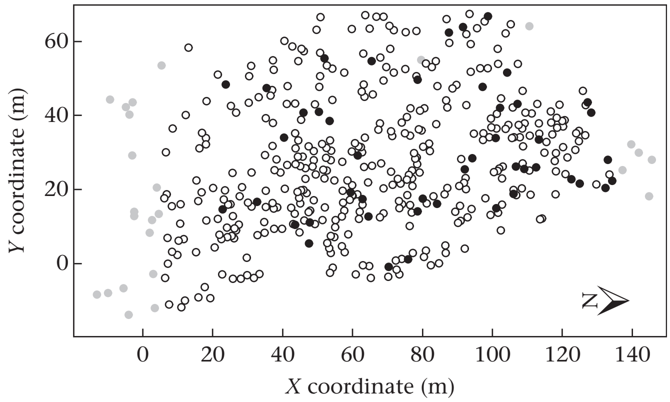

Figure 1. Distribution of blue-footed booby nests with extrapair (EP) chicks in the sampling area. Focal nests included 46 nests with EP chicks (black dots) and 377 nests without EP chicks (white dots). Grey dots represent 25 nests that were included in the analysis only as neighbours because proximity to the sampling area boundary prevented calculation of local nest density. The shoreline runs roughly north–south, about 20 m beyond the lower (eastern) boundary of the plot.

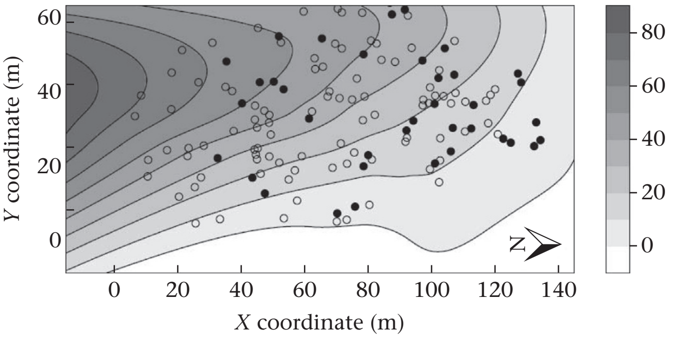

Figure 2. Extrapair paternity and obstacle density in blue-footed boobies. Focal nests comprised 99 nests without extrapair (EP) chicks (open dots) and 39 nests with EP chicks (solid dots). Scale shows number of trees and rocks within 5 m of focal nests. Contour plot created with lattice package of R shows estimated obstacle density in each greyscale band (Sarkar, 2008). The shoreline runs roughly north–south, about 20 m beyond the lower (eastern) boundary of the plot.

The probability of EPP was marginally related to quadratic local nest density (GLM: $P = 0.052$; Fig. 3), and piecewise regression (Crawley, 2007) showed that although the initial increase with density in Fig. 3 was not significant (density <26: intercept = −2.21, slope = 0.012, $N = 273$, $P = 0.72$), the probability of EPP declined significantly above 26 nests/neighbourhood (density ≥26: intercept = 3.49, slope = −0.18, $N = 150$, $P = 0.025$). Moreover, visual inspection suggests that, with only one exception, nests with EP chicks did not occur within nest clusters, but rather at their edges and in more isolated nests (Fig. 1).

Extrapair Sires

We successfully assigned paternity of 17 of the 55 EP chicks genotyped in the sampled area. One of these EP fathers sired two EP chicks in nests that were 33.9 m apart.

The probability of a male breeder in the sampling area siring a chick at another nest in the sampling area was not related to his nest's Y or X coordinates (GLM: Y coordinate, $P = 0.21$; X coordinate, $P = 0.43$), nor to his social partner's laying date (GLM: $P = 0.56$). It was significantly related to the quadratic local nest density (GLM: deviance = 6.49, $N = 423$, $P = 0.010$; Fig. 4) but not to linear local density (GLM: $P = 0.37$). The probability of siring an EP chick

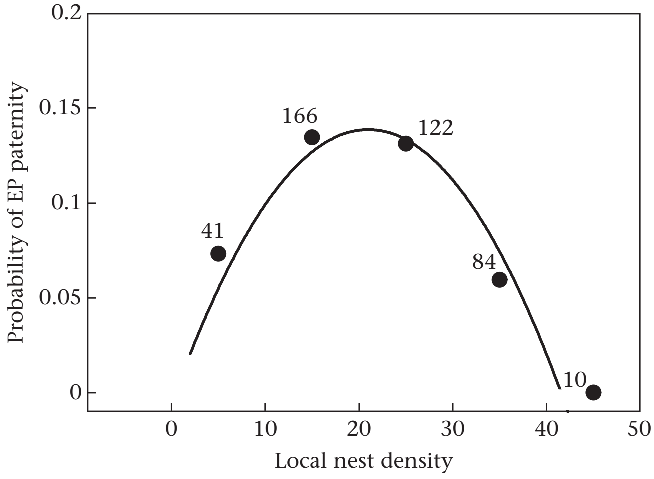

Figure 3. Probability of extrapair paternity (EPP) in a female blue-footed booby's nest as a function of local nest density (neighbours within 10 m). Points show mean probabilities at each of five nest density intervals; numbers represent sample sizes at each density interval. We binned the (binomial) data to improve visualization.

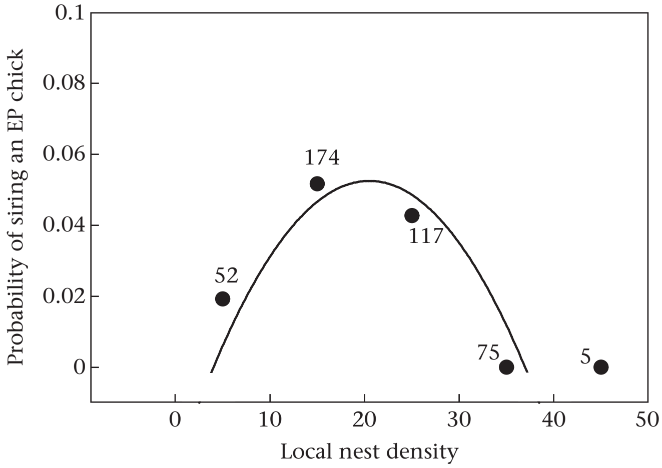

Figure 4. Probability of male's gaining extrapair paternity as a function of local nest density (i.e. neighbours within 10 m). Points show mean probabilities at each of five nest density intervals; numbers represent sample sizes at each density interval. We binned the (binomial) data to improve visualization.

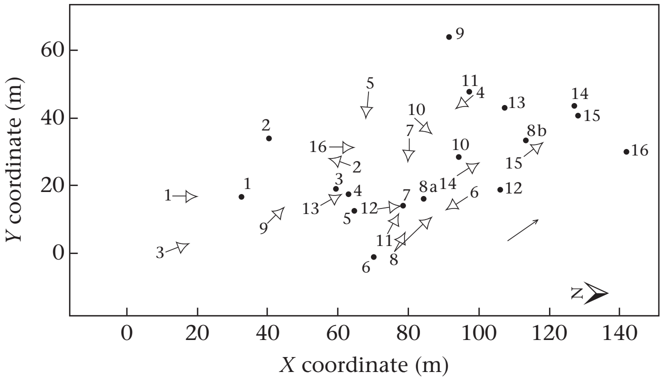

Figure 6. Spatial relationship between nests of extrapair (EP) sires and nests of their EP partners. Locations of nests with EP chicks (dots) and nests of the corresponding EP sires (at origin of each arrow). Arrows show the directions of movement of sires, assuming they moved directly from their own territories to the territories of their EP partners to inseminate them. The nest of each EP chick bears the same number as the corresponding EP sire. The large arrow shows the mean movement bearing of 328.8°, assuming that sires moved to the territories of their EP partners. The shoreline runs roughly north–south, about 20 m beyond the lower (eastern) boundary of the plot.

declined beyond 19 nests/neighbourhood (density ≥19: intercept = 1.02, slope = −0.16, $N = 226$, $P = 0.043$), but the initial increase seen in Fig. 4 was not significant (density <19: intercept = −5.41, slope = 0.16, $N = 197$, $P = 0.21$). Conspicuously, nests of EP sires did not occur within nest clusters, but only at or near their edges and in more isolated sites (Fig. 5). Of the habitat structure variables tested, only density of obstacles came close to showing a significant relationship to the probability of siring chicks elsewhere (GLM: $N = 113$: density of obstacles, deviance = 3.29, $P = 0.069$; grass coverage, $P = 0.81$; rock coverage, $P = 0.34$; visibility, $P = 0.66$); hinting that the more obstacles around a male's nest, the less likely he was to sire an EP chick elsewhere.

Surprisingly, EP sires were not neighbours of their EP partners: the 17 EP sires were located an average of 43.7 m from the nests of the EP partners they fertilized, at distances ranging from 14 to 105 m (median = 39 m; Fig. 6). Assuming that EP sires moved directly from their own territories to the territories of their EP partners to inseminate them, we tested randomness of their directions of movement against a circular uniform distribution (Watson, 1967). Directions were not random and followed a mean bearing of 328.8° (test statistic = 0.71, $N = 17$, $P < 0.001$; Fig. 6); this could result from nests with EPP being concentrated in the relatively boulder-free north while EP sires were distributed heterogeneously along the north–south axis.

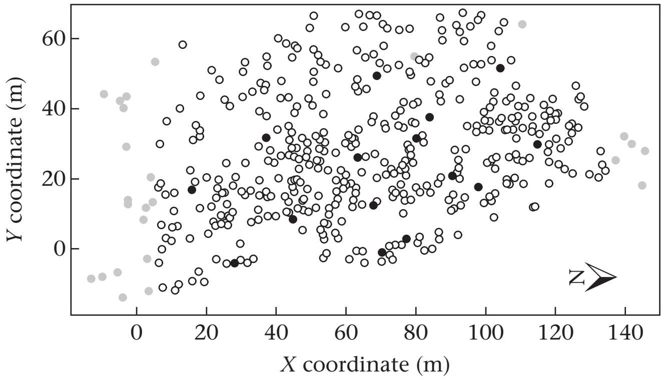

Figure 5. Distribution of blue-footed booby nests sired by extrapair (EP) males in the sampling area. Focal nests included 15 nests with EP sires (black dots) and 408 nests with no identified EP sires (white dots). Grey dots show 25 nests that were included in the analysis only as neighbours since they were too close to the sampling area's edge. The shoreline runs roughly north–south, about 20 m beyond the lower (eastern) boundary of the plot.

Seven EP chicks were from clutches started 6.57 ± 4.66 days before their sires' social partners started laying (range 2–16 days) and the other 10 were from clutches started 15.80 ± 9.60 days after the sires' social partners started laying (range 2–30 days). Thus, the range of start dates of EP clutches spanned a total 46 days, starting 16 days before the sires' clutches with their social partners.

DISCUSSION

EPP was more common in nests in areas where obstacles to locomotion were sparse and it increased northward, just as obstacle density around nests declined northward. Obstacles in the vicinity of a booby's nest probably make it more difficult for potential EP mates to approach and for EP interactions to occur, either because boobies circumventing them expose themselves to injury or aggression from guarding males or neighbours, or because obstacles complicate performance of courtship components such as the parading display (Nelson, 1978). It is unlikely that this pattern was driven by an association between nest location and breeder quality (as suspected in oystercatchers, *Haematopus ostralegus*; van de Pol, Bakker, Saaltink, & Verhulst, 2006), because for neither sex was there an association between nest location and any measure of individual quality (previous breeding success, current age, body size or body condition).

Density of sexually active male neighbours (and their partners) within 10 m of a female's nest had a quadratic effect on the probability of EPP. In contrast, nest density is positively related to EPP in many avian species (Griffith et al., 2002), but negative effects of very high density may have been missed because tests of a quadratic relationship are rare. At densities of over 0.082 nests/m^2, the probability of EPP declined as the number of neighbours increased, and females nesting within clusters of nests did not have EP chicks. Very high-density neighbourhoods in a booby colony may be difficult for foraying individuals of either sex to penetrate and sample because of frequent agonistic encounters with territory-defending neighbours of both sexes. In addition, male partners in dense neighbourhoods possibly increase mate guarding effort in response to the high risk of cuckoldry (Komdeur, 2001; Mayer & Pasinelli, 2013). The quadratic effect of density on EPP could imply that neighbourhoods with fewer than 0.082 nests/m^2

are less attractive to foraying males, although the decline in EPP at lower densities was not significant. Foraying males may be most successful in neighbourhoods of medium density because female breeders there are both relatively numerous and relatively accessible.

The average distance between nests of females and their EP sires was 43.7 m, and not a single EP sire was a near neighbour. Fertilization by distant rather than nearby EP males has been detected in other avian species (e.g. Dunn, Robertson, Michaud-Freeman, & Boag, 1994; Hung, Tarof, & Stutchbury, 2009; Stewart, Hanschu, Burke, & Westneat, 2006), although EP fertilization by near neighbours is also common (e.g. Perreault, Lemon, & Kuhnlein, 1997; Webster, Chuang-Dobbs, & Holmes, 2001; Woolfenden, Stutchbury, & Morton, 2005). Mating with distant EP partners may incur increased travel costs for the foraying sex, but if females are more closely related to near neighbours, then mating with distant EP partners could potentially increase offspring heterozygosity (Foerster, Delhey, Johnsen, Lifjeld, & Kempenaers, 2003). Studies of numerous species have reported positive relationships between heterozygosity and fitness traits such as embryo, offspring and adult survival, health and reproductive success (reviewed in Kempenaers, 2007). On average, male and female boobies disperse only 30.5 m and 36.6 m, respectively, from their natal site to their first breeding site, and they breed thereafter within 19.0–28.9 m and 22.5–30.5 m, respectively, of that first site (Kim, Torres, Rodriguez, & Drummond, 2007; Osorio-Beristain & Drummond, 1993), so a heterozygosity benefit to females is plausible.

Foraying by paired boobies has not been observed, and copulations between breeders with territories distant from each other could take place at the territory of the male or the female, or in other areas. It is likely that EP fertilizations mostly occur when foraying males approach the territories of paired females because (1) among avian species with EPP, foraying has been nearly universally documented in males and much less often documented in females (whose foraying may, however, be less detectable; Westneat & Stewart, 2003), (2) six non-neighbouring male boobies of unknown breeding status were observed approaching, courting and copulating with paired females beside those females' territories before they laid in 2011 (Kiere & Drummond, 2013) and (3) location of an individual's own nest in the study plot affected the probability of a female having an EP chick but not the probability of a male siring an EP chick elsewhere. Boobies probably foray by walking through the colony, but they could also access distant parts of the colony by flying.

It is remarkable that male neighbours were almost absent from the sample of identified EP sires despite predominating among EP partners directly observed in other years. Paired and unpaired territorial neighbours represented 60.0% of observed extrapair copulatory partners in the study plot in 2011 (Kiere & Drummond, 2013) and 86.7% in 1991 and 1997 (Osorio-Beristain & Drummond, 1998, 2001; Pérez-Staples & Drummond, 2005; Pérez-Staples et al., 2013). This disjunction could arise partly from movement of unpaired males to new territories after EP copulations, although EP sires' own clutches were mostly laid before, not after, the clutches containing their EP eggs. A more straightforward explanation is that females' EP partners include both local and distant territorial males (paired and unpaired) and female postcopulatory choice among ejaculates may favour distant EP partners. Ejaculate retention and sperm competition in red junglefowl, *Gallus gallus domesticus*, and ruffs, *Philomachus pugnax*, favour males that are more genetically different from the female (Pizzari, Lø, & Cornwallis, 2004; Thuman & Griffith, 2005). Hence, multiple EP mating by female boobies with neighbours and non-neighbours could be followed up by cryptic selection of sperm to optimize genetic compatibility, either by avoiding inbreeding or by achieving complementarity of major histocompatibility complex haplotypes (Ball & Parker, 2003; Griffith & Immler, 2009; Hasson & Stone, 2011).

Identified sires were breeders (only breeders were blood-sampled) from distant nests that fertilized eggs in clutches laid up to 16 days before and 30 days after their own partners laid, implying that they engaged in EP interactions during their within-pair courtship period and during the time when they were alternating incubation shifts with their social partners (although female seabirds can store sperm for at least 1 month (Hatch, 1983). A male breeder's probability of siring EP chicks at another nest was not related to the location of his nest within the study plot but increased with local nest density up to ≥ 0.06 nests/m^2, then declined at higher values, similar to the effect of local nest density on a female's probability of producing EP chicks. This could imply that male breeders are visited at their own territories by female breeders and that foraying females are attracted by clusters of sexually active males but are unable to access individuals in the densest neighbourhoods successfully. However, prevalence of male foraying is indicated by the strong relationship between the location of a female's nest in the colony and the probability of EPP there, and the absence of a similar relationship for males.

Different potential of different parts of the nesting habitat for EP interactions could influence foraying patterns and territory selection. Nesting in the southern, boulder-strewn part of the study plot appeared to constrain the EPP opportunities of females more than males. Assuming that foraying was mostly done by males, it appears that males in the south forayed elsewhere, in parts of the study plot where females were less constrained by obstacle density, and that this movement towards abundant nests of unconstrained females (in the north and northwest) imparted an average foraying direction of 328.8° to the sample of males that achieved EPP. In some avian species, males or females may prefer to nest in social environments that either propitiate or render unlikely encounters with potential EP partners (Danchin & Wagner, 1997); likewise, boobies may show similar preferences in relation to features of habitat structure and colony structure that facilitate or constrain EP interactions. For example, males with attractive partners could nest preferentially where abundant obstacles or high breeder density will limit access of other males (without foreclosing their own EP options), and females with poor-quality partners could select locations where obstacles are scarce and they are not enclosed within clusters of conspecifics. It will be a challenge to determine whether individual boobies selectively locate their territories and nests in habitats and social contexts that allow them to pursue their own extrapair interests while limiting those of their partners.

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