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Is kin cooperation going on undetected in marine bird colonies?

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Abstract In multitudinous breeding colonies, kin interactions could go unnoticed because we are unaware of the kinship among adults we observe. Evidence of cooperation and competition between close adult kin in a blue-footed booby colony was sought by analyzing patterns of natal dispersal and proximity of nests. Male and female recruits nested closer to their own natal sites than to their parents' current sites. Males (only) dispersed less far when both parents were present than when no parent or one parent was present, but not selectively close to fathers versus mothers when these were divorced. Neither parental presence nor parental proximity affected breeding success of recruits of either sex. Although distances between the nests of simultaneously recruiting broodmates were unrelated to their sex, males dispersed 13.1 m less when a sister was present than when a brother was present. Neither sex was affected in its dispersal distance by the presence or hatching order/dominance of a broodmate. Neither sex was affected in its breeding success by the presence versus absence of a broodmate, although female success increased with proximity of their brothers. Parents and sisters may actively or passively help males establish their first territories near their natal sites and nearby brothers may help females in their first breeding attempts; otherwise, boobies do not influence each other's natal dispersal and first breeding success. It appears that boobies do not nest selectively close to or far from their parents, offspring, or broodmates. Why there is apparently so little cooperation and altruism between close adult relatives in booby colonies is puzzling.

Keywords Colonial nesting · Kin proximity · Kin structure · Dispersal

Introduction

Although reproductive colonies of philopatric vertebrates, particularly long-lived species, provide a favorable context for the evolution of adaptations for cooperation and competition with adult kin, evidence for such adaptations is scarce. Interactions among adult kin are seldom sought and are likely to go undetected because observers seldom know the kinship of colony members and large colony size can deter investigation. However, patterns of dispersal and spatial distribution within colonies can potentially reveal whether animals seek or avoid kin, and give clues to the associated costs and benefits (Bowler and Benton 2005).

Kin structures of animal populations are intimately related to the evolution of natal and breeding dispersal (Hamilton and May 1977) and of competition and cooperation over habitats, mates, and food (West et al. 2002). Social interactions among siblings and between parents and offspring potentially influence natal dispersal and territory settlement (Gandon and Michalakis 1999; Perrin and Goudet 2001; Eikenaar et al. 2007) and in long-lived organisms especially, natal dispersal can determine opportunities for interactions among kin (Pomeroy et al. 2000; Baglione et al. 2003). Positive interactions between

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neighboring kin potentially give rise to associations of kin in neighborhoods (Lambin et al. 2001) marked by improved survival and reproductive success (Lambin and Krebs 1993; Lambin and Yoccoz 1998), whereas competitive interactions between kin can favor dispersal from the natal site (Hamilton and May 1977). Kin competition could cause both sexes to disperse (Léna et al. 1998), but differential dispersal will arise when one sex faces greater competition from (same sex) relatives (Payne 1991) or benefits more from cooperation with relatives (Perrin and Goudet 2001; Perrin and Lehmann 2001).

Many marine birds are long-lived and often faithful to their natal colony or sub-colony, where they reproduce in the midst of numerous conspecifics, some of whom are kin. Through familiarity, many bird species can learn to recognize close relatives (Beecher 1981, 1982, and familiarity recognition is the most likely mechanism of kin recognition in avian societies (Komdeur and Hatchwell 1999), so social evolution in marine bird colonies is likely to be based on kin recognition rather than on the generalized altruism toward neighbors (e.g., Queller 1992, 1994; Taylor 1992). Cohabitation of nestling broodmates and extensive parental care by both parents provide opportunity for learning individual identifying cues. In all phases of the reproductive cycle there is scope for helping or collaborating with kin, or selectively mitigating hostility to kin, whenever kin are colony neighbors. Kin interactions beyond parental care and broodmate competition have not been sought in marine bird colonies although highly varied kin interactions occur in a minority of non-marine birds, including cooperative breeding, clustering of relatives in adjoining territories, territorial and non-territorial post-breeding family groups and diverse male kin groupings (e.g., Watts and Stokes 1971; Williams and Rabenold 2005; review in Ekman 2006).

To evaluate whether kin cooperation or competition may be occurring in a marine bird colony, we analyzed kin-related spatial patterns in a long-lived, philopatric species that reproduces in colonies comprising hundreds or thousands of nests. Blue-footed boobies *Sula nebouxii* (Milne-Edwards) show biparental care and their offspring show aggressive broodmate dominance throughout the nestling period care. Social interactions in neighborhoods of the blue-footed booby include vigorous territorial defense against neighbors and passers-by, killing or adoption of neighbors' chicks, group defense against allospecific egg predators, extrapair courtship and copulation with neighbors, eggdumping, and destruction of probable extrapair eggs and dumped eggs (Drummond et al. 1986; Osorio-Beristain and Drummond 1998, 2001; Osorio-Beristain et al. 2006). Boobies could benefit by modifying these behaviors when interacting with kin and also by sharing information on their ephemeral fishing grounds with kin (cf. Ward and Zahavi 1973; Richner and Heeb 1996). If so, then selection could favor them seeking or avoiding proximity with kin when choosing a nest site.

We scrutinized a colony of marked boobies for patterns of natal dispersal and nesting proximity indicating possible cooperation or conflict between parents and offspring and between broodmates. The parental cooperation hypothesis predicts that if one or both parents are nesting in the colony when an offspring recruits, the offspring will show shorter natal dispersal, nest closer to the parental site than to its own natal site, and show higher breeding success. The parental competition hypothesis predicts longer natal dispersal, greater proximity to the natal site than the parental site, and lower breeding success when parents are present, particularly same-sex parents. As parents get older and more experienced, they become more effective cooperators or competitors and their effects on natal dispersal distance are predicted to increase.

If its broodmate is nesting when a booby recruits, the broodmate cooperation hypothesis predicts that natal dispersal of the recruit will be shorter, whereas the broodmate competition hypothesis predicts that it will be longer. More particularly, the same-sex broodmate cooperation hypothesis predicts that on recruitment, same-sex broodmates will nest closer to each other than different-sex broodmates and show shorter natal dispersal and higher breeding success than recruits nesting with no broodmate present or a different-sex broodmate present. The same-sex broodmate competition hypothesis predicts the opposite effects. Pairs of blue-footed booby broodmates always show marked dominance-subordination throughout the nestling period, with the elder chick usually in the dominant role (Drummond et al. 1986; Drummond and Osorno 1992). Therefore, we also examined whether younger broodmates (presumed subordinates during infancy) dispersed further than elder broodmates (presumed dominants), limiting the comparison to pairs of brothers and pairs of sisters in which both are recruited in the same year.

Materials and methods

Study species

We studied blue-footed boobies on Isla Isabel, Nayarít, off the Pacific Coast of Mexico (21°52′N, 105°54′W). These boobies are socially monogamous and their ground level nests are widely distributed in the forests and adjacent grasslands of the 82-ha island. Generally, males obtain nesting territories (of an average 7.6 m^2) then pair with females (Nelson 1978; Gonzalez and Osorno 1987; Stamps et al. 2002). After this, male and female jointly select the location of the breeding site (nest scrape) within the territory (Stamps et al. 2002). Although a minority of boobies nest in relative isolation, most nest sites are grouped in neighborhoods (Kim et al.

2009), where densities of 0.032 nests per square meter are commonplace (Chavez-Peón and Castillo-Alvarez 1983).

Interactions occur mostly between close neighbors but also between distant neighbors. In the study colony, during the entire incubation and broodcare periods, at least one parent is always on the territory, often both. Boobies whose nests are within 10 m of each other commonly engage in territorial disputes and respond to the same conspecific and allospecific intruders and predators (Montes-Medina et al. 2009). Boobies whose nests are >10 m apart potentially interact when approaching or leaving their territories, particularly if their walking access routes converge or approach/intersect each other's territories. Boobies in most parts of the forest interior walk to the shore before take-off. There is a further scope for interacting with distant neighbors once chicks begin to wander away from their family territories, particularly when they aggregate with their peers while continuing to be fed by parents.

Female boobies disperse an average 6 m further from natal sites than males (Kim et al. 2007b). Over at least the first 8 years of life, the blue-footed boobies of Isla Isabel show attachment to the site where they first nested, itself only 30.5±1.7 m (mean ± SE) in males and 36.6±1.4 m in females from the site where they hatched (natal site; Kim et al. 2007b). Osorio-Beristain and Drummond (1993) found that the boobies' first nest sites were a similar distance from their natal sites and their parents' current sites, but their samples were too small to determine whether recruits and experienced breeders nest selectively close to or far from relatives. These boobies generally start reproduction (recruit) at age 3–5 years (Drummond et al. 2003) and can continue on a roughly annual basis up to at least age17 years, although most die before then (S.-Y. Kim, A. Velando, R. Torres and H. Drummond unpublished). Reproductive success of males and females improves with age/experience up to roughly age 10–12 years then declines progressively with senescence (Velando et al. 2006; S.-Y. Kim, A. Velando, R. Torres and H. Drummond unpublished). Mate fidelity from year-to-year is common, but by no means universal (unpublished data). Most broods are of one or two chicks, and in two-chick broods, the dominant (usually elder) chick grows faster and is more likely to fledge than its subordinate broodmate, which nonetheless catches up with the dominant chick in body size and mass before fledging (Drummond et al. 1986, 2003).

Field procedures

Starting in 1989, all breeding sites (scrapes with a clutch or brood) in a 20,800 m^2 study area were recorded every year in relation to a grid of permanent plots of roughly 20×20 m defined by marker trees (Drummond et al. 2003). All fledglings and most breeders were marked with numbered metal bands. Nests of all banded breeders with sites within 20 m of the study area were also recorded. In 1993 and subsequent years, each breeding site was mapped by measuring the distance (nearest 10 cm) and direction (nearest 2°) of its center from the ground-level estimated center of the closest marker tree's trunk (Kim et al. 2007a, b). For analysis, breeding site locations were expressed in two linear coordinates originating at the marker tree in one corner of the study area.

Every year, breeding sites were surveyed every few days from shortly after the start of hatching in early nests, in late February, until each chick died or fledged (reached age 70 days), the last chicks fledging in late July. Each breeder's band number was confirmed by independent readings on up to 3 days to minimize reading errors. Recruits were sexed by their voices (males whistle and females grunt). Hatching date of each chick at each site was recorded during the surveys or estimated from length of ulna and culmen at first encounter (Drummond et al. 2003).

Sampling and statistical analyses

We used data from all fledglings of the 1993–2002 natal cohorts with banded parents and which bred for the first time between 1996 and 2005 when 1–6 years old (median ages, 4 and 3 years for males and females, respectively). The sample comprised 607 males and 575 females from 1,015 broods of one, two, or (rarely) three fledglings. Natal dispersal was the distance between their natal sites and their first breeding sites. Distances were calculated between the recruits' first breeding sites and the current breeding sites of their parents and broodmates. By limiting the sample of siblings analyzed to broodmates rather than also including full-sibs and half-sibs from reproductive events in successive years, we tested for sibling interactions in the context where they are most likely to be present; that is, between full-sibs who are familiar with each other because they cohabited together during the first 3–4 months of life. If any family member attempted to breed more than once in a year, then the first event was selected for analysis. Breeding success of individuals (number of chicks fledged) at the first reproduction was standardized within years with a z transformation to take variation among years into account (Zar 1999).

Dispersal to sites >20 m from the study area perimeter goes unrecorded, and this potentially biases the distributions of observed dispersal distances because recorded dispersal from peripheral sites can occur over longer distances than from central sites. To determine whether location in the study area was related to observed dispersal distance, we included distance of the natal site from the centroid of the area as a variable in analyses of natal dispersal distances (following van Noordwijk 1984). The boobies nest most densely along the eastern margin of the study area, where the sloping shoreline of the island permits easy take-off into the wind, and most sparsely in the southwestern corner where denser forest limits both access and amount of suitable nesting terrain (map in Kim et al. 2009).

Breeding year and distance of the natal nest from the study area centroid were included (whenever their effects were significant) in all models testing for a relationship between natal dispersal distance and parental or broodmate presence. Cohort effect could not be taken into account in the models as it is highly correlated both statistically and biologically with breeding year, because individual variation in age at first breeding is limited (see above). We tested for effects of current presence of parents and broodmates on natal dispersal distance and standardized breeding success at the first reproduction using generalized linear models (GLMs) with a gamma error distribution and a log link because distribution of natal dispersal distance was not normal in the study population (Kim et al. 2007b). In the models for natal dispersal distance, first all explanatory variables (parental or broodmate presence, sex, breeding year, and distance from the centroid) and a two-way interaction (parental or broodmate presence × sex) were fitted to pooled data of males and females, then the models were refitted to males and females separately where the interaction was significant. For breeding success, we analyzed males and females separately to avoid replication of data points from paired birds. Initially, all explanatory variables and two-way interactions of interest were fitted in the maximal model; then, nonsignificant terms were dropped sequentially to simplify the model. We used *F* tests to assess the significance of the increase in *F* value that resulted when a given term was removed from the minimal adequate model (Crawley 2005). Analyses were carried out with R v2.5.1 (R Development Core Team 2006), and we report means ± SE throughout.

Results

Natal dispersal distance in relation to parental presence and age

In the model with male and female dispersers pooled, the interaction between sex and parental presence was significantly related to natal dispersal distance (GLM: $F_{2,1179}$= 3.829, P=0.022). In males, natal dispersal distances did not differ among breeding years but were positively related to distance of their natal sites from the study area centroid (Table 1a). Natal dispersal distances differed significantly among male offspring with both parents nesting (BP), one parent nesting (OP), and no parent nesting (NP) when distance of their natal sites from the study area centroid was taken into account (Table 1a). BP males dispersed less far from the natal site to the first breeding site than OP and NP males (Fig. 1; GLM: submodel with OP and NP combined versus main model with separate groups: $F_{1,605}$=0.159, P= 0.690; submodel with BP and OP combined: $F_{1,605}$=7.707, P=0.006; submodel with BP and NP combined: $F_{1,605}$= 3.926, P=0.048). And there was no difference between the natal dispersal distances of BP males whose two parents were re-paired and BP males whose parents were divorced (GLM: $F_{1,191}$=0.147, P=0.701). Among BP males whose two parents were divorced, distance from the divorced father and distance from the mother did not differ (distance from father: 33.73±2.23 m, distance from mother: 31.49± 2.17 m; Paired *t* test: t_{113}=0.854, P=0.395). In females, natal dispersal distance was not related to parental presence (Fig. 1), breeding year, or distance of natal site from the study area centroid (Table 1b).

Table 1 Summary of GLMs with a gamma error distribution and a log link examining the effects of parental presence, breeding year, and distance from the study area centroid on natal dispersal distance in **a** males and **b** females

	F	d.f.	*P*
Males			
Parental presence	4.363	2,604	0.013
Breeding year	0.997	9,597	0.441
Distance from the centroid	6.322	1,605	0.012
Females			
Parental presence	0.495	2,572	0.610
Breeding year	1.001	9,565	0.438
Distance from the centroid	1.009	1,573	0.316

The significance reported is the *F* value when the explanatory variable of interest is dropped from the model

Both sons and daughters nested an average 2–4 m closer to their natal sites than to their parents' current sites, whether one or both parents were nesting currently (Table 2).

Maternal age was unrelated to natal dispersal distance of either males or females (GLM: males: $F_{1,231}$=0.876, P= 0.350; females: $F_{1,255}$=0.059, P=0.808). Paternal age was related to natal dispersal distances but only those of sons (GLM: males: $F_{1,252}$=5.603, P=0.019; females: $F_{1,260}$= 1.039, P=0.309) when the significant effect of distance of natal site from the study area centroid was taken into account (GLM: $F_{1,252}$=7.444, P=0.007). Sons of older males dispersed less far (Fig. 2). The interaction between paternal age and paternal presence (presence/absence) was not significantly related to natal dispersal distance of sons ($F_{1,252}$=0.239, P=0.625); hence, sons of older males dispersed over shorter distances whether their fathers were present or absent.

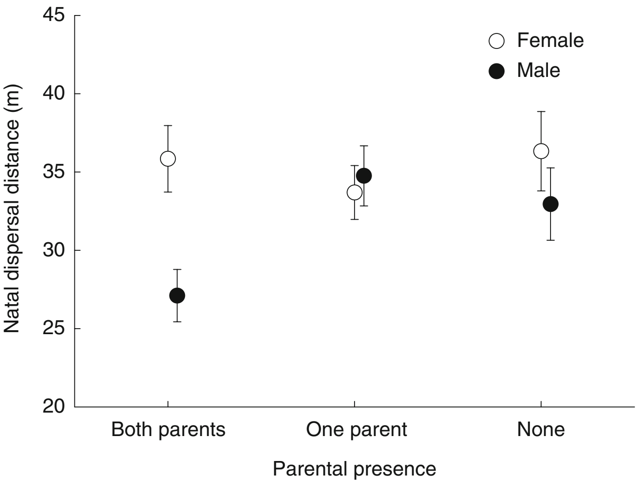

Fig. 1 Natal dispersal distance of female and male recruits (means ± SE) in relation to presence of nesting parents in each recruit's first breeding season

Parental presence and breeding success

Standardized breeding success (number of chicks fledged) at the first reproduction did not differ significantly among BP, OP and NP groups in either males or females (GLM: males: $F_{2,604}$=1.637, P=0.196; females: $F_{2,572}$=0.109, P=0.897). Furthermore, among first breeding males and females whose father and/or mother was present, neither distance from the father's current breeding site nor distance from mother's current breeding site was related to standardized breeding success (GLM: males: distance from father: $F_{1,305}$=3.746, P=0.054; distance from mother: $F_{1,327}$=2.221, P=0.137; females: distance from father: $F_{1,299}$=0.003, P=0.957; distance from mother: $F_{1,323}$=1.989, P=0.159).

Siblings and natal dispersal distance

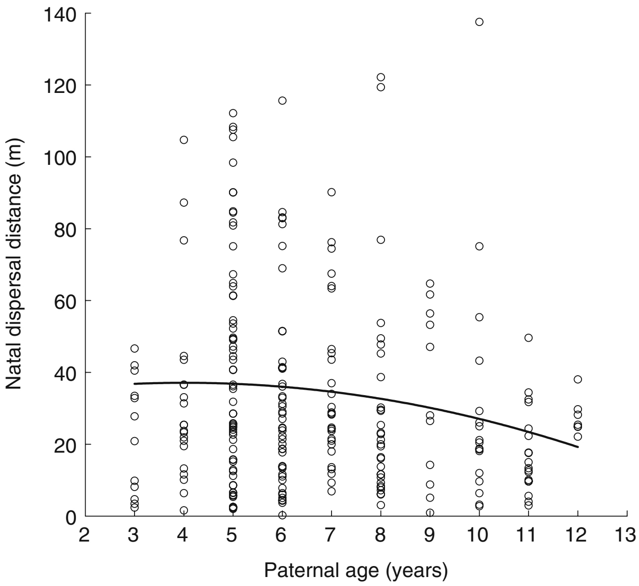

Fig. 2 Relationship between natal dispersal distance of male recruits (n=254) and age of their fathers at hatching

We contrasted natal dispersal distances of birds that first bred in the same year that a broodmate first bred (77 males and 62 females from 68 broods of two siblings of all possible sex combinations and one brood of three brothers) with birds that first bred when no broodmate was breeding, whether the latter had fledged alongside a broodmate or alone (490 males and 495 females).

In the model with males and females pooled, natal dispersal distance did not differ between recruits with broodmate present (breeding) and those without broodmate present (Fig. 3; GLM: $F_{1,1122}$=0.012, P=0.911) when significant effects of sex (GLM: $F_{1,1122}$=4.451, P=0.035) and distance between natal sites and the study area centroid (GLM: $F_{1,1122}$=7.888, P=0.005) were taken into account. Neither breeding year nor interaction between sex and broodmate presence was related with natal dispersal distance (GLM: breeding year: $F_{9,1114}$=1.412, P=0.178; sex × broodmate presence: $F_{2,1121}$=0.001, P=0.977). However, among recruits with broodmates present, males dispersed an average 13.1 m less when a sister was present than when a brother was present (Fig. 3; GLM: $F_{1,75}$=4.891, P=0.030), but

Table 2 Comparisons of distance between recruit's natal site and its first breeding site (natal dispersal distance) and distance between recruit's first breeding site and current breeding sites of its parents according to sex of recruit and which parents were present (breeding)

Sex of recruit	Parental presence	Distance from	Distance (m)		Paired t test		
			Natal site	Parent	t	d.f.	P
Male	Both parents	Father	27.1±1.7	31.0±1.8	2.907	192	0.004
		Mother		29.7±1.7	2.012	192	0.046
	One parent	Father	35.2±3.1	38.5±3.2	2.262	113	0.026
		Mother	34.4±2.4	36.6±2.6	1.216	135	0.226
Female	Both parents	Father	35.8±2.1	38.5±2.3	2.375	192	0.019
		Mother		41.4±2.3	3.361	192	<0.001
	One parent	Father	32.2±2.5	35.2±2.7	2.211	107	0.029
		Mother	34.9±2.4	38.6±2.5	1.978	131	0.050

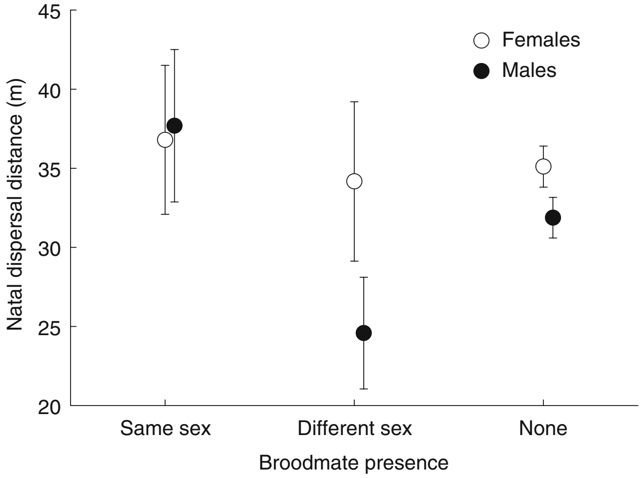

Fig. 3 Natal dispersal distances of female and male recruits (means ± SE) in relation to broodmate presence (nesting by same-sex broodmate, different sex broodmate or no broodmate) in the recruit's first breeding season

females were not similarly affected (Fig. 3; GLM: $F_{1,60}$= 0.131, P=0.719). Natal dispersal distance did not differ between elder and younger brothers that bred for the first time in the same year (Wilcoxon signed-ranks test: Z_{19}= 0.672, P=0.502), nor between elder and younger sisters that bred for the first time in the same year (Z_{12}=0.874, P= 0.382). Distances between the nest sites of broodmates that bred for the first time in the same year did not differ significantly with the sexual composition of the brood: 45.3 m for two brothers, 33.3 m for two sisters, and 40.0 m for brother-sister pairs (n=20, 13, 36, respectively; Kruskal–Wallis test: H_2=0.468, P=0.791).

Siblings and breeding success

Standardized breeding success (number of chicks fledged) did not differ significantly among birds with same-sex broodmates present, those with the different sex broodmates present and those with no broodmate present, in either males or females (GLM: males: $F_{2,564}$=2.871, P=0.057; females: $F_{2,554}$=2.172, P=0.115). In males with a broodmate present, neither distance from a brother's current breeding site nor distance from a sister's current breeding site was related to their standardized breeding success (GLM: distance from brother: $F_{1,39}$=0.212, P=0.648; distance from sister: $F_{1,34}$= 0.418, P=0.522). In females with a broodmate present, distance from a brother's current breeding site was negatively correlated with their standardized breeding success ($F_{1,34}$=5.281, P=0.028; Fig. 4), but distance from a sister's current breeding site had no effect ($F_{1,24}$=0.033, P=0.857). A female recruit whose brother was nesting less than about 30 m away was likely to be relatively successful and even outperform the average pair in the colony (Fig. 4).

Discussion

Cooperation and competition with parents

Natal philopatry and lifetime philopatry (Kim et al. 2007b) generally keep adult blue-footed boobies within tens of meters of their close kin, and therefore create a context in which selection could act on social interactions among kin. The observed patterns of natal dispersal distance and kin proximity provide no support for the parental competition hypothesis and limited support for the parental cooperation hypothesis. In contrast with some passerine first-breeders that disperse further when parents of the same sex are present on the natal territory due to kin competition for breeding sites (e.g., Wheelwright and Mauck 1998), first-breeding male boobies (but not females) dispersed less far from natal sites when both parents were present and sons of divorced parents did not nest farther from fathers than mothers. The tendency of both sexes to nest 2–4 m closer to their natal sites than to parents' current sites implies that male and female recruits are more attracted by their natal sites and may not be attracted to their parents at all. The presence of both parents may enable first-breeding sons to secure territories closer to their natal sites. Parents could support or tolerate first-breeding sons in the competitive colony environment where breeders typically repel others that enter or traverse their territories.

The positive relationship between natal dispersal of male boobies and distance of their natal nests from the study area centroid probably reflects a sampling bias arising from failure to sample dispersal of recruits that bred outside the study area. The differences in dispersal distance and kin proximity reported are unlikely to be due to this bias, but all mean distances reported may be underestimates.

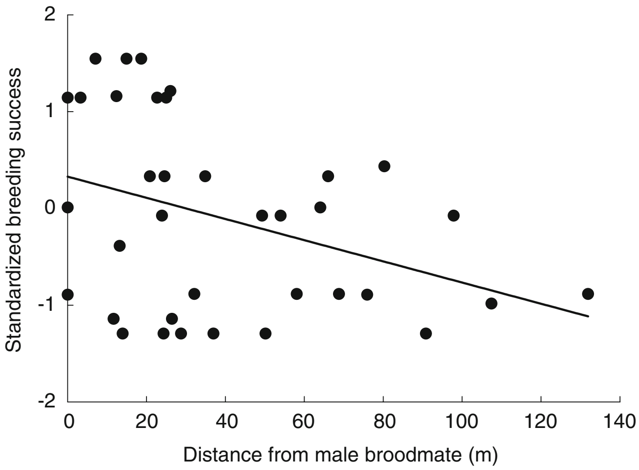

Fig. 4 Standardized breeding success of female recruits in relation to distance from the nest sites of their male broodmates. The fitted line is a linear regression

Sons of older males showed reduced natal dispersal but this does not imply either father-son cooperation or decline in father-son competition as aging males face higher mortality (Ronce et al. 2000), because it did not depend on paternal presence. More likely, as boobies gain in age and experience, they father higher quality offspring that are more competitive and consequently disperse over shorter distances (cf., Massot and Clobert 2000). Breeding success of male blue-footed boobies improves progressively over the first 10–12 years of life (Velando et al. 2006) and offspring quality could improve too. Daughters, on the other hand, did not disperse less in the presence of both parents or when fathered by older males, possibly because parental influence is attenuated or absent in the sex that joins a territory rather than establishing its own.

The observed patterns of breeding success provide no evidence that parents compete or cooperate with adult offspring. It made no difference to the success of male or female recruits whether both, one or no parents were breeding in the colony or how far away their parents nested.

Cooperation and competition with broodmates

The recruits' patterns of dispersal and proximity provide no support for the broodmate competition hypothesis and limited support for the broodmate cooperation hypothesis. Recruits whose broodmate recruited in the same year dispersed a similar distance to recruits with no broodmate or whose broodmate was absent, and when broodmates recruited in the same year, sex was important in one combination: males dispersed 13.1 m less when the nesting broodmate was a sister than when it was a brother. A sister could help a brother to establish a territory nearer his natal site by actively supporting or tolerating him. Modification of dispersal distance when opposite sex relatives are alive implies kin recognition (Payne 1991), possibly through familiarity or phenotype matching (Nakagawa and Waas 2004). It is conceivable that only males are helped because generally only males establish territories, and that only sisters help male broodmates because brothers are in competition with male broodmates. Importantly, whatever their gender, recruits did not select nest sites selectively close to or far from their broodmates. In the presence of a sister, some juvenile male rodents disperse less far (Le Galliard et al. 2006; but see Jacquot and Vessey 1995).

Although recruiting broodmates generally appeared not to prejudice or enhance each other's reproductive success, the closer her brother nested the more fledglings a female recruit produced, implying that brothers somehow assist their sisters. This effect was most evident when the brother nested <30 m away, a distance that might well propitiate social interaction. Assistance might involve collective nest defense, tolerance of territorial incursions during transit through the colony, refraining from infanticide, and sharing of information on fishing grounds or foraging together. We cannot explain why assistance should be limited to this particular sexual combination.

Junior (generally subordinate) fledglings dispersed no further than their senior (generally dominant) same-sex broodmates when both recruited in the same year. Apparently, subordination throughout infancy neither degrades the ability to nest near the natal site nor favors dispersal away from the natal site in response to current or potential competition with a formerly dominant sibling (cf. Gayou 1986; Ekman et al. 2002). In this respect, blue-footed boobies contrast with species in which dominance status among juveniles appears to affect dispersal, for example eliciting early dispersal in western screech owl *Otus kennicottii* dominants (Ellsworth and Belthoff 1999) and gray jay *Perisoreus canadiensis* and Siberian jay *Perisoreus infaustus* subordinates (Strickland 1991; Ekman et al. 2002), and greater dispersal in great tit *Parus major* subordinates (Dhondt 1979).

Inbreeding avoidance

Even though female biased natal dispersal in the blue-footed booby (Kim et al. 2007b) may function partly to avoid inbreeding, there was no persuasive evidence of facultative adjustment of natal dispersal to reduce the risk of breeding with broodmates or parents. Male recruits did disperse less far when a sister was also nesting, but opposite sex broodmates that recruited in the same season were no further apart than same-sex broodmates. Some non-colonial birds disperse further when they recruit in the same season when broodmates and opposite-sex parents nest (Wheelwright and Mauck 1998) but others do not (Payne 1991), and similar variation is present among species of rodents (Le Galliard et al. 2006).

Conclusions

Failure of boobies to nest away from relatives may reflect minimal competition between relatives and minimal risk of inbreeding. Competition effects on natal dispersal (review in Lambin et al. 2001) have been inferred for some birds and mammals whose territories contain food and are often retained over successive seasons. Such competition may be absent or minimal in booby colonies because breeding territories contain no food and relatives are generally kept apart by interannual movements (natal and breeding dispersal) of all individuals over a scale of several territory diameters. When population structure is such that most competitive interactions are with non kin, selection for dispersal away from kin should be very weak (Comins et al. 1980).

Failure of boobies to nest near close relatives is more puzzling. The reported correlations could imply tolerance or assistance of territory establishing male recruits by parents and sisters and facilitation of female's first breeding by nearby brothers. Alternatively, they could arise from unidentified processes not embraced by our study rather than reflecting any causal relationship. It is noteworthy that neither correlation is accompanied by any evidence that the supposed beneficiaries seek proximity to their supposed benefactors.

It is possible that kin cooperation and competition affect older boobies, occur between other relatives or influence other variables. However, if parents do not help their offspring at recruitment, when their youth and inexperience make them most needy, then it is unlikely that they help them at later ages. And if boobies do not help broodmates, who are recognizable full-sibs, then it is unlikely that they help sibs of other cohorts, who are more likely to be half-sibs, or more distant relatives. Patterns of dispersal and spatial separation suggest that there is little kin cooperation in booby colonies, even though limited natal dispersal and lifetime philopatry create kin proximities that set the scene for the evolution of kin cooperation. What we need to explain is why kin selected cooperation and altruism have not evolved in blue-footed boobies and, possibly, many other colonial breeders. Our understanding of the evolution of altruism between adult kin will be incomplete until we can explain why it is absent from some species in which kin live in proximity and apparently stand to benefit from helping each other. Lack of heritability in traits that serve helping and/or weak selection on helping in the colonial context are likely explanations although they will be challenging to examine.

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