



Females of a polymorphic seabird dislike foreign-looking males



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Sexual selection may facilitate speciation if it promotes divergence in attributes used in mate choice, causing prezygotic isolation between populations. Brown boobies, *Sula leucogaster*, are seabirds that can be grouped into four genetic clusters and two male plumage morphs: brown-headed sexually monomorphic and white-headed male dimorphic. The extent of white on the head (white hood) of a male may reflect parenting ability and be sexually selected. Colour morphs have been geographically isolated, but contact has been recently reported. We manipulated male hood colour in two dimorphic populations (at Islas Marietas National Park (hereafter Marietas), which is close to the contact zone of San Benedicto Island, and San Jorge Island, which is away from the contact zone) to establish whether female preference for male hoods can function as a reproductive barrier. Females from Marietas were more aggressive towards male mates whose white hoods were painted brown (allopatric-looking) than were females from San Jorge. Although experimental females from both islands courted less than females from control pairs, experimental females from Marietas were five times less likely to copulate than control females, whereas there were no differences between treatments in propensity to copulate by females in San Jorge. Thus, in the brown booby, female dislike of foreign males may function as a reproductive barrier in populations close to contact zones, where the risk of possibly maladaptive hybridization is highest.

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A crucial step in the process of speciation is the evolution of reproductive isolation, that is, of barriers that prevent fertilization between diverging populations. Thus, geographically separated populations that have diverged through genetic drift or selection must, in order to remain distinct upon secondary contact, evolve prezygotic isolation (members of one population are unlikely to mate/fertilize members of the other population) or postzygotic isolation (allelic or genetic incompatibilities between isolated populations that promote maladaptive offspring; Dobzhansky, 1937). Reproductive isolation can evolve as a by-product of adaptation to different niches if traits used in mate choice are those that are diverging through natural selection (i.e. 'magic traits'; Gavrillets, 2004; Schluter, 2000, 2001), through reinforcement when reduced hybrid fitness leads to the evolution of a stronger prezygotic isolation (Dobzhansky, 1940; see Noor, 1995) and by direct selection on mating preferences (Servedio, 2001). However, divergence in courtship traits and associated preferences is the most common

cause of premating reproductive isolation in animals (Ritchie, 2007) and may arise from disruptions in sexual communication (Coyne & Orr, 2004; Dobzhansky, 1937; Fisher, 1930). Hence, sexual selection has been deemed an important evolutionary force driving speciation since it can lead to rapid diversification of mate recognition systems (Paterson, 1985; see also Ryan & Rand, 1993), resulting in premating isolation between populations (Boul, Funk, Darst, Cannatella, & Ryan, 2007; Fisher, 1930; Kraaijeveld, Kraaijeveld-Smit, & Maan, 2011; Lande, 1981; Panhuis, Butlin, Zuk, & Tregenza, 2001; West-Eberhard, 1983).

Mate signals and preferences are under ecological and sexual selection simultaneously (Kirkpatrick & Ravigné, 2002; Maan & Seehausen, 2010; Weissing, Edelaar, & Van Doorn, 2011); therefore, environmental conditions experienced by allopatric populations may drive divergence in mate recognition signals and influence the strength or direction of sexual selection (e.g. Boughman, 2002; Fuller, 2002; Seehausen, et al., 2008). Sexual isolation may occur if mate recognition signals evolve within one population but remain unchanged or evolve differently in other populations (Lande, 1982). Thus, if mate signals and preferences covary between populations, divergence may be accelerated through positive assortative mating because of the development of

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a genetic correlation between female preferences and male traits (Lande, 1982). Moreover, if mate choice is based on condition-dependent ornaments, female preference may intensify assortative mating upon secondary contact due to the advantages of mating with a locally adapted partner (Lorch, Proulx, Rowe, & Day, 2003; Proulx & Servedio, 2009; Van Doorn, Edelaar, & Weissing, 2009). Indeed, when crosses between recently diverged species produce unfit offspring, the spread and fixation of alleles that confer mating discrimination is favoured (Noor, 1999), leading to reproductive character displacement (greater divergence in mate recognition signals in sympatry than in allopatry, but note that an alternative outcome is the spread of alleles that rescue hybrid viability, thus removing postmating barriers; Ritchie & Hewitt, 1995). The expression of adaptive female preferences for local over allopatric mates would be facilitated if local partners can be identified by either arbitrary or (better) condition-dependent signals (Van Doorn et al., 2009; Weissing et al., 2011). Preference for a locally adapted partner may be particularly advantageous in philopatric species, or in species occupying heterogeneous ranges, where offspring are likely to breed in the same habitat as their parents (Van Doorn et al., 2009; Weissing et al., 2011).

In birds, one of the more frequently reported pre-mating barriers involves plumage coloration (Price, 2008). Divergence in coloration may directly cause reproductive isolation when individuals mate assortatively by phenotype, because of the coevolution between traits and preferences (Lande, 1981), sexual imprinting on parental phenotypes (Plenge, Curio, & Witte, 2000; Witte & Sawka, 2003), or differential fitness related to colour variants in different habitats (Roulin, 2004). Recently it has been shown that speciation rates are higher in colour-polymorphic clades than in monomorphic clades (Hugall & Stuart-Fox, 2012), suggesting that differences in coloration among individuals may directly promote speciation (Gray & McKinnon, 2007). Moreover, since selection against the production of unfit hybrids may reinforce barriers to gene flow, the occurrence of pre-mating reproductive isolation depends critically on how females choose mates according to plumage colour, as shown in flycatchers, in which female choice selected for divergence in male plumage colour and the resulting character displacement reduced the frequency of hybridization (Sætre et al., 1997).

Brown boobies, *Sula leucogaster*, constitute a convenient system to evaluate the role of female preferences in the divergence of male plumage. The brown booby is a pantropical, colonial philopatric seabird (Nelson, 1978) whose populations can be grouped into four major genetic clusters of plumage differentiation that correspond closely to geography (Morris-Pocock, Anderson, & Friesen, 2011). Birds from populations in the Caribbean, Central Atlantic and Central Indo-Pacific are all brown with white bellies, whereas males from the Eastern Pacific, which diverged from the Central Indo-Pacific lineage about 1 million years ago (Morris-Pocock et al., 2011), have a white hood that varies in length and whiteness (Nelson, 1978). This variation appears to be positively linked to parenting ability and to be under current sexual selection (Tereshy, 1998).

Dispersal between Central Indo-Pacific and Eastern Pacific populations has recently been documented in both directions and has led to interbreeding at Hawaii (Vanderwerf, Becker, Eijzena, & Eijzena, 2008) and at San Benedicto Island following a volcanic eruption in 1952 (Morris-Pocock et al., 2011; Pitman & Balance, 2002). A detailed genetic analysis of eight individuals from San Benedicto revealed one white-headed male with Eastern Pacific mtDNA but nuclear Central Indo-Pacific haplotypes (no individuals with mtDNA from Central Indo-Pacific have been found at this locality). This, together with the fact that two (presumably male) chicks 'appeared to have brown-headed feathers' (Morris-Pocock

et al., 2011), suggests that viable hybrids of Eastern Pacific and Central Indo-Pacific *S. leucogaster* have been produced at San Benedicto. Although based on a small sample size, this information suggests that no postzygotic barriers have evolved between the white-headed Eastern Pacific and the brown-headed Central Indo-Pacific brown boobies and that, at least in some circumstances (such as the recolonization of an island following a catastrophic event), plumage differentiation may not be sufficient to prevent interbreeding between these two clades. In birds, the time span for the loss of intrinsic hybrid fertility and viability among sister species is often longer than the time to evolve prezygotic isolation (Price & Bouvier, 2002), so it is not surprising that brown boobies from different genetic clusters can produce viable hybrids. However, although apparently viable, hybrids seem to be uncommon (but no systematic quantification of their occurrence has been conducted; see above). Hence, other factors such as low hybrid fitness under local ecological conditions (Gow, Peichel, & Taylor, 2007), genetic incompatibilities arising in the F2 (Rosas, Barton, Copley, Barbier de Reuille, & Coen, 2010) or backcrosses (Orr & Presgraves, 2000), or sexual selection against hybrids (Ritchie, 2007; Servedio, 2004) may be hampering interbreeding between brown boobies from the Eastern Pacific and the Central Indo-Pacific at the contact zones. Here, we attempted to elucidate whether male plumage and female preferences may function as reproductive barriers against immigrating males in Eastern Pacific brown booby colonies.

We manipulated male head colour to assess whether Eastern Pacific females prefer local (white-headed) to allopatric (experimentally painted brown-headed) male phenotypes, and whether such female preference varies in relation to geographical proximity to the contact zone. The study was carried out at two Eastern Pacific colonies: Islas Marietas National Park (hereafter Marietas), which is close to the contact zone of San Benedicto Island, and San Jorge Island, which is away from the contact zone (Fig. 1) and probably geographically isolated by the Baja California peninsula, because boobies (as other seabirds) do not normally fly across large inland areas (e.g. Friesen, Burg, & McCoy, 2007). If avoiding heterospecific matings promotes higher fitness, we expected female preference (female courtship and frequency of copulations) for local male phenotypes over allopatric male phenotypes on both islands. If the risk of maladaptive hybridization increases with geographical proximity to a contact zone, we expected females breeding at Marietas to show a stronger preference for local male phenotypes than females breeding at San Jorge (which together with larger white hoods would be in line with reproductive character displacement; see above).

METHODS

The study was carried out during the brown booby reproductive season of 2011 at two breeding colonies from the Mexican Eastern Pacific. San Jorge Island (31°01'N, 113°15'W) is located in the northern Gulf of California approximately 10 km off the Sonora coast, whereas the Marietas Islands (20°42'N, 105°34'W) are located 6 km southeast from the coast of Nayarit State (Fig. 1). The Marietas Islands are closer to the contact zone of San Benedicto (19°19'N, 110°49'W) than is San Jorge (Fig. 1).

During the courtship period, we captured both members of each pair from San Jorge ($N = 33$) and Marietas ($N = 30$) by night lighting (i.e. dazzling each bird with a torch, then capturing it) and randomly assigned pairs to the experimental group ($N = 17$ pairs from San Jorge, $N = 15$ pairs from Marietas) or the control group ($N = 16$ and 17 pairs, respectively). A female and a male were deemed to constitute a pair if they were standing within 20 cm of each other before capture and were observed performing sexual

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