

*The Condor* 110(3):544–548  
 © The Cooper Ornithological Society 2008

## MAINTENANCE OF PLUMAGE POLYMORPHISM IN RED-FOOTED BOOBIES IN THE GALÁPAGOS ARCHIPELAGO: OBSERVATIONS OF MATE CHOICE AND HABITAT ASSOCIATION

PATRICIA C. BAIÃO<sup>1,3</sup> AND PATRICIA G. PARKER<sup>1,2</sup>

<sup>1</sup>*Department of Biology, University of Missouri-St. Louis, One University Blvd., R223, St. Louis, MO, 63121*

<sup>2</sup>*St. Louis Zoo, 1 Government Drive, St. Louis, MO, 63110*

**Abstract.** The Red-footed Booby (*Sula sula*) is considered one of the most polymorphic seabirds, with three adult plumage types recognized: white, white-tailed brown, and brown, as well as several degrees of intermediates. Here we show that there is no evidence of deviation from random mating according to plumage color in the largest population of Red-footed Boobies in the Galápagos Archipelago, based on a random sample of approximately 300 pairs, which agrees with previous results found in the Indian Ocean. We also found that the ratio of color morphs varies among islands within this archipelago, with the populations of Islas Genovesa and Wolf presenting a reversed ratio (90% brown, and 10% white) when compared to the majority of Red-footed Boobies populations worldwide. Furthermore, there was no indication of differential habitat association among morphs. We concluded that plumage color does not play an important role in mate choice, and as a result, nonrandom mating based on plumage color is likely not a selective mechanism maintaining the plumage polymorphism in this population.

**Key words:** *Galápagos Archipelago, habitat selection, non-random mating, plumage polymorphism, Sula sula, Sulidae.*

### Manutenção do Polimorfismo de Plumagem em *Sula sula* no Arquipélago de Galápagos: Observações de Preferência Sexual e Habitat

**Resumo.** *Sula sula* é considerada uma das espécies mais polimórficas de aves marinhas, com três padrões de plumagem reconhecidos: branco, marrom-de-rabo-branco e marrom, além de vários graus de intermediários. Nesse estudo, nós mostramos que não há evidências de desvios do padrão de pareamento randômico baseado na coloração da plumagem na maior população de *Sula sula* no arquipélago de Galápagos, baseado em uma amostragem randômica de aproximadamente 300 pares. Também mostramos que a proporção de indivíduos com padrões de plumagem diferentes varia entre ilhas no arquipélago de Galápagos, com as populações das Ilhas Genovesa e Wolf apresentando proporção inversa daquela encontrada na maioria das populações de *Sula sula* ao longo da área de distribuição da espécie (90% marrom e 10% branco). Além disso, não encontramos nenhuma indicação de associações diferenciadas de habitat entre indivíduos de diferentes padrões de plumagem. Concluímos que a coloração da plumagem não é de importância para a escolha de parceiros sexuais, e como resultado, o processo de pareamentos não-randômico baseado na coloração da plumagem possivelmente não funciona como mecanismo de manutenção do polimorfismo nessa população.

Manuscript received 18 September 2007; accepted 30 June 2008.

<sup>3</sup>E-mail: [pccg24@umsl.edu](mailto:pccg24@umsl.edu)

Plumage coloration and patterns are extremely diverse among birds. Feathers may have two different types of colors: structural colors, which are the result of structural changes in the shape and orientation of barbules; and pigmented colors, which are the result of the deposition of pigments on the follicles at the time of feather growth (Tickell 2003). Melanin, the pigment responsible for brown or black coloration, is one of the most common of the many pigments shown to be related to feather coloration (Tickell 2003). For several bird species, control of melanin synthesis, and therefore of melanic and white phenotypes, has been demonstrated to have a straightforward genetic basis, with associations between point substitutions at the melanocortin-1 receptor (MC1R) locus and phenotypes (Theron et al. 2001, Mundy et al. 2004, Baião et al. 2007).

Plumage polymorphisms based on differential deposition of melanin on the feathers are known to occur in a number of families of birds, including four seabird families: Procellariidae, Hydrobatidae, Stercorariidae, and Sulidae (Nelson 1978, Le Corre 1999). The Red-footed Booby (*Sula sula*) belongs to the Sulidae, along with nine other species of gannets and boobies (Nelson 1978, Friesen and Anderson 1997, Friesen et al. 2002). It is a pantropic species, and it is considered one of the most polymorphic seabirds (Le Corre 1999, Galeotti et al. 2003), with such distinct differences that the different color morphs could be mistaken to be two different species (Nelson 1968). While Nelson (1978) recognized three major adult plumage types in Red-footed Boobies (white, white-tailed brown, and brown) as well as several intermediates, Schreiber et al. (1996) recognized five color morphs (white, light, mixed, brown, and dark).

The white morph is the most common along the species' range, and the brown morph is the rarest, known to occur commonly only in the Galápagos Archipelago and Cocos Island, both in the eastern Pacific (Nelson 1978). All Red-footed Boobies begin their independent lives as brown juveniles and gain full adult plumage at about three to four years of age (Nelson 1978, Schreiber et al. 1996). Since juvenile immature white-morph birds progressively develop their white plumage, there is an inherent confusion in distinguishing the permanent brown birds from these immature whites. However, physiologically mature adults attain bright red feet, bright blue beaks, and brightly colored facial skin, and these characters can be used to distinguish age classes and correctly categorize adult plumage types.

The color morphs usually coexist and interbreed throughout the species' range, and no deviations from random mating based on plumage color were found in a population in the Indian Ocean (Le Corre 1999). The proportions of color morphs vary throughout the species' distribution; for most islands where types coexist, the white morph is the predominant morph, on average accounting for 95% of the birds, while the white-tailed brown morph accounts for the remaining 5% (Nelson 1968). The Red-footed Booby population on Isla Genovesa, in the Galápagos Archipelago, is composed of two main color morphs, brown and white (as defined by Nelson 1978) and several intermediates, which are brown-bodied birds that vary in the number of white feathers on the scapular region (Nelson 1968). Interestingly, the white morph that occurs in the Galápagos Archipelago differs from white morphs elsewhere in having a blackish tail. Nelson (1978) reported a reversed ratio of color morphs on Isla Genovesa, with white-morph birds accounting for approximately 5% of the population and the remaining 95% brown or intermediate. Red-footed Boobies also breed on Islas San Cristóbal, Darwin, and Wolf in the Galápagos Archipelago, and there have been only anecdotal accounts of the composition and the ratio of color morphs on these islands. The largest colony of Red-footed Boobies in the Galápagos Archipelago is found on Genovesa, where

the population size was estimated to be around 140 000 breeding pairs in 1964 (Nelson 1978). Taken altogether, the four islands were thought to hold approximately a quarter of a million breeding pairs in the 1960s and 1970s (Nelson 1978). There are no current estimates of population sizes on this archipelago.

In this study, we tested possible selective mechanisms maintaining the plumage polymorphism in Red-footed Boobies, such as mate choice and habitat selection. The probability of mating between two individuals can be influenced by traits or phenotypes displayed by potential mates, such as plumage color; in fact, it has been shown for several species of birds, such as Lesser Snow Geese (*Anser caerulescens*; Cooch and Beardmore 1959), Arctic Skuas (*Stercorarius parasiticus*; Phillips and Furness 1998), Barn Owls (*Tyto alba*; Roulin 1999), Common Buzzards (*Buteo buteo*; Krüger et al. 2001), and Magellanic Penguins (*Spheniscus magellanicus*; Forero et al. 2001), that mate choice is a nonrandom process based on sexual preferences for specific colors or color patterns. Deviations from random mate choice, assortative or disassortative mating, can affect genotype and phenotype frequencies, as compared to those of Hardy-Weinberg equilibrium, as well as the distribution of mating types, given an association between genotype and phenotype (Templeton 2006). Baião et al. (2007) determined that the plumage polymorphism observed in Red-footed Boobies has a genetic basis, finding a perfect association between color morph and allelic variation at the melanocortin-1 receptor (MC1R) locus. Two point substitutions were associated with melanic phenotypes, and most of the intermediate individuals were found to be heterozygous for those sites. Thus, an association between genotype and phenotype can be established for this species.

In this study, we performed censuses to determine color morph ratios of Red-footed Boobies on three islands in the Galápagos Archipelago, and tested for: (1) nonrandom mate choice based on plumage color on Isla Genovesa; (2) differences in overall body condition between color morphs in order to eliminate a possible effect of body condition on mate choice; (3) associations between color morphs and sex; and (4) habitat associations of color morphs relative to the two main vegetation zones present on Isla Genovesa, the arid zone and the littoral zone.

## MATERIALS AND METHODS

We visited the Galápagos Archipelago in three consecutive years, 2004, 2005, and 2006, during the month of July. We collected data from three islands in this archipelago: Genovesa, Darwin, and Wolf. Genovesa was visited during the 2004 and 2006 field seasons, while Darwin and Wolf were visited during the 2005 season.

All Red-footed Boobies included in this study fell into three color categories (according to Nelson [1978]): white, brown, or intermediate. We could readily differentiate white individuals from brown and intermediate; however, the differentiation between brown and intermediate individuals was not always possible from the distance used for the census. Since intermediate individuals are mostly brown with various degrees of white patches on the scapular region, we classified all birds for the scope of this analysis into two color categories: (1) white and (2) melanic, which included all brown and intermediate individuals. Only adult birds were included in this analysis; juveniles were recognized by their brown feet and beaks, in contrast to the red feet and blue beaks of adults.

The ratio of color morphs in the three populations studied was determined by a derivation of the double-observer approach for estimating probability (Nichols et al. 2000), in which two observers followed a transect, and one observer counted the birds in each of the two categories (melanic and white) while pointing

TABLE 1. Frequencies of mating types among Red-footed Boobies on Isla Genovesa in the Galpagos archipelago, in 2004 and in 2006. Expected frequencies were calculated from Hardy-Weinberg equilibrium model from general population ratio of color morphs. M indicates melanic; W indicates white.

Year	Number of pairs	Number of mating types						$\chi^2$	P
		M × M		M × W		W × W			
		Observed	Expected	Observed	Expected	Observed	Expected		
2004	153	117	115.6	32	34.8	4	2.6	1	>0.75
2006	48	41	40.3	6	7.3	1	0.3	1.6	>0.25
Years combined	201	158	155.9	38	42.3	5	2.9	2.1	>0.25

to them. The other observer recorded and counted any bird that was missed by the first. The census on Genovesa was performed in July of 2004 ( $n = 463$ ), while the censuses on Darwin ( $n = 181$ ) and Wolf ( $n = 128$ ) were performed in July of 2005. During the 2004 census on Genovesa, we determined the ratio of color morphs in the two vegetation zones, the arid zone and the littoral zone; these two ratios were pooled and later used as the general population ratio of color morphs for this island. The littoral zone lines the beach with evergreen vegetation, while the vegetation atop the cliff in the arid zone is dominated by thickets of palo santo (*Bursera graveolens*). Since most Red-footed Boobies build their nests in palo santo in the arid zone (PCB, pers. obs.), likely due to the availability of nesting materials as well as nest sites, associations among color morphs and these vegetation zones could give us insight into differential habitat selection among the morphs. For the analysis of associations of color morphs with the two main vegetation types on Isla Genovesa, we included observations of a total of 463 birds, from which 321 individuals were from the arid zone and 142 were from the littoral zone.

On Isla Genovesa, the breeding population was assessed by censusing birds found on nests. We tagged a total of 246 and 53 nests in 2004 and 2006, respectively, with flagging material. Because pairs are rarely found together on a nest, the first individual found in each nest was temporarily marked with a semipermanent marker on the webbing of the foot, which was proven to last for the duration of the study, based on observations of two individuals marked as controls. Subsequent visits to the nests allowed us to determine the color morph of the second parent. Since we could not determine the color morphs of both individuals on several nests ( $n = 93$  and  $n = 5$  in 2004 and 2006, respectively), some of our analyses were based on the ratio of color morphs calculated from the subset of the breeding population from which mating types were known (153 pairs in 2004 and 48 pairs in 2006).

To determine whether plumage color was independent of sex, we collected blood samples from the brachial veins of breeding birds. We extracted DNA using standard phenol and chloroform extraction protocols, and we amplified sex specific loci through polymerase chain reaction (Fridolfsson and Ellegren, 1999). We successfully obtained results from 47 birds (24 melanic and 23 white) in 2004, and 86 birds (77 melanic and 9 white) in 2006 from Isla Genovesa, 37 birds from Isla Darwin (22 melanic and 15 white), and 33 from Isla Wolf (22 melanic and 11 white) in 2005. In order to assess differences in body condition between color morphs, two measurements were taken from birds sampled on Genovesa and Wolf: wing chord length and total body weight ( $n = 194$ ).

#### STATISTICAL ANALYSIS

There are three possible mating types within our color morph categories: (1) melanic × melanic, (2) melanic × white, and (3) white × white. The ratio of mating types was recorded only on Isla Genovesa during two field seasons, July of 2004 and July of 2006 ( $n = 153$  pairs in 2004, and  $n = 48$  pairs in 2006). Observed ratios of mating types were compared with expected frequencies calculated from the Hardy-Weinberg equilibrium model based on the ratio of color morphs in the subsample of the breeding population for which mating types were known for both years. A post hoc power analysis was conducted using G\*Power (Erdfelder et al. 1996) for  $\alpha = 0.01$  and a medium effect size of  $w = 0.3$ .

The ratios of color morphs among islands were compared using a chi-square test. Since Islas Genovesa and Wolf presented equal proportions of color morphs, the data from those two islands were pooled and compared to the ratio on Isla Darwin. We also tested the association between color morphs and sex and the association between color morph and vegetation type using chi-square tests. A general linear model (GLM) in SPSS 16.0 (SPSS, Chicago, Illinois), specifically an analysis of covariance (ANCOVA), was used in order to compare the overall body condition among melanic and white individuals (García-Berthou 2001). We used log-transformed weight as the dependent variable, the log-transformed wing chord length as a covariable, and both sex and color morph as fixed factors. Significance level for all analysis was set at  $P = 0.05$ .

#### RESULTS

##### RATIO OF COLOR MORPHS

On Isla Genovesa, we performed a census of 463 birds, of which 426 (92%) were melanic and 37 (8%) were white. On Isla Darwin, of 181 birds censused, 127 (70%) were melanic and 54 (30%) were white. Finally, of 128 birds censused on Isla Wolf, 118 (92%) were melanic and 10 (8%) were white. There is a significant difference in the ratio of color morphs between Darwin and the other two studied islands ( $\chi^2_1 = 49.4$ ,  $P < 0.001$ ); the white morph represents a greater proportion in the Darwin island population.

##### DEVIATIONS FROM RANDOM MATING

We found no significant deviations from random mating based on color morph for either of the two years sampled (power = 0.9). The distribution of the breeding population among the three mating types (melanic × melanic, melanic × white, and white × white) showed evidence of neither assortative nor disassortative mating (Table 1).

TABLE 2. Analysis of Covariance (ANCOVA) in Red-footed Boobies on Isla Genovesa in 2004 and 2006 and on Isla Wolf in 2005. Measurements are log-transformed weight with respect to sex and color morph, using log-transformed wing chord length as a covariate of weight.

	SS	df	MS	F	P
Corrected model	0.05 <sup>a</sup>	4	0.01	7.9	<0.001
Intercept	0.08	1	0.08	47.2	<0.001
Log (chord length)	0.00	1	0.00	1.2	0.27
Sex	0.02	1	0.02	14.2	<0.001
Color morph	0.00	1	0.00	0.1	0.75
Sex * color morph	0.00	1	0.00	0.9	0.34
Error	0.28	166	0.00		
Total	1581.92	171			
Corrected total	0.33	170			

<sup>a</sup> $R^2 = 0.16$  (adjusted  $R^2 = 0.14$ ).

#### SEX DISTRIBUTION, HABITAT ASSOCIATIONS, AND BODY CONDITION BETWEEN COLOR MORPHS

We found color morph to be independent of sex ( $\chi^2_1 = 0.3$ ,  $P > 0.5$ ). Additionally, we found that the ratio of melanin to white birds did not differ significantly between the littoral zone (136 brown [96%], to 6 white [4%]) and the arid zone (290 brown [90%] to 31 white [10%];  $\chi^2_1 = 3.2$ ,  $P > 0.05$ ) and therefore concluded that there is no evidence of habitat association relative to color morph. We found no significant differences in body condition among color morphs (Table 2).

#### DISCUSSION

Our analysis showed a significant difference in the ratio of color morphs between Isla Darwin and the other two studied islands, Genovesa and Wolf. However, we did not find any indication of nonrandom mating according to plumage color, based on a random sample of approximately 300 pairs, which excludes nonrandom mating as a possible mechanism for the maintenance of the different color morph ratios in these different locations. Individuals of the two color morph categories did not differ significantly in body condition, and color morph was found to be independent of sex. Moreover, we found no specific association of color morph categories with the two main habitat types present on Genovesa, the littoral and the arid zones.

The variation in color morph ratios among relatively close islands is intriguing, since these results suggest three possible scenarios: (1) that these populations were established through a founder event that created isolated populations, (2) that these populations have become genetically isolated through the lack of effective gene flow among islands despite their proximity, or (3) that there are differential selective pressures acting on plumage color in these different locations. A previous study revealed maternal gene flow among populations in the Pacific Ocean, using mitochondrial cytochrome *b* as a genetic marker (Steeves et al. 2003). On the other hand, Schreiber et al. (1996) suggested a lack of effective gene flow among populations in that same ocean, based on morphological differences among different populations. Therefore, analyses of the pattern of gene flow among Genovesa, Darwin, and Wolf are necessary to determine if restricted gene flow could be responsible for the observed differences in color morph ratio among islands.

Our findings of random mating are in accordance with those of Le Corre (1999), who also found random mating among different color morphs of Red-footed Boobies in the Indian Ocean. Although striking, this plumage variation does not appear to affect the way birds choose their mates and therefore does not act as a mechanism maintaining plumage polymorphism in the population of Isla Genovesa. However, due to the fact that the white morph is relatively rare in the population of Isla Genovesa, the lack of detectable nonrandom mating could be the result of limited mate choice. It could also be that there is only a slight deviation from random mating, which would be difficult to demonstrate statistically. If choice were limited by the availability of white individuals, other mechanisms such as higher occurrence of extra-pair paternity in certain pair combinations (e.g., brown  $\times$  brown) could play a role in the maintenance of the plumage polymorphism observed in this species. We (Baião and Parker in press) found no evidence of extra-pair paternity among 14 families of Red-footed Boobies, corroborating the observed pattern of random mating.

Seabirds' plumages are usually not very colorful; for instance, they do not typically feature bright feather ornaments (Pierotti 1987). In contrast, unfeathered parts of seabirds, such as the beaks and feet, can become highly pigmented. As a result, seabirds may use traits other than plumage color as cues for mate selection. This is particularly true for boobies, which show a very diverse array of colors on both feet and beak, and display these body parts during courtship. Red-footed Boobies show very intensely red feet as well as pinkish faces and blue beaks. Therefore, it is possible that other characters, such as colors of unfeathered parts, are cues for mate choice instead of plumage color in this species.

There are no other studies of the possible adaptive significance of plumage color in Red-footed Boobies. One mechanism that has been suggested to explain the maintenance of plumage polymorphism is disruptive selection, in which extreme individuals of a normally distributed population are favored (Galeotti et al. 2003). In the case of Red-footed Boobies, this selection might act through a visual effect of melanin pigmentation, namely crypsis. Nelson (1978) suggested that the less conspicuous morph, the brown or the white-tailed brown, would be favored in populations that are sympatric to frigatebirds because of the risk of kleptoparasitism by these birds. On Genovesa, Magnificent (*Fregata magnificens*) and Great Frigatebirds (*F. minor*) are present, indicating that kleptoparasitism could be playing a role in maintaining the polymorphism, favoring the brown morph on this island. However, the conspicuousness of a bird may be altered by its environment; if the island it inhabits is dark in color, as is common among volcanic islands, then dark birds will be less conspicuous. On the other hand, if the island were lighter, such as in sand-dominated environments, white birds would be less conspicuous. Therefore, we should be careful in making assumptions of the adaptive value of plumage colors based on these general rules.

Disruptive selection through crypsis can also play an important role in avoiding detection by potential prey. Red-footed Boobies feed mainly on flying fish and flying squid. The birds have a specific prey-capture technique, which consists of shallow dive movements that allow them to pursue and capture these mobile prey at or above sea surface (Weimerskirch et al. 2006). Therefore, differences in plumage color might have an impact on the chance of a bird being seen by its prey. Specific studies that investigate differential feeding success among color morphs would be necessary to evaluate this as a mechanism for the maintenance of the plumage polymorphism in this species.

Disruptive selection can also act on pigmentation through nonvisual properties such as thermoregulation, promotion of optimal water balance, mechanical protection against feather abrasion, or protection against ultraviolet radiation (Heppner 1970, Bonser 1995, Galeotti et al. 2003). To the best of our knowledge, none of these has been evaluated as a possible maintenance mechanism for the plumage polymorphism in Red-footed Boobies.

Aside from disruptive selection, frequency-dependent selection and no selection have been invoked to explain the maintenance of plumage polymorphisms (Roulin 2004). Our study evaluated mating preferences and habitat preferences as possible selective mechanisms that could be responsible for the maintenance of the plumage polymorphism in Red-footed Boobies. However, many other mechanisms, both selective (e.g., differential survival or fecundity) and neutral (e.g., lack of effective gene flow or founder effect events) remain to be evaluated before we can have a definite explanation for the striking phenotypic variation observed in this species.

We would like to express our gratitude to the Whitney R. Harris World Ecology Center, the Faucett family, the Des Lee professorship in Zoological Studies, the St. Louis Zoo Field Research in Conservation Program, and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the funding provided for this study. We would also like to thank the Galápagos National Park and the Charles Darwin Foundation for support during fieldwork. For all their help and encouragement we would like to thank the field crew members: Sandra Bahr, Marilyn Cruz, Nicole Gottdenker, Jessica Rabenold, Diego Santiago, Rebecca Wright, Iain Love, Galo Buitron, Jane Merkel, Shari Harden, Gavin O'Connor, Michele Rutledge, and Kelly Halbert and Paulo Câmara. Lastly, we would like to thank the two anonymous reviewers from *The Condor* for all their very helpful comments.

#### LITERATURE CITED

- BAIÃO, P. C., AND P. G. PARKER. In press. No evidence of extra-pair fertilization in Red-footed Boobies (*Sula sula*). *Waterbirds*.
- BAIÃO, P. C., E. A. SCHREIBER, AND P. G. PARKER. 2007. The genetic basis of the plumage polymorphism in Red-footed Boobies (*Sula sula*): a melanocortin-1 receptor (*MC1R*) Analysis. *Journal of Heredity* 98:287–292.
- BONSER, R. H. C. 1995. Melanin and the abrasion resistance of feathers. *Condor* 97:590–591.
- COOCH, F. G., AND J. A. BEARDMORE. 1959. Assortative mating and reciprocal difference in the Blue-Snow Goose complex. *Nature* 183:1833–1834.
- ERDFELDER, E., F. FAUL, AND A. BUCHNER. 1996. GPOWER: a general power analysis program. *Behavior Research Methods, Instruments, and Computers* 28:1–11.
- FORERO, M. G., J. L. TELLA, J. A. DONAZAR, G. BLANCO, M. BERTELOTTI, AND O. CEBALLOS. 2001. Phenotypic assortative mating and within-pair sexual dimorphism and its influence on breeding success and offspring quality in Magellanic Penguins. *Canadian Journal of Zoology* 79:1414–1422.
- FRIDOLFSSON, A. K., AND H. ELLEGREN. 1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* 30:116–121.
- FRIESEN, V. L., AND D. J. ANDERSON. 1997. Phylogeny of the Sulidae (Aves: Pelicaniformes): a test of alternative modes of speciation. *Molecular Phylogenetics and Evolution* 7:252–260.
- FRIESEN, V. L., D. J. ANDERSON, T. E. STEEVES, H. JONES, AND E. A. SCHREIBER. 2002. Molecular support for the species status of the Nazca Booby (*Sula granti*). *Auk* 119:820–826.
- GALEOTTI, P., D. RUBOLINI, P. O. DUNN, AND M. FASOLA. 2003. Colour polymorphism in birds: causes and functions. *Journal of Evolutionary Biology* 16:635–646.
- GARCÍA-BERTHO, E. 2001. On the misuse of residuals in ecology: testing regression residuals vs. the analysis of covariance. *Journal of Animal Ecology* 70:708–711.
- HEPPNER, F. 1970. The metabolic significance of differential absorption of radiant energy by black and white birds. *Condor* 72:50–59.
- KRUGER, O., J. LINDSTROM, AND W. AMOS. 2001. Maladaptive mate choice maintained by heterozygote advantage. *Evolution* 55:1207–1214.
- LE CORRE, M. 1999. Plumage polymorphism of Red-footed Boobies (*Sula sula*) in the western islands in the western Indian Ocean: an indicator of biogeographic isolation. *Journal of Zoology* 49:411–415.
- MUNDY, N. I., N. S. BADCOCK, T. HART, K. SCROBNER, K. JANSSEN, AND N. J. NADEAU. 2004. Conserved genetic basis of a quantitative plumage trait involved in mate choice. *Science* 303:1870–1873.
- NELSON, J. B. 1968. *Galápagos: island of birds*. William Morrow, New York.
- NELSON, J. B. 1978. *The Sulidae: gannets and boobies*. Oxford University Press, Oxford, UK.
- NICHOLS, J. D., J. E. HINES, J. R. SAUER, F. W. FALLON, J. E. FALLON, AND P. J. HEGLUND. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *Auk* 117:393–408.
- PHILLIPS, R. A., AND R. W. FURNESS. 1998. Polymorphism, mating preferences and sexual selection in the Arctic Skua. *Journal of Zoology* 245:245–252.
- PIEROTTI, R. 1987. Isolating mechanisms in seabirds. *Evolution* 41:559–570.
- ROULIN, A. 1999. Nonrandom pairing by male Barn Owls (*Tyto alba*) with respect to a female plumage trait. *Behavioral Ecology* 10:688–695.
- ROULIN, A. 2004. The evolution, maintenance, and adaptive function of genetic colour polymorphism in birds. *Biological Reviews* 79:815–848.
- SCHREIBER, E. A., R. W. SCHREIBER, AND G. A. SCHENK. 1996. The Red-footed Booby (*Sula sula*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 241. The Academy of Natural Sciences, PA, and The American Ornithologists' Union, Washington, DC.
- STEEVES, T. E., D. J. ANDERSON, H. McNALLY, M. H. KIM, AND V. L. FRIESEN. 2003. Phylogeography of *Sula*: the role of physical barriers to gene flow in the diversification of tropical seabirds. *Journal of Avian Biology* 34:217–223.
- TEMPLETON, A. R. 2006. *Population genetics and microevolutionary theory*. John Wiley and Sons, Hoboken, NJ.
- THERON, E., K. HAWKINS, E. BERMINGHAM, R. E. RICKLEFS, AND N. I. MUNDY. 2001. The molecular basis of an avian plumage polymorphism in the wild: a melanocortin-1-receptor point mutation is perfectly associated with the melanic plumage morph of the Bananaquit, *Coereba flaveola*. *Current Biology* 11:550–557.
- TICKELL, W. L. N. 2003. White plumage. *Waterbirds* 26:1–12.
- WEIMERSKIRCH, H., M. LE CORRE, Y. ROPERT-COUDERT, A. KATO, AND F. MARSAC. 2005. The three-dimensional flight of Red-footed Boobies: adaptations to foraging in a tropical environment? *Proceedings of the Royal Society of London Series B* 272:53–61.