

Phylogeography of *Sula*: the role of physical barriers to gene flow in the diversification of tropical seabirds

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We examined mitochondrial cytochrome *b* sequence variation in masked *Sula dactylatra*, red-footed *S. sula*, and brown *S. leucogaster* boobies sampled from islands in the central and eastern Pacific Ocean and in the Caribbean Sea. Each species showed a different phylogeographic pattern. Whereas haplotypes in masked and red-footed boobies were shared across the central and eastern Pacific (i.e., across the Eastern Pacific Basin), brown booby haplotypes were not shared across the Eastern Pacific Basin. Although most masked booby haplotypes from the Pacific were distinct from those in the Caribbean, one haplotype was shared across the Isthmus of Panama. Red-footed and brown boobies, however, did not share haplotypes across the Isthmus of Panama. We estimate that divergence of these regional populations occurred within the last 560,000 years. Thus, the Isthmus of Panama and the Eastern Pacific Basin (albeit to a lesser degree) appear to have played a role in the diversification of these species.

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In the allopatric model of population differentiation, gradual divergence of populations occurs via genetic drift and selection during extended periods of separation by physical barriers to gene flow (Mayr 1963). Despite the high vagility of seabirds, several genetic studies of temperate and arctic species indicate that physical barriers to gene flow (e.g., glaciers) have played an important role in the divergence of many populations (e.g., Kidd and Friesen 1998, Congdon et al. 2001, Liebers et al. 2001, Moum and Árnason 2001). The role that physical barriers played in shaping biogeographic patterns in tropical species is relatively unknown (e.g., Avise et al. 2000). Although glaciers did not reach the tropics, associated climatic changes caused fluctuations in ocean circulation patterns, sea-surface temperatures, and sea-levels (Williams et al. 1998). Thus, physical barriers that are no longer obvious, in addition to those that are presently obvious, may have contributed to the diversification of many tropical seabird species.

One potential physical barrier to gene flow is a 5400 km zone of island-free, deep water between the Line Islands in the central Pacific and Clipperton Atoll in the eastern Pacific, i.e., the Eastern Pacific Basin. Several biogeographic studies indicate that this area, often called the Eastern Pacific Barrier, presents a formidable barrier to gene flow for many shallow-water marine species (e.g., Ekman 1953, Briggs 1961, Vermeij 1987). More recent phylogenetic studies, however, indicate that larvae of some species are able to disperse across this area (e.g., Lessios et al. 1996, 1998). Thus, the Eastern Pacific “Barrier” appears to act more like a filter than a barrier because it has allowed larval dispersal of some species but not others (Lessios et al. 1996, 1998, McCartney et al. 2000). No phylogenetic study to date has tested the hypothesis of restricted gene flow across the Eastern Pacific Basin in tropical seabirds.

Another potential barrier to gene flow is the Isthmus of Panama. Numerous genetic studies indicate that its emergence approximately 3 million years ago (Coates

and Obando 1996) isolated many marine taxa in the Pacific and in the Atlantic (e.g., sea urchins – Lessios et al. 1999, *Eucidaris* spp., McCartney et al. 2000, *Echinometra* spp.; fishes – Muss et al. 2001, *Ophioblennius* spp.; sea turtles – Bowen et al. 1992, *Chelonia* spp., Bowen et al. 1998, *Lepidochelys* spp.). Only one study to date has explicitly examined whether the closure of the Isthmus of Panama similarly isolated tropical seabirds: Avise et al. (2000) found distinct phylogeographic differences between sooty terns *Sterna fuscata* nesting in the Pacific and in the Atlantic. Specifically, birds nesting on either side of the Isthmus of Panama did not share any of the 47 mitochondrial control region haplotypes found. However, unlike other marine taxa that have been studied, the divergence of these populations did not occur when the Isthmus of Panama initially closed. Rather, it appears to have occurred between 7,500 and 187,000 years ago. These results suggest that the Isthmus of Panama has restricted female-mediated gene flow in sooty terns in one of two ways. It has either always been an effective barrier (e.g., sooty terns arose in the Pacific following the emergence of the isthmus and subsequently invaded the Atlantic via the Indian Ocean or vice versa), or it has usually been an effective barrier (e.g., sooty terns arose in the Pacific and subsequently invaded the Atlantic via a one-time dispersal event, likely during a severe storm, across the Isthmus of Panama or vice versa). Regardless, female-mediated gene flow across the Isthmus of Panama has been restricted long enough for population differentiation to occur.

Boobies (Pelecaniformes: Sulidae) provide an excellent opportunity to test the hypothesis that the Eastern Pacific Basin and the Isthmus of Panama influenced diversification in tropical seabird populations. Specifically, the three pantropical species exhibit different patterns of morphological variation in the central and eastern Pacific and in the Caribbean. Masked boobies *Sula dactylatra* (excluding Nazca boobies *S. granti* – Pitman and Jehl 1998, American Ornithologists' Union 2000, Friesen et al. 2002) display the least morphological variation. Although birds often have different foot colours, these colour variants cannot be grouped by region, and essentially no variation in plumage colouration exists across either the Eastern Pacific Basin or the Isthmus of Panama (Nelson 1978, Anderson 1993, but see Murphy 1936). Red-footed boobies *S. sula* display great variation in plumage colouration: birds may be mostly white, all brown, or brown with white scapular feathers and/or a white tail (Nelson 1978, Schreiber et al. 1996). However, these variants cannot easily be grouped by region. For example, although mostly-white birds nest on islands around the world, all-brown birds do not nest in the Caribbean (Nelson 1978). Brown boobies *S. leucogaster* display striking plumage variation that can partially be grouped by region. Both female and male birds nesting in the central Pacific and

in the Caribbean are all brown with white bellies, whereas male birds nesting in the eastern Pacific have varying degrees of white on their heads and necks (Nelson 1978).

Given these patterns of morphological variation, the role that the Eastern Pacific Basin and the Isthmus of Panama may have played in the divergence of populations in these three closely related species is unclear. A recent molecular study that evaluated the species status of Nazca boobies included masked booby samples from the central Pacific ($n = 20$), eastern Pacific ($n = 4$), and the Caribbean ($n = 5$; Friesen et al. 2002). Although the study did not specifically address the influence of the Eastern Pacific Basin and the Isthmus of Panama in the diversification of masked boobies, Friesen et al. (2002) found little phylogeographic differentiation between the central and eastern Pacific (i.e., the majority of birds sampled from both regions shared the same mtDNA cytochrome *b* haplotype). Friesen et al. (2002) did, however, find phylogeographic differences between the Pacific and the Atlantic (i.e., birds sampled in the Pacific and the Atlantic did not share any cytochrome *b* haplotypes). These results suggest that the Isthmus of Panama, but not the Eastern Pacific Basin, may be an effective barrier to female-mediated gene flow in masked boobies. In this study, we used cytochrome *b* sequence data to test the hypothesis that the Eastern Pacific Basin and the Isthmus of Panama have restricted gene flow in masked, red-footed, and brown boobies.

Methods

Sampling and laboratory protocols

Blood, feather, muscle, embryo, or unfertilized egg samples were collected from 64 masked, 89 red-footed, and 78 brown boobies on islands in the central and eastern Pacific and in the Caribbean (Table 1). DNA was purified from samples using standard proteinase K digestion, organic extraction, and isopropanol precipitation (Sambrook et al. 1989). A 450 bp fragment of the mitochondrial cytochrome *b* gene was amplified and screened for single-stranded conformational polymorphisms (SSCPs) using the methods described in Friesen et al. (1996) and Friesen and Anderson (1997). SSCP provide an efficient and sensitive tool for detecting sequence variation in fragments ≤ 500 bp (e.g., Lessa and Applebaum 1993, Friesen et al. 1996). With the exception of SSCP variants detected in one individual only, two representatives of each SSCP variant were sequenced using standard cycle sequencing protocols (Mobix, McMaster University) and visualized using an ABI 373A automated sequencer (Perkin Elmer Corporation, Applied Biosystems Division).

Table 1. Sample numbers and frequencies of cytochrome *b* haplotypes among masked, red-footed, and brown boobies. Subspecies designations from Nelson (1978). Haplotypes correspond to names used in Fig. 1.

Masked boobies *Sula dactylatra*

Subspecies	Sampling Location	Region	Haplotype Frequency					Total
			m-A	m-B4	m-B	m-C	m-D	
<i>S. d. personata</i>	Johnston Atoll	central Pacific	1	4	25			30
<i>S. d. californica</i>	Isla San Benedicto	eastern Pacific			2			2
<i>S. d. californica</i>	Clipperton Atoll	eastern Pacific			2			2
<i>S. d. dactylatra</i>	Isla Monito	Caribbean			9	14	7	30
		Total	1	4	38	14	7	64

Red-footed boobies *Sula sula*

Subspecies	Sampling Location	Region	Haplotype Frequency			Total
			r-A	r-A1	r-B	
<i>S. s. rubripes</i>	Johnston Atoll	central Pacific	30			30
<i>S. s. websteri</i>	Isla Genovesa	eastern Pacific	28	1		29
<i>S. s. sula</i>	Isla Monito	Caribbean			30	30
		Total	58	1	30	89

Brown boobies *Sula leucogaster*

Subspecies	Sampling Location	Region	Haplotype Frequency					Total
			b-A1	b-A2	b-C2	b-B	b-D	
<i>S. l. plotus</i>	Johnston Atoll	central Pacific		25	5			30
<i>S. l. brewsteri</i>	Isla San Pedro Martir	eastern Pacific	8					8
<i>S. l. brewsteri</i>	Piedra Blanca	eastern Pacific	6					6
<i>S. l. brewsteri</i>	Clipperton Atoll	eastern Pacific	5					5
<i>S. l. leucogaster</i>	Isla Monito	Caribbean				21	8	29
		Total	19	25	5	21	8	78

Data analysis

Relationships among haplotypes for each species were inferred by constructing minimum spanning trees (Excoffier et al. 1992) using the default settings in ARLEQUIN (version 2.001; Schneider et al. 2001). Support for clades was estimated from bootstrapping with 1000 replications using maximum parsimony methods in PAUP* (version 4.0 beta; Swofford 2002).

For each species, samples were grouped into three regions: central Pacific, eastern Pacific and Caribbean (Table 1). The extent of genetic differentiation among regions was indexed using Φ_{ST} , estimated by analysis of molecular variance (AMOVA; Excoffier et al. 1992) using ARLEQUIN. The statistical significance of Φ_{ST} estimates was assessed by randomization using 1,000 permutations. Female-mediated gene flow was estimated as $N_m = 1/2([1/\Phi_{ST}] - 1)$ (Crow and Aoki 1982). The genetic distance (δ) among regional samples was estimated as in Wilson et al. (1985) and statistical significance of genetic distances was assessed by randomization using 1,000 permutations. For significant genetic distances, time since divergence was estimated as $t = \delta/r$, where r is sequence divergence rate (Wilson et al. 1985). Friesen and Anderson (1997) estimated a

divergence rate of 2.8% per million years (my) for cytochrome *b* for sulids, but we also calculated t assuming a more typical avian rate of 2%/my (e.g., Nunn et al. 1996).

Results and discussion

Phylogenetic structure

Among the 66 masked booby samples, we found the same five cytochrome *b* haplotypes described by Friesen et al. (2002). Two haplotypes (m-A and m-B4) were restricted to the central Pacific, one (m-B) was shared among all regions, and the remaining two were restricted to the Caribbean (Table 1). Among the 89 red-footed booby samples, we found three cytochrome *b* haplotypes, defined by six variable sites and all six polymorphisms were synonymous third position transitions. One haplotype (r-A) was shared between the central and eastern Pacific, haplotype r-A1 was unique to one individual in the eastern Pacific, and the remaining haplotype (r-B) was restricted to the Caribbean (Table 1). We found five cytochrome *b* haplotypes, defined by seven variable sites, among the 78 brown

booby samples and three of the polymorphisms were synonymous third position transitions, two were non-synonymous first position transitions, one was a non-synonymous second position transition, and the last was a synonymous third position transversion. Two haplotypes (b-A2 and b-C2) were restricted to the central Pacific, haplotype A1 was restricted to the eastern Pacific, and the remaining two (b-B and b-D) were restricted to the Caribbean (Table 1). All haplotype sequences were submitted to GenBank (Accession numbers: AY156695-AY156707).

The minimum spanning trees revealed a different phylogeographic pattern in each species (Fig. 1). In masked boobies, as in Friesen et al. (2002), we found two well supported clades (Fig. 1). However, our larger sample size revealed that haplotype m-B is shared among all three regions. Since haplotype m-B is distantly related to haplotype m-C and m-D, this pattern may reflect secondary contact between masked boobies in the Pacific and in the Caribbean. In red-footed boobies, we found two distinct phylogeographic clades, one clade was found in the Pacific and the other was restricted to the Caribbean (Fig. 1). Unlike Nazca boobies, which nest mainly in the Galápagos and on Malpelo Island (Pitman and Jehl 1998) and form a distinct clade when compared to masked boobies nesting elsewhere in the Pacific (Friesen et al. 2002), red-footed boobies nesting in the Galápagos do not form a distinct clade on the minimum spanning network. This pattern suggests that the evolutionary forces that caused Nazca boobies to speciate did not cause a

similar diversification event in red-footed boobies. Like in masked and red-footed boobies, we found two phylogenetic clades in brown boobies (Fig. 1). However, unlike in masked and red-footed boobies, the distinction between the clades was not well supported. In addition, one clade was restricted to the central Pacific whereas the other was found in the eastern Pacific and in the Caribbean.

Population genetic structure

Genetic differentiation among regional samples is strong in all three species ($\Phi_{ST} = 0.62, 0.99$ and 0.94 for masked, red-footed, and brown boobies, respectively; $P < 0.001$ for all three species). Despite this, three different patterns of gene flow are apparent. Gene flow for brown boobies across the Eastern Pacific Basin is essentially zero ($N_m = 0$), but is unrestricted for both masked and red-footed boobies ($N_m = \infty$). Gene flow across the Isthmus of Panama is essentially zero for red-footed and brown boobies ($N_m = 0$), although gene flow across the Isthmus of Panama was detected in masked boobies, it was low ($\Phi_{ST} = 0.65, P < 0.001, N_m = 0.27$) and likely due to secondary contact between the Pacific and the Caribbean (see above).

In masked and red-footed boobies, genetic distances were statistically significant between the central Pacific and the Caribbean, and between the eastern Pacific and the Caribbean, but not between the central and eastern Pacific (Fig. 2). However, in brown boobies, genetic

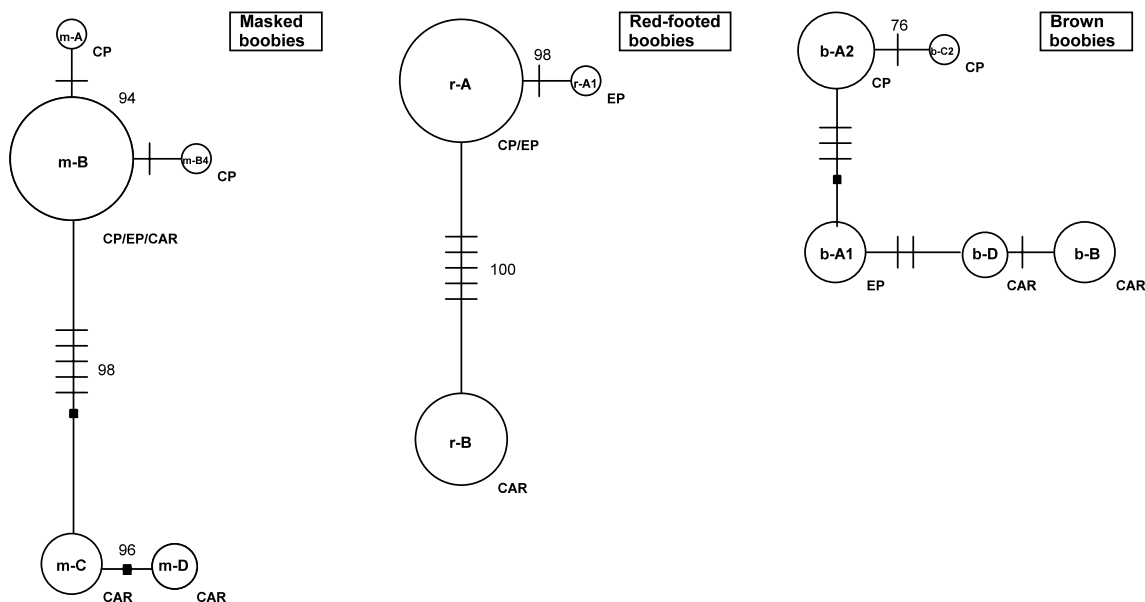


Fig. 1. Minimum spanning trees for cytochrome *b* haplotypes among masked, red-footed, and brown boobies. Circle sizes are proportional to frequencies of haplotypes given in Table 1. CP = central Pacific, EP = eastern Pacific, CAR = Caribbean). Crosshatches and filled squares indicate transitions and transversions, respectively. Numbers indicate support for clades that occurred in over 50% of 1000 bootstrap replications.

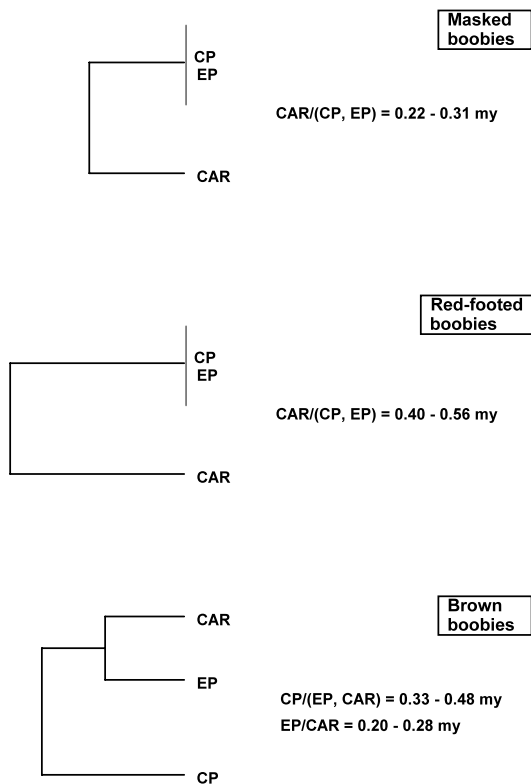


Fig. 2. UPGMA trees based on genetic distances (δ) among regional samples of masked, red-footed, and brown boobies. Branch lengths are proportional to genetic distance. Genetic distances indicated by black lines are significantly different from zero at $\alpha = 0.05$; grey lines are not significantly different. Numbers indicate time since divergence assuming divergence rates of 2.8%/my and 2%/my, respectively. For other details, see Fig. 1.

distances among all three regions were significant (Fig. 2). Assuming divergence rates of 2.8%/my and 2%/my, we estimate that these regional populations diverged within the last 0.56 my (Fig. 2). However, if the presence of haplotype m-B in the Caribbean is due to secondary contact between the Pacific and the Caribbean (see above), our estimate of time since divergence of these populations is likely an underestimate. Excluding haplotype m-B from the Caribbean, our estimate of time since *initial* divergence of masked boobies in the Pacific and the Caribbean (i.e., prior to the introgression of haplotype m-B) is approximately 0.46–0.64 my.

Conclusions

Despite limited sampling within each region, our results for masked, red-footed, and brown boobies, and those obtained by Avise et al. (2000) for sooty terns, suggest that the Isthmus of Panama is an effective barrier to female-mediated gene flow in several species of tropical

seabirds. However, whether the Isthmus of Panama has ever been breached by any of these species is unclear. As described in the introduction, each of these species may have spread between the Pacific and the Atlantic (and the Caribbean) either via the Indian Ocean or via a one-time dispersal event over the Isthmus of Panama. Regardless, female-mediated gene flow across the Isthmus of Panama has been restricted long enough for population differentiation to occur in at least four species of tropical seabirds.

The Eastern Pacific Basin, however, seems to have played a lesser role in the diversification of pantropical boobies. A potential explanation for this may be differences in foraging and dispersal patterns among species (e.g., Mouv and Arnason 2001, Burg and Croxall 2002). Whereas brown boobies tend to forage inshore and near breeding colonies, masked and red-footed boobies tend to forage offshore and away from breeding colonies (Nelson 1978, Anderson 1993, Schreiber et al. 1996). Thus, brown boobies may be less likely than masked or red-footed boobies to cross the Eastern Pacific Basin and discover new breeding habitat. In addition, although subadults of all three species are capable of long distance (> 1000 km) movements (Nelson 1978), band recovery data suggest that breeding dispersal in brown boobies is more limited than in masked and red-footed boobies (Woodward 1972, Amerson and Shelton 1976). If brown boobies exhibit a stronger tendency to return to their natal colonies to breed, then they may be less likely to colonize new breeding habitat than are masked and red-footed boobies.

However, recent observational data indicate that brown boobies can disperse across the Eastern Pacific Basin. Prior to the eruption of the Bárceña volcano in 1952 on Isla San Benedicto (a small, oceanic island in the eastern Pacific), only white-headed males nested on the island, but since the eruption, Isla San Benedicto has been re-colonized by both white-headed and brown-headed males (Pitman and Ballance 2003). Pitman and Ballance (2003) assume that brown-headed males are from the central Pacific because at least two central Pacific seabird species (Laysan albatross *Phoebastria immutabilis* and black-footed albatross *P. nigripes*), and possibly three (red-tailed tropicbirds *Phaethon rubricauda*) have also recently colonized the island. Pitman and Ballance (2003) further suggest that this pattern may be due to recent changes in the marine environment.

Although dispersal does not necessarily lead to gene flow (e.g., selection against dispersers may prevent contribution of their genes to future generations), Pitman and Ballance (2003) observations suggest that the Eastern Pacific Basin may no longer be an effective barrier to gene flow in brown boobies. Our results, however, indicate that female-mediated gene flow has been restricted long enough in the past for population differen-

tiation to occur. Thus, it appears that the Eastern Pacific Basin may be a “dynamic barrier” and perhaps brown boobies are able to disperse across the Eastern Pacific Basin under some oceanographic conditions but not others.

If future work indicates that this is indeed the case (and that the Isthmus of Panama has been breached by one or more species in the past), then several types of physical “barriers” to gene flow in tropical seabirds may exist: (1) dynamic, oceanic barriers that restrict gene flow in some species and not others (i.e., dispersal across them is dictated by life history parameters such as foraging and dispersal patterns), (2) static, geological barriers that always restrict gene flow, and (3) static, geological barriers that usually restrict gene flow (i.e., dispersal across them is dictated by stochastic events such as severe storms). In the meantime, however, it is apparent that the Isthmus of Panama and the Eastern Pacific Basin (albeit to a lesser degree) have played a role in the diversification of several species of tropical seabirds.

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References

American Ornithologists’ Union 2000. Forty-second supplement to the American Ornithologists’ Union Check-list of North American Birds. – *Auk* 117: 847–858.

Amerson Jr, A. B. and Shelton, P. C. 1976. The natural history of Johnston Atoll, central Pacific Ocean. – *Atoll Res. Bull.* 192.

Anderson, D. J. 1993. Masked booby (*Sula dactylatra*). – In: Poole, A. and Gill, F. (eds). *The Birds of North America*, Vol. no. 73. The American Ornithologists’ Union, Washington, DC.

Avise, J. C., Nelson, W. S., Bowen, B. W. and Walker, D. 2000. Phylogeography of colonially nesting seabirds, with special reference to global matrilineal patterns in the sooty tern (*Sterna fuscata*). – *Mol. Ecol.* 9: 1783–1792.

Bowen, B. W., Meylan, A. B., Ross, P., Limpus, C. J., Balazs, H. and Avise, J. C. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. – *Evolution* 46: 865–881.

Bowen, B. W., Clark, A. M., Abreu-Grobois, F. A., Chaves, A., Reichart, H. A. and Ferl, R. J. 1998. Global phylogeography of the ridley sea turtles (*Lepidochelys* spp.) as inferred from mitochondrial DNA sequences. – *Genetica* 101: 179–189.

Briggs, J. C. 1961. The East Pacific Barrier and the distribution of marine shore fishes. – *Evolution* 15: 545–554.

Burg, T. M. and Croxall, J. P. 2002. Global relationships amongst black-browed and grey-headed albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. – *Mol. Ecol.* 10: 2647–2660.

Coates, A. G. and Obando, J. A. 1996. The geologic evolution of the Central American Isthmus. – In: Jackson, J. B. C., Budd, A. F. and Coates, A. G. (eds). *Evolution and Environment in Tropical America*. Univ. of Chicago Press, IL, pp. 21–56.

Congdon, B. C., Piatt, J. F., Martin, K. and Friesen, V. L. 2001. Mechanisms of population differentiation in marbled murrelets: historical versus contemporary processes. – *Evolution* 54: 974–986.

Crow, J. F. and Aoki, K. 1982. Group selection for a polygenic trait: a differential proliferation model. – *Prod. Natl. Acad. Sci. USA* 79: 2628–2631.

Ekman, S. 1953. *Zoogeography of the sea*. – Sidgwick and Jackson, London.

Excoffier, L., Smouse, P. E. and Quattro, J. M. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. – *Genetics* 131: 479–491.

Friesen, V. L., Piatt, J. F. and Baker, A. J. 1996. Evidence from cytochrome *b* sequences and allozymes for a “new” species of alcid: The long-billed murrelet (*Brachyramphus perdix*). – *Condor* 98: 681–690.

Friesen, V. L. and Anderson, D. J. 1997. Phylogeny and evolution of the Sulidae (Aves: Pelecaniformes): a test of alternative modes of speciation. – *Mol. Phylogenet. Evol.* 7: 252–260.

Friesen, V. L., Anderson, D. J., Steeves, T. E., Jones, H. and Schreiber, E. A. 2002. Molecular support for species status of the Nazca booby. – *Auk* 119: 820–826.

Kidd, M. G. and Friesen, V. L. 1998. Analysis of mechanisms of microevolutionary change in *Cephus* guillemots using patterns of control region variation. – *Evolution* 52: 1158–1168.

Lessa, E. P. and Applebaum, G. 1993. Screening techniques for detecting allelic variation in DNA sequences. – *Mol. Ecol.* 2: 121–129.

Lessios, H. A., Kessing, B. D., Wellington, G. M. and Graybeal, A. 1996. Indo-Pacific echinoids in the tropical eastern Pacific. – *Coral Reefs* 15: 133–142.

Lessios, H. A., Kessing, B. D. and Robertson, D. R. 1998. Massive gene flow across the world’s most potent marine biogeographic barrier. – *Proc. R. Soc. Lond. B* 265: 583–588.

Lessios, H. A., Kessing, B. D., Robertson, D. R. and Paulay, G. 1999. Phylogeography of the pantropical sea urchin *Euclidaris* in relation to land barriers and ocean currents. – *Evolution* 53: 806–817.

Liebers, D., Helbig, A. J. and De Knijff, P. 2001. Genetic differentiation and phylogeography of gulls in the *Larus cachinnans-fuscus* group (Aves: Charadriiformes). – *Mol. Ecol.* 10: 2447–2462.

Mayr, E. 1963. *Populations, species and evolution*. – Harvard Univ. Press, MA.

McCartney, M. A., Keller, G. and Lessios, H. A. 2000. Dispersal barriers in tropical oceans and speciation in Atlantic and eastern Pacific sea urchins of the genus *Echinometra*. – *Mol. Ecol.* 9: 1391–1400.

Moum, T. and Arnason, E. 2001. Genetic diversity and population history of two related seabird species based on mitochondrial DNA control region sequences. – *Mol. Ecol.* 10: 2463–2478.

Murphy, R. C. 1936. *Oceanic birds of South America*. – MacMillan, NY.

Muss, A., Robertson, D. R., Stepien, C. A., Wirtz, P. and Bowen, B. W. 2001. Phylogeography of *Ophioblennius*: the role of ocean currents and geography in reef fish evolution. – *Evolution* 55: 261–272.

Nelson, J. B. 1978. *The Sulidae*. – Oxford Univ. Press, Oxford.

- Nunn, G. B., Cooper, J., Jouventin, P., Robertson, C. J. R. and Robertson, G. C. 1996. Evolutionary relationships among extant albatrosses (Procellariiformes: Diomedidae) established from complete cytochrome-*b* gene sequences. – *Auk* 133: 784–801.
- Pitman, R. L. and Ballance, L. T. 2003. The changing status of marine birds breeding at San Benedicto Island, Mexico. – *Wilson Bull.* 114: 11–19.
- Pitman, R. L. and Jehl, J. R. 1998. Geographic variation and reassessment of species limits in the “masked” boobies of the eastern Pacific Ocean. – *Wilson Bull.* 110: 155–170.
- Sambrook, J., Fritsch, E. F. and Maniatis, T. 1989. *Molecular Cloning: a Laboratory Manual*, 2nd ed. – Cold Spring Harbor Laboratory Press, NY.
- Schneider, S., Roessli, D. and Excoffier, L. 2001. Arlequin ver. 2.001: a software for population genetics data analysis. – Genetics and Biometry Laboratory, Univ. of Geneva, Switzerland.
- Schreiber, E. A., Schreiber, R. W. and Schenk, G. A. 1996. Red-footed booby (*Sula sula*). – In: Poole, A. and Gill, F. (eds). *The Birds of North America*, no. 241. The American Ornithologists’ Union, Washington, DC.
- Swofford, D. L. 2002. PAUP* ver. 4: Phylogenetic Analysis Using Parsimony (* and Other Methods). – Sinauer Associates, MA.
- Vermeij, G. J. 1987. The dispersal barrier in the tropical Pacific: implication for molluscan speciation and extinction. – *Evolution* 41: 1046–1058.
- Williams, M., Dunkerley, D., De Deckker, P., Kershaw, P. and Chappell, J. 1998. *Quaternary Environments*, 2nd ed. – Arnold Publishers, NY.
- Wilson, A. C., Cann, R. L., Carr, S. M., George, M., Gyllenstein, U. B., Helm-Bychowski, K. M., Higuchi, R. G., Palumbi, S. R., Prager, E. M. and Stoneking, M. 1985. Mitochondrial DNA and two perspectives on evolutionary genetics. – *Biol. J. Linn. Soc.* 26: 375–400.
- Woodward, P. W. 1972. The natural history of Kure Atoll, northwestern Hawaiian Islands. – *Atoll Res. Bull.* 164.

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Invited by the Institute of Avian Research “Vogelwarte Helgoland”, Wilhelmshaven, and the Deutsche Ornithologen-Gesellschaft (German Ornithologists’ Society) the 24th International Ornithological Congress will be held at the Congress Centrum Hamburg, Germany, 13–19 August 2006. For further details contact the IOC home page at <http://www.i-o-c.org>, or Institute of Avian Research, An der Vogelwarte 21, D-26386 Wilhelmshaven, Germany, Fax +49 4421-968955; e-mail: info@i-o-c.org.