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POPULATION GENETICS OF THE GALÁPAGOS HAWK (*BUTEO GALAPAGOENSIS*): GENETIC MONOMORPHISM WITHIN ISOLATED POPULATIONS

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ABSTRACT.—Because of their smaller size and isolation, island populations tend to be more divergent and less genetically variable than mainland populations. We collected DNA samples from nine Galápagos Hawk (*Buteo galapagoensis*) island populations, covering the species' entire range. Neutral minisatellite DNA markers were used to calculate within-island genetic diversity and between-island genetic differentiation (F_{ST}). Typically, these markers mutate too quickly to be informative in such studies. However, in very small, isolated populations, concerns about high mutational rate are obviated by the relative force of genetic drift. Individuals within islands had the highest levels of reported genetic uniformity of any natural bird population, with mean within-population band-sharing similarity values ranging from 0.693 to 0.956, increasing with decreasing island size. Galápagos Hawks exhibit cooperative polyandry to varying degrees across islands; however, we did not find an association between degree of polyandry and genetic variability. Between-island F_{ST} values ranged from 0.017 to 0.896, with an overall archipelago value of 0.538; thus, most populations were genetically distinct. Also, we documented higher levels of genetic similarity between nearby populations. Our results indicated negligible gene flow among most Galápagos Hawk populations, and genetic drift has played a strong role in determining structure at these minisatellite loci. Received 16 April 2004, accepted 5 April 2005.

Key words: *Buteo galapagoensis*, cooperative polyandry, Galápagos Hawk, Galápagos Islands, genetic drift, minisatellites.

Genética de Poblaciones de *Buteo galapagoensis*: Monomorfismo Genético dentro de Poblaciones Aisladas

RESUMEN.—Debido al tamaño más pequeño y al aislamiento de las poblaciones de las islas, éstas tienden a ser más divergentes y menos variables genéticamente que las poblaciones continentales. Recolectamos muestras de ADN de nueve poblaciones isleñas de *Buteo galapagoensis*, cubriendo el rango total de distribución de la especie. Usamos marcadores neutrales de ADN minisatelital para calcular la diversidad genética dentro de las islas y la diferenciación genética (F_{ST}) entre islas. Típicamente, estos marcadores mutan demasiado rápido como para ser relevantes en estos estudios. Sin embargo, en poblaciones aisladas muy pequeñas, las preocupaciones sobre altas tasas de mutación son descartadas por la fuerza relativa

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de la deriva génica. Los individuos dentro de las islas presentaron los niveles más altos de uniformidad genética que se conocen actualmente para poblaciones naturales de aves, con valores de similitud promedio de bandas compartidas dentro de las poblaciones que fluctuaron entre 0.693 y 0.956. Estos valores se incrementaron al disminuir el tamaño de la isla. *B. galapagoensis* exhibe poliandria cooperativa de varios niveles en distintas islas; sin embargo, no encontramos una asociación entre el grado de poliandria y la variabilidad genética. Los valores de F_{ST} entre las islas fluctuaron entre 0.017 y 0.896, con un valor global para el archipiélago de 0.538. Por lo tanto, la mayoría de las poblaciones fueron genéticamente distintas. Además, documentamos niveles más altos de similitud genética entre poblaciones vecinas. Nuestros resultados indican que el flujo génico entre la mayoría de las poblaciones de *B. galapagoensis* es despreciable, y que la deriva génica ha jugado un rol importante determinando la estructura en estos loci minisatelitales.

POPULATION GENETIC STRUCTURE reflects a number of processes, including mutation rate, genetic drift, gene flow, natural selection, and phylogeographic history (Bohonak 1999, Ouborg et al. 1999). Genetic variability is lost through genetic drift and selection against some genotypes. Generally, genetic drift has a stronger effect in smaller populations; thus, a positive relationship between population size and genetic variation is expected (Nevo et al. 1984, Frankham 1996). Populations may diverge because of random fixation of different alleles, differences in selective pressures, or addition of novel mutations. Gene flow, however, can have a homogenizing effect among populations and mitigate the loss of intrapopulation variation by adding new alleles or replacing alleles lost through drift (Slatkin 1985).

Populations on islands often have lower levels of genetic variation than those on the mainland (Frankham 1997). Populations of birds on island archipelagos tend to be more strongly differentiated than geographically separate mainland populations, because water is an effective barrier against gene flow in many species (Williamson 1981, Boag 1988, Baker et al. 1990). These patterns of decreased genetic variation and increased differentiation may result from founder events that occurred at the time of colonization. In many cases, though, founding flock sizes may be large enough that founder effects are negligible (e.g. Clegg et al. 2002). Even when the number of founders is known to be small, subsequent arrival of additional immigrants may prevent a measurable founder effect (Grant et al. 2001). Alternatively, lower variability and increased differentiation on islands may be attributable to sequential founder events (Clegg

et al. 2002), long-term genetic drift working in small isolated populations (Baker et al. 1990, Mundy et al. 1997), or a combination of the two.

The Galápagos Hawk (Falconiformes: *Buteo galapagoensis*) is endemic to the Galápagos archipelago located ~1,000 km west of South America. The islands are volcanic in origin, having arisen from a mantle hotspot (Morgan 1971), and they have never been connected to the mainland. The oldest of the present islands is ~4 million years old (White et al. 1993). However, older, now-submerged seamounts to the southeast of the archipelago indicate that islands have been present over the hotspot for at least 17 million years and probably for much longer (Christie et al. 1992, Werner and Hoernle 2003).

Galápagos Hawks are presently found on nine islands: Santa Fe, Española, Pinzón, Santiago, Santa Cruz, Isabela, Fernandina, Pinta, and Marchena (Fig. 1). Historically, humans have shot them, and the species has been extirpated from two human-inhabited islands, San Cristóbal and Floreana. The population on Santa Cruz (another human-inhabited island) may also have been extirpated; no adults have been seen on the island in recent years, but juveniles are seen periodically. Distances of <5 km to ~240 km separate islands with Galápagos Hawk populations (Fig. 1). The migration rate between islands is unknown but presumed to be low (de Vries 1975), given that most *Buteo* species are reluctant to cross large bodies of water (Kerlinger 1985). Swainson's Hawks (*B. swainsoni*) are the Galápagos Hawk's closest mainland relatives (Riesing et al. 2003), and they migrate long distances over land (from North America to Argentina) but avoid flying over water (Fuller et al. 1998).

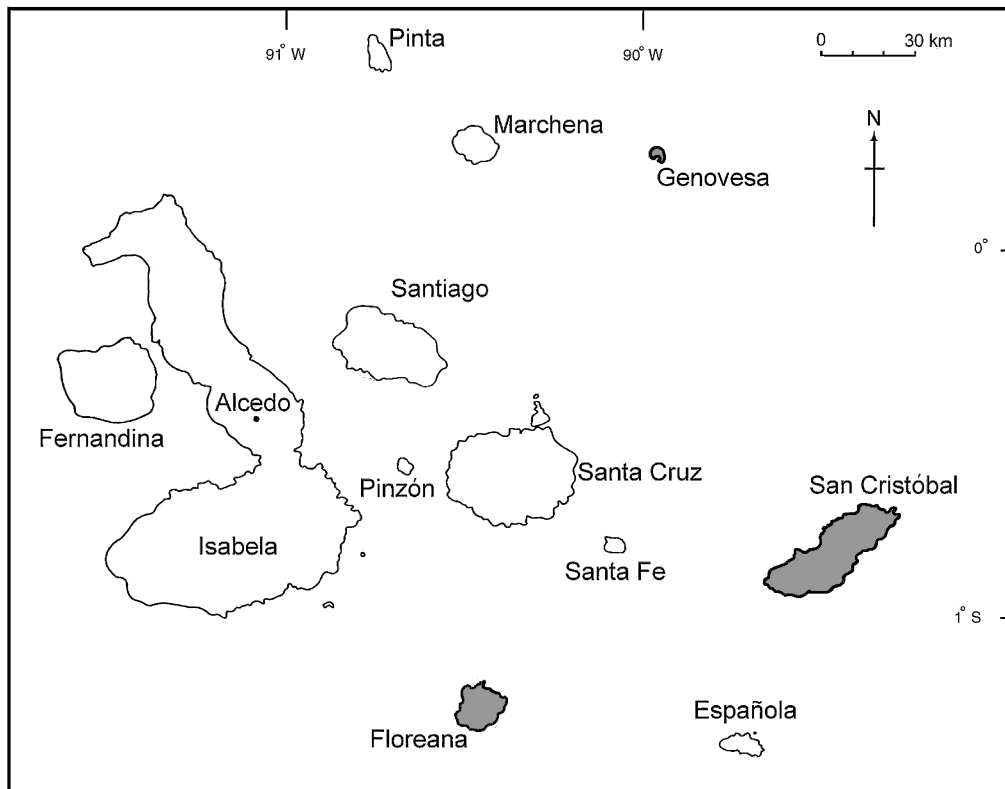


FIG. 1. Distribution of the Galápagos Hawk on the Galápagos Islands. All labeled islands currently have Galápagos Hawk populations, except for the three islands that are shaded. Genovesa has never supported a Galápagos Hawk population, and the populations on San Cristóbal and Floreana have been extirpated by humans.

Morphological and behavioral variation in Galápagos Hawk populations also suggests that they are genetically isolated. Galápagos Hawks differ in overall body size, and in allometry to a lesser degree, among islands (de Vries 1973, Bollmer et al. 2003). The species exhibits cooperative polyandry; territorial groups consist of one female and up to eight (usually two or three) unrelated males (Faaborg and Patterson 1981, Faaborg et al. 1995). Paternity is shared within and among broods, though there are often more males in a group than the number of chicks produced per brood (one or two); all birds in the group defend the communal territory and care for the brood, including males that are not the genetic sires of the offspring (Faaborg et al. 1995, DeLay et al. 1996). One Galápagos Hawk population appears to be monogamous (Española), but the rest exhibit cooperative polyandry to varying degrees, with mean group sizes ranging

from 2.5 to 4.5 birds (de Vries 1975, Faaborg et al. 1980, Bollmer et al. 2003). The factors contributing to this variation in mating system (e.g. sex ratio, survivorship) are unstudied but are likely associated with differences in habitat structure and resource availability.

Here, we describe the genetic structure of all nine populations of Galápagos Hawks (the entire range of the species) using multilocus minisatellite DNA markers. Minisatellites—hypervariable regions of DNA consisting of tandem repetitions of short units of nucleotides (Jeffreys et al. 1985)—have been used in other studies to characterize population structure (e.g. Freeman-Gallant 1996, Carneiro da Silva and Granadeiro 1999, Gullberg et al. 1999, Tarr and Fleischer 1999). We describe the amount of genetic variation present in populations and measure the degree of differentiation among populations using Wright's F_{ST} , the standardized

variance in allele frequencies among populations (Wright 1951, 1978). We test the prediction that genetic variation increases with population size by using total island area and total area of appropriate habitat as indices of population size. Variation in mating system also is predicted to partly determine genetic variability by influencing effective population size, mostly through biased sex ratios and variance in reproductive success (Nunney 1993, Parker and Waite 1997). In the more polyandrous populations of Galápagos Hawks, there may be increased variance in reproductive success and more skewed sex ratios, which would lead to decreased effective population sizes in relation to total population size and a more rapid loss in variation. We test for an effect of mating system (degree of polyandry) on genetic variability after controlling for island area. Finally, we ask whether geographically closer populations are more similar genetically because of increased gene flow or more recent separation (isolation by distance).

METHODS

Field methods.—We visited the Galápagos Islands for two to three months between May and August each year from 1998 to 2003. Galápagos Hawks ($n = 541$) were captured on nine islands: 25 individuals from Santa Fe, 23 from three sites on Española (Gardner Bay, Punta Suarez, and Punta Cevallos), 287 from three sites on Santiago (James Bay, Sullivan Bay, and the highlands), 93 from Volcan Alcedo on Isabela, 41 from Pinta, 26 from Marchena, 10 from Pinzón, 32 from Fernandina, and 4 from Santa Cruz. Birds were caught using two methods: a bal-chatri trap baited with a live prey animal such as a rat (Berger and Mueller 1959), or a rope noose on a stick to capture perched birds (Faaborg et al. 1980). We banded each bird with an aluminum or anodized color band (or both) and took two 50- μ L blood samples via venipuncture of the brachial vein. Samples were immediately put into 500 μ L of lysis buffer (100 mM Tris, pH 8.0, 100 mM EDTA, 10 mM NaCl, 0.5% SDS; Longmire et al. 1988), shaken, and stored at ambient temperature.

Minisatellite DNA markers.—Use of hypervariable multilocus minisatellite profiles (VNTRs) in studies of population genetic differentiation is typically problematic, because of constraints imposed, in part, by a high mutational rate at

these loci (Flint et al. 1999). Moreover, Flint et al. (1999) cautioned that calculating F_{ST} values between human populations using minisatellites yielded an underestimate of genetic differentiation as compared with the level found using other markers. Therefore, their use in characterizing population genetic differentiation, at least in light of this finding, is a statistically conservative methodology. However, in special cases, such as those involving isolated island vertebrate populations, “the fixation of restriction-fragment polymorphisms can outpace the generation of fragment-length variability through recombination” (Gilbert et al. 1990:764). This claim was buttressed by the finding that all bands were fixed within one population of the Channel Island fox (*Urocyon littoralis*), and that individual foxes within each island had diagnostic, island-specific bands. Clearly, in this and analogous special cases, “differences among hypervariable restriction-fragment profiles can be used to estimate relative genetic variability and to reconstruct the evolutionary relationships of natural populations” (Gilbert et al. 1990:764), because concerns related to a high mutational rate are largely obviated by the relative force of genetic drift in small populations.

In the present study, we extracted DNA and performed multilocus minisatellite DNA fingerprinting using the restriction endonuclease *Hae*III and Jeffreys’ probe 33.15 (Jeffreys et al. 1985), following procedures described in Parker et al. (1995). After hybridization, we used a Storm 820 Phosphorimager (Amersham Biosciences, Buckinghamshire, United Kingdom) to visualize fingerprints. For most populations, we used only a subset of the samples ($n = 163$) for genetic analyses: 15 from Santa Fe, 15 from Española, 37 from Santiago, 22 from Isabela, 20 from Pinta, 20 from Marchena, and 20 from Fernandina. From Pinzón and Santa Cruz, we used all birds sampled (10 and 4, respectively), and they were all juveniles. For the other populations, we randomly selected individuals from the pool of sampled territorial adults (the class most likely to consist of nonrelatives). We did not run all samples; however, fewer individuals are necessary to get a representative sample when, as here, populations are lacking in genetic variability. We ran nine gels with 17 to 26 lanes each. We ran samples in alternating blocks of three to seven individuals from each island, so that multiple islands were represented on

each gel. We chose four individuals from different islands as ladders and ran them on each of the gels. From the banding patterns, we created a presence-absence matrix of bands (alleles) encompassing all individuals. Because of high within-population genetic uniformity, the presence of a number of bands fixed across populations, and the ladders on each of the gels, we were able to reliably score across gels.

We assumed that bands were assorting independently and calculated within- and between-island similarity indices as $S = 2S_{AB}/(2S_{AB} + N_A + N_B)$, where S is the proportion of bands shared, S_{AB} is the number of bands shared by individuals A and B, N_A is the number of bands unique to individual A, and N_B is the number of bands unique to individual B (Wetton et al. 1987; Lynch 1988, 1990). We calculated these from our presence-absence matrix using GELSTATS, version 2.6 (Rogstad and Pelikan 1996).

In fingerprinting, individuals often are used in multiple pairwise comparisons, which results in nonindependence of band-sharing values (Danforth and Freeman-Gallant 1996, Call et al. 1998, Leonard et al. 1999). We used the *p-dif* test (Bertorelle et al. 1999) in the program WATSON (Bucchini et al. 1999), a test that permutes individuals, not band-sharing values, to ask whether within-island band-sharing values significantly differed from between-island values. We calculated F_{ST} values for each pairwise comparison of islands, as well as an overall archipelago value, according to Lynch (1990, 1991). The maximum value of F_{ST} is 1 when two subpopulations are fixed for different alleles (complete differentiation), and 0 when alleles are distributed randomly among subpopulations (no differentiation).

We used a linear regression to test the prediction that population genetic uniformity (as measured by within-island similarity indices) decreases with increasing island area. We calculated total island area in ARCMAP, version 9.0, using digitized vegetation coverage maps obtained from the Charles Darwin Research Station. Projections were in decimal degrees, so we converted the areas to square kilometers (1 degree \approx 111 km) and used the log of island area in the regression. Large portions of some of these islands ($\leq 75\%$ of total island area) are barren of vegetation, which makes them less suitable for Galápagos Hawk territories. Total island area may, therefore, overestimate population size in some cases, so we performed a second

regression using the log of total vegetated area (excluding lava and beaches). We tested for an effect of mating system with a general linear model, using band-sharing values as the dependent variable, mean group size as a fixed factor, and log of total island area as a covariate. Because of the nonindependence of minisatellite band-sharing values, we first randomly selected a subset of independent values (using each individual once) from each population. For mating system, we classified each island as having a mean group size of less than two males or more than two males, using published data from de Vries (1975) and Bollmer et al. (2003) and new data collected from Fernandina in 2003 (1.4 ± 0.5 males per group, $n = 10$ groups). Thus, we classified Española, Santa Fe, Pinzón, and Fernandina as less polyandrous (mean group sizes of 1–1.5 males), and Isabela, Santiago, Marchena, and Pinta as more polyandrous (mean group sizes of 2.3–3.5 males). We used a Mantel (1967) test to examine isolation by distance (Slatkin 1993), testing the prediction that genetic differentiation among populations (F_{ST}) should increase with increasing geographic distance between them. We log-transformed the distance between islands as measured between nearest points. We performed these analyses in SPSS, version 10.0.5 for Windows (SPSS, Chicago, Illinois) and IBDWS, version 2.0 beta (Bohonak 2002). We excluded Santa Cruz from the above analyses because of its small sample size.

Because there does not appear to be a breeding population on Santa Cruz, we performed an assignment test to see whether the juveniles we captured on Santa Cruz closely matched any of the other populations, which would indicate that they could be migrants. Although there are no tests designed for codominant minisatellite data, the online program DOH (Brzustowski 2002), as first described in Paetkau et al. (1995), can accommodate data from dominant markers by treating each band as a separate locus. We performed a segregation analysis by tallying, within each population, the co-occurrences of each band with every other band to note cases of linkage (bands always appearing together within individuals) and allelism (individuals always having one or the other band but never both, indicating that they belong to the same locus). We found no cases of linkage, and we eliminated all cases of allelism (most attributable to rare bands) by removing the less-frequent band from

each allelic dyad. We entered the remaining 23 independent bands into the DOH program as presence-absence data for each individual. The program assigns each individual into the population in which its genotype has the highest probability of occurring.

RESULTS

Within-population similarity.—We scored an average (\pm SD) of 14.1 ± 1.42 bands for each individual. Within-island similarity indices were high, ranging from 0.693 for Isabela to 0.956 for Santa Fe (Table 1 and Fig. 2). The mean similarity index for Santa Cruz was slightly lower (0.657), but this is based on only six pairwise comparisons. Birds from Santa Fe were particularly lacking in genetic variation, having only a few variable bands. Specifically, 13 of the 16 Santa Fe bands scored were fixed in the population. All 15 Santa Fe birds were identical to two or three other birds, resulting in only four different genotypes in that population. In addition, 4 of the 10 birds on Pinzón were identical, whereas there were two sets of identical birds (2 and 3 birds each) out of 15 individuals sampled on Española and four sets of identical birds (2 or 3 birds each for 9 total) on Marchena. The other populations (Isabela, Fernandina, Santiago, and Pinta) were more variable and had no identical individuals.

Regression analyses supported our prediction that genetic similarity among individuals in a population decreases with increasing total island

area ($r = -0.844$, $df = 7$, $P = 0.008$; Fig. 3) and vegetated area ($r = -0.846$, $df = 7$, $P = 0.008$), though there was no substantial difference between the two measures. A general linear model showed no effect of degree of polyandry on genetic variability after controlling for island area ($F = 0.537$, $P = 0.466$, $n = 78$), whereas there was still a strong island area effect after controlling for mating system ($F = 32.1$, $P < 0.0001$, $n = 78$).

Population differentiation.—Between-island F_{ST} values ranged from 0.017 to 0.896 (Table 2), with an overall archipelago value of 0.538. We performed pairwise permutation tests to test whether populations were significantly distinct from each other. There were 28 pairwise comparisons, so we used a Bonferroni correction to avoid Type I errors, which brought our alpha level down to 0.002. Twenty-three of the 28 comparisons still showed significant differences among populations ($P < 0.001$ for all). Four of the five nonsignificant values involved Pinzón compared with Isabela ($P = 0.058$), Fernandina ($P = 0.021$), Santiago ($P = 0.820$), and Pinta ($P = 0.006$). The remaining comparison, Isabela versus Fernandina ($P = 0.203$), had the lowest F_{ST} value (0.017; Table 2). Three of the five nonsignificant values also represent the three smallest interisland distances.

We had predicted that populations would exhibit isolation by distance. A Mantel test confirmed this, showing a significant pattern of increasing genetic differentiation with increasing distance between islands ($r = 0.626$, $P \leq 0.003$; Fig. 4).

Between-island dispersal.—Over the past few decades, juveniles have occasionally been seen on islands where there was no resident Galápagos Hawk population, but no individual banded on one island had ever been observed on another island. In 2003, however, we observed two banded individuals on Fernandina, an island where Galápagos Hawks had not previously been studied. One individual, a territorial adult female, had been banded by us as a second-year juvenile on Volcan Alcedo, Isabela, in 1998. The other bird was a territorial male whose band could not be read. It is very likely that he was also banded as a juvenile on Alcedo in 1998, given that 70 birds were caught there in two days, 64 of which were juveniles. Also, it is unlikely that he came from an island other than Isabela, because Isabela separates Fernandina from all the other islands (Fig. 1).

TABLE 1. Mean within-island Galápagos Hawk minisatellite band-sharing value (\pm SD), total island area, and percentage of each island that is vegetated (not lava or beach); islands are listed in order of increasing area as calculated from digitized maps.

Island	Within-island S	Area (km ²)	Percentage vegetated
Pinzón	0.903 \pm 0.067	18.1	95.2
Santa Fe	0.956 \pm 0.032	24.8	100.0
Pinta	0.765 \pm 0.083	59.4	62.0
Española	0.900 \pm 0.052	61.1	98.2
Marchena	0.891 \pm 0.047	128.8	25.4
Santiago	0.711 \pm 0.086	577.5	68.6
Fernandina	0.719 \pm 0.101	647.6	30.5
Santa Cruz	0.657 \pm 0.157	984.1	100.0
Isabela	0.693 \pm 0.086	4,710.7	66.5

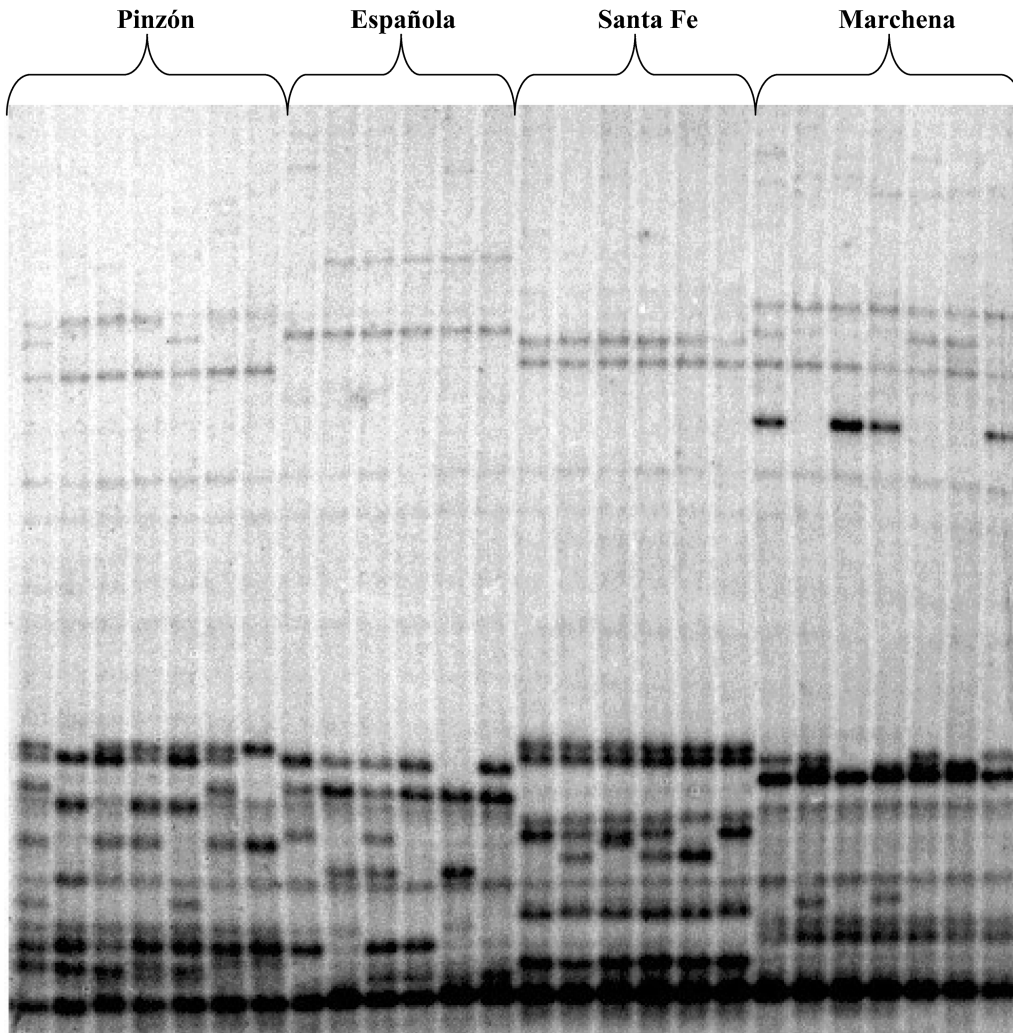


FIG. 2. An example of a multilocus minisatellite DNA fingerprinting gel of Galápagos Hawks. Each lane represents the fingerprint of an individual randomly selected from those sampled on the four study islands named above the gel. Some of these populations exhibit the highest levels of monomorphism at minisatellite loci of any natural bird population studied. Note that several bands are unique to or fixed in their respective island populations, highlighting the powerful effect that genetic drift has had in this system in limiting neutral genetic variance within islands and increasing it among islands.

In Table 3, we present the results of the assignment test for each population. The program accurately assigned all the individuals from the more genetically monomorphic Española, Santa Fe, Pinzón, and Marchena populations to their home islands, though there were misassignments among the larger populations, likely owing to their greater genetic variability. The assignment test placed the four Santa Cruz

juveniles into the populations they most closely matched. One of the four individuals caught on Santa Cruz had a banding pattern identical to that of one of the Santa Fe genotypes, and the assignment test placed it within the Santa Fe population. Another of the Santa Cruz individuals had a banding pattern very similar to those on Pinzón (mean band-sharing between it and the Pinzón individuals was 0.911 ± 0.03), and

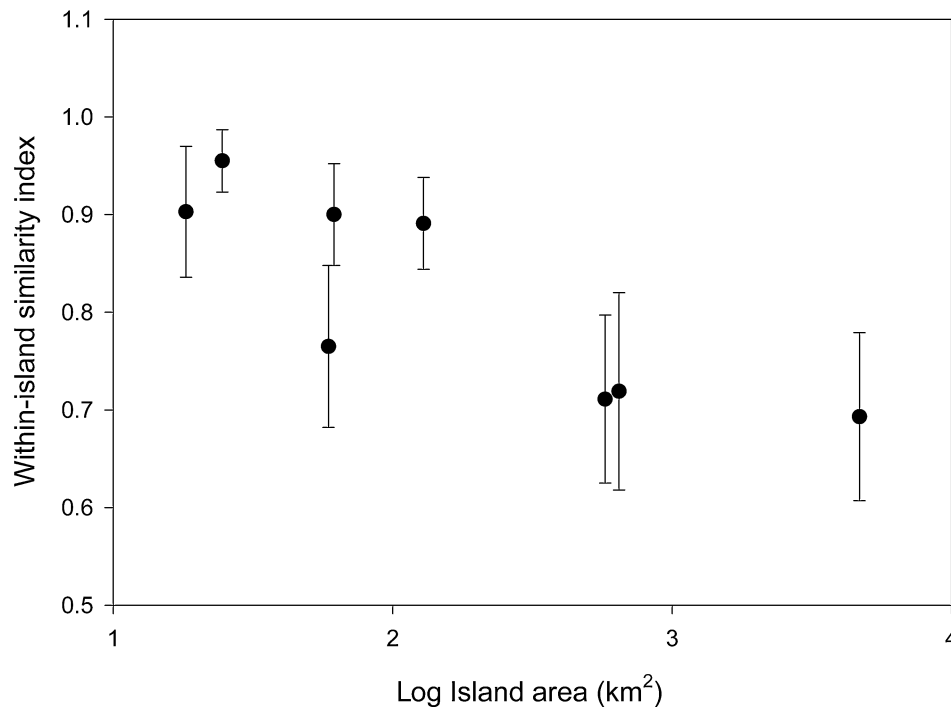


FIG. 3. Plot of mean genetic similarity (\pm SD) of Galápagos Hawk individuals within islands against the log of island area (km²). Data support our prediction that within-population genetic similarity should decrease with increasing island size.

the assignment test placed it within the Pinzón population. The last two Santa Cruz individuals matched Santiago best, though the chance for an assignment error is higher for the more variable populations.

DISCUSSION

Genetic variation within populations.—We were able to characterize population genetic structure of nine Galápagos Hawk populations, covering the entire species range. The populations exhibited very little genetic variation, having within-population similarity indices ranging from 0.6 to >0.9 at hypervariable minisatellite loci. To our knowledge, the smaller Galápagos Hawk populations have the highest reported levels of monomorphism at minisatellite loci of any natural bird population, though some populations of New Zealand birds (reviewed in Miller et al. 2003) and other endangered island bird species (e.g. Rave 1995, Caparroz et al. 2001) are nearly as inbred. Gilbert et al. (1990) found

even higher mean band-sharing values for populations of Channel Island foxes, another top predator, ranging from 0.75 up to 1.00. By contrast, unrelated birds in outbred mainland populations typically have band-sharing values around 0.2 and 0.3 (Parker Rabenold et al. 1991, Papangelou et al. 1998). Although there are no published studies using minisatellites in other *Buteo* species, mean band-sharing within a small sample of overwintering Swainson's Hawks was 0.374 ± 0.10 ($n = 8$; J. L. Bollmer et al. unpubl. data). So the Galápagos Hawk's ancestral mainland polymorphism was likely much higher.

Extremely low genetic variability within this species is probably the result of a single founder event coupled with long-term genetic drift. The *Buteo* phylogeny by Riesing et al. (2003) shows a very recent divergence between Galápagos and Swainson's hawks, and mitochondrial DNA (mtDNA) work underway on the Galápagos Hawks indicates a single colonization event from the mainland (J. L. Bollmer et al. unpubl. data).

TABLE 2. Pairwise comparisons of between-island differentiation in Galápagos Hawks. Mean between-island band-sharing values (\pm SD) are above the diagonal, with total number and number of independent pairwise comparisons scored in parentheses. F_{ST} values are reported below the diagonal.

	Española	Santa Fe	Pinzón	Isabela	Fernandina	Santiago	Marchena	Pinta
Española	–	0.306 \pm 0.03 (225, 15)	0.656 \pm 0.04 (150, 10)	0.546 \pm 0.08 (330, 15)	0.534 \pm 0.10 (300, 15)	0.593 \pm 0.08 (555, 15)	0.579 \pm 0.05 (300, 15)	0.563 \pm 0.70 (300, 15)
Santa Fe	0.896	–	0.489 \pm 0.04 (150, 10)	0.485 \pm 0.08 (330, 15)	0.443 \pm 0.08 (300, 15)	0.509 \pm 0.07 (555, 15)	0.404 \pm 0.05 (300, 15)	0.470 \pm 0.07 (300, 15)
Pinzón	0.714	0.862	–	0.702 \pm 0.08 (220, 10)	0.716 \pm 0.09 (200, 10)	0.737 \pm 0.07 (370, 10)	0.753 \pm 0.05 (200, 10)	0.748 \pm 0.07 (200, 10)
Isabela	0.551	0.659	0.322	–	0.701 \pm 0.09 (440, 20)	0.669 \pm 0.09 (814, 22)	0.641 \pm 0.08 (440, 20)	0.632 \pm 0.09 (440, 20)
Fernandina	0.591	0.708	0.335	0.017	–	0.675 \pm 0.09 (740, 20)	0.631 \pm 0.08 (400, 20)	0.636 \pm 0.10 (400, 20)
Santiago	0.522	0.661	0.266	0.100	0.123	–	0.672 \pm 0.07 (740, 20)	0.667 \pm 0.08 (740, 20)
Marchena	0.752	0.872	0.583	0.421	0.472	0.393	–	0.753 \pm 0.08 (400, 20)
Pinta	0.617	0.737	0.341	0.264	0.291	0.213	0.304	–

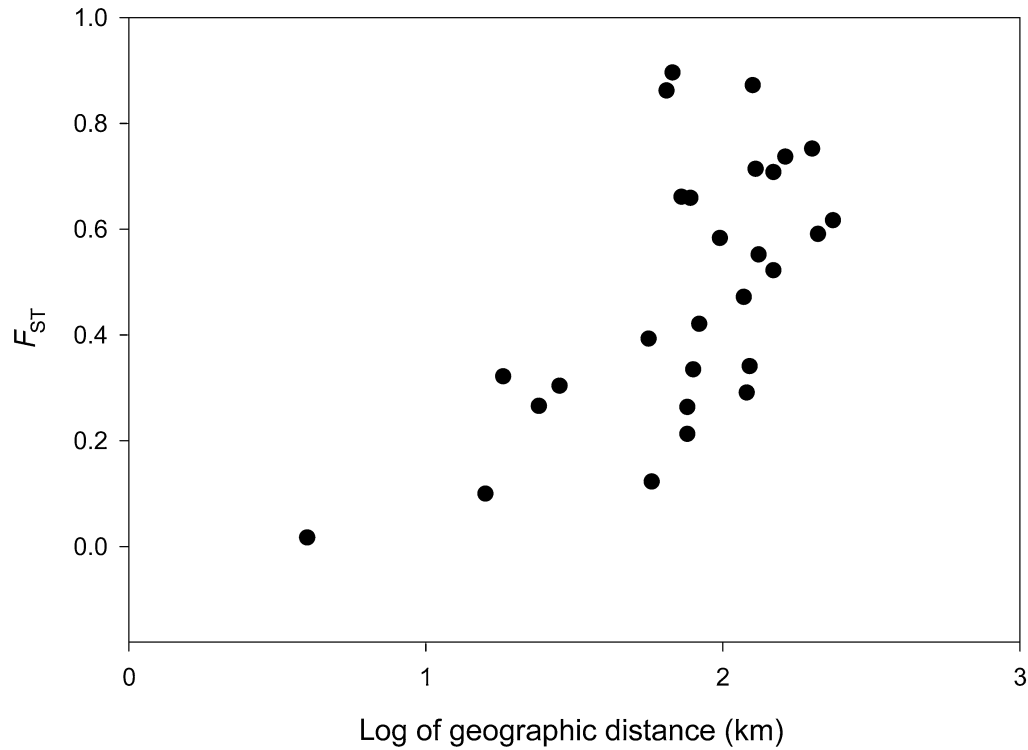


FIG. 4. Plot of pairwise interisland F_{ST} values against the log of geographic distances (km) between islands for Galápagos Hawks. Degree of genetic differentiation between populations increases with increasing geographic distance.

TABLE 3. Results of Galápagos Hawk assignment test using minisatellite data. Rows represent the populations in which we sampled the individuals, and columns represent the populations to which DOH assigned the individuals. Santa Cruz is listed only as an island of capture, because there is no resident Galápagos Hawk population there with which possible migrants could be compared.

	Española	Santa Fe	Pinzón	Isabela	Fernandina	Santiago	Marchena	Pinta
Española	15	0	0	0	0	0	0	0
Santa Fe	0	15	0	0	0	0	0	0
Pinzón	0	0	10	0	0	0	0	0
Isabela	0	0	2	10	8	2	0	0
Fernandina	0	0	0	5	13	2	0	0
Santiago	0	0	1	5	5	23	0	3
Marchena	0	0	0	0	0	0	20	0
Pinta	0	0	1	1	0	0	5	13
Santa Cruz	0	1	1	0	0	2	0	0

Although there is evidence that island colonizations may not always result in a significant decrease in genetic diversity (Clegg et al. 2002, Grant 2002), in the present case, the founding population may have been small enough that

a severe bottleneck occurred. The high mean interisland band-sharing (0.617) and the presence of bands that are fixed across all populations (even though most populations are currently genetically isolated) suggest that Galápagos

Hawks became inbred early in their colonization of the islands. The close relationship between island area and genetic variation across populations indicates that long-term genetic drift has also been an important factor influencing the level of variability in Galápagos Hawks. The smallest populations have become fixed or nearly fixed for many of their bands, with different bands being common in different populations.

Within-island genetic uniformity decreased significantly with increasing population size, as approximated by total island area and vegetated area. Although total island area explained a large portion of the variance in genetic similarity ($r = -0.844$), we had supposed that population size (and thus genetic variability) would correlate even more strongly with vegetated area, given the presence of large tracts of barren lava on some islands. Using only vegetated area, however, did not substantially improve the correlation ($r = -0.846$), even though five of the islands are <70% vegetated, two greatly less. We excluded Santa Cruz from this analysis because it differs from the other islands, in that human activities have made the population on this large island artificially small. Even though the Santa Cruz population is almost certainly the smallest in the archipelago, the four juvenile Galápagos Hawks sampled there exhibited the lowest mean similarity of any of the populations, probably because of interisland movements of birds, which we will discuss below.

We found that there was no effect of mating system on genetic variability of Galápagos Hawk populations. We had predicted that increased polyandry might result in lowered effective population sizes in relation to total population size because of increased variance in male reproductive success or more strongly biased sex ratios. The lack of difference between low- and high-polyandry populations shows that mating system is not a strong determinant of genetic variability in the Galápagos Hawk; shared paternity may mitigate the effects of increased polyandry. Also, population size accounts for such a large portion of the variance in within-island genetic similarity that there is little remaining variability on which other forces might act.

Genetic divergence among populations.—Overall, the high F_{ST} values indicate that Galápagos Hawks are reluctant to cross large stretches of water, which is consistent with the

migratory behavior of their closest mainland relatives (Fuller et al. 1998). Most Galápagos Hawk populations appear to be significantly genetically different from each other, with the exception of the interaction between Isabela and Fernandina and four comparisons involving Pinzón. The comparisons involving Pinzón are more suspect, given that we sampled only 10 individuals on Pinzón, all of which were floater juveniles instead of territorial adults. Also, the use of the Bonferroni correction increased the probability of Type II errors, especially for the two comparisons with P -values of 0.006 (Pinzón vs. Pinta) and 0.021 (Pinzón vs. Fernandina). These two comparisons are also the most geographically distant of the nonsignificant values.

The populations were divergent to varying degrees, as indicated by the pattern of isolation by distance. Lower F_{ST} values between nearby populations may be the result of ongoing (albeit relatively rare in most cases) gene flow between them, more recent population separation, or a combination of the two. Española and Santa Fe were the most divergent from the rest of the archipelago, with F_{ST} values between them and the other islands ranging from 0.5 to 0.9. Their relatively extreme divergence (especially from each other) is likely attributable to the random fixation of alleles in these populations that are not common on other islands.

Fernandina and Isabela were indistinguishable at these minisatellite loci. Of all island pairs, they are separated by the shortest distance (<5 km), and we observed a bird banded on Isabela residing in a territory on Fernandina. The lack of differentiation between these two populations, therefore, may be attributable to ongoing gene flow. Alternatively, their similarity may have resulted from more recent separation or from drift acting more slowly in larger populations. With the present data, we are unable to distinguish among these scenarios.

The four juveniles we captured on Santa Cruz are likely migrants from neighboring islands. When fledglings leave their territories, they spend at least three or four years in a nonterritorial floater population, roaming all over their native island and occupying areas not used by territorial birds (de Vries 1975). Because of this nomadic behavior, we suggest that juveniles are much more likely than adults to move between islands. Dispersal of juveniles to Santa Cruz may be more probable

than movement to other islands, because Santa Cruz is mostly or entirely uninhabited by a territorial adult population, which means that suitable habitat is vacant, and juveniles are not likely to be harassed and driven away by adults. The assignment test placed two of the birds into the Santa Fe and Pinzón populations with high degrees of probability. The other two were most similar to Santiago, though there is more likely to be a misassignment when dealing with more variable populations. Santiago is a likely source population because it supports a large floater population and is an adjacent island. We cannot eliminate the possibility that one or more of these birds was born on Santa Cruz, because we could not compare them to a sample of resident Santa Cruz territorial birds, given the lack of known breeding adults there.

Archipelagoes are well known as arenas for species radiations (e.g. Darwin's finches, Hawaiian honeycreepers). Although we have described morphological and behavioral differences (Bollmer et al. 2003) and genetic differentiation (present study) among populations of Galápagos Hawks, these differences are on a microevolutionary scale. Presumably, Galápagos Hawks are one of the more recent arrivals to the archipelago, and have not been there long enough to diverge into subspecies or new species. Drift has had a strong influence on divergence at these neutral minisatellite markers, but the importance of drift in speciation is debatable (Barton 1998). Given the genetic isolation of many of these populations, the Galápagos Hawk may one day match the patterns seen in other sedentary species groups in the archipelago (e.g. Galápagos tortoises [*Geochelone elephantopus* subspp.], lava lizards [*Microlophus* spp.]), with multiple subspecies or species restricted to one or a few islands.

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LITERATURE CITED

- BAKER, A. J., M. D. DENNISON, A. LYNCH, AND G. LE GRAND. 1990. Genetic divergence in peripherally isolated populations of Chaffinches in the Atlantic islands. *Evolution* 44:981–999.
- BARTON, N. H. 1998. Natural selection and random genetic drift as causes of evolution on islands. Pages 102–123 *in* *Evolution on Islands* (P. R. Grant, Ed.). Oxford University Press, Oxford.
- BERGER, D. D., AND H. C. MUELLER. 1959. The bal-chatri: A trap for the birds of prey. *Bird Banding* 30:18–26.
- BERTORELLE, G., L. BUCCHINI, A. PILASTRO, AND C. MATESSI. 1999. DNA fingerprinting data and the analysis of population genetic structure by comparing band-sharing patterns. *Molecular Ecology* 8:1851–1866.
- BOAG, P. T. 1988. The genetics of island birds. Pages 1550–1563 *in* *Acta XIX Congressus Internationalis Ornithologici* (H. Ouellet, Ed.). National Museum of Natural Sciences, Ottawa.
- BOHONAK, A. J. 1999. Dispersal, gene flow, and population structure. *Quarterly Review of Biology* 74:21–45.
- BOHONAK, A. J. 2002. IBD (isolation by distance): A program for analyses of isolation by distance. *Journal of Heredity* 93:153–154.
- BOLLMER, J. L., T. SANCHEZ, M. DONAGHY CANNON, D. SANCHEZ, B. CANNON, J. C. BEDNARZ, T. DE VRIES, M. S. STRUVE, AND P. G. PARKER. 2003. Variation in morphology and mating system among island populations of Galápagos Hawks. *Condor* 105:428–438.
- BUCCHINI, L., A. LISA, AND C. MATESSI. 1999.

- WATSON: A tool to analyse DNA fingerprinting data. [Online.] Available at www.igm.cnr.it/watson/manualwatson.html.
- BRZUSTOWSKI, J. 2002. DOH assignment test calculator. [Online.] Available at www2.biology.ualberta.ca/jbrzusto/Doh.php.
- CALL, D. R., J. G. HALLETT, S. G. MECH, AND M. EVANS. 1998. Considerations for measuring genetic variation and population structure with multilocus fingerprinting. *Molecular Ecology* 7:1337–1346.
- CAPARROZ, R., C. Y. MIYAKI, M. I. BAMPI, AND A. WAJNTAL. 2001. Analysis of the genetic variability in a sample of the remaining group of Spix's Macaw (*Cyanopsitta spixii*, Psittaciformes: Aves) by DNA fingerprinting. *Biological Conservation* 99:307–311.
- CARNEIRO DA SILVA, M., AND J. P. GRANADEIRO. 1999. Genetic variability and isolation of Cory's Shearwater colonies in the Northeast Atlantic. *Condor* 101:174–179.
- CHRISTIE, D. M., R. A. DUNCAN, A. R. MCBIRNEY, M. A. RICHARDS, W. M. WHITE, K. S. HARPP, AND C. G. FOX. 1992. Drowned islands downstream from the Galápagos hotspot imply extended speciation times. *Nature* 355:246–248.
- CLEGG, S. M., S. M. DEGNAN, J. KIKKAWA, C. MORITZ, A. ESTOUP, AND I. P. F. OWENS. 2002. Genetic consequences of sequential founder events by an island-colonizing bird. *Proceedings of the National Academy of Sciences USA* 99:8127–8132.
- DANFORTH, B. N., AND C. R. FREEMAN-GALLANT. 1996. DNA fingerprinting data and the problem of non-independence among pairwise comparisons. *Molecular Ecology* 5: 221–227.
- DE LAY, L. S., J. FAABORG, J. NARANJO, S. M. PAZ, T. DE VRIES, AND P. G. PARKER. 1996. Paternal care in the cooperatively polyandrous Galápagos Hawk. *Condor* 98:300–311.
- DE VRIES, T. 1973. The Galápagos Hawk, an ecological study with special reference to its systematic position. Ph.D. dissertation, Vrije University, Amsterdam.
- DE VRIES, T. 1975. The breeding biology of the Galápagos Hawk, *Buteo galapagoensis*. *Le Gerfaut* 65:29–57.
- FAABORG, J., T. DE VRIES, C. B. PATTERSON, AND C. R. GRIFFIN. 1980. Preliminary observations on the occurrence and evolution of polyandry in the Galápagos Hawk (*Buteo galapagoensis*). *Auk* 97:581–590.
- FAABORG, J., P. G. PARKER, L. DELAY, T. DE VRIES, J. C. BEDNARZ, S. M. PAZ, J. NARANJO, AND T. A. WAITE. 1995. Confirmation of cooperative polyandry in the Galápagos Hawk (*Buteo galapagoensis*). *Behavioral Ecology and Sociobiology* 36:83–90.
- FAABORG, J., AND C. B. PATTERSON. 1981. The characteristics and occurrence of cooperative polyandry. *Ibis* 123:477–484.
- FLINT, J., J. BOND, D. C. REES, A. J. BOYCE, J. M. ROBERTS-THOMSON, L. EXCOFFIER, J. B. CLEGG, M. A. BEAUMONT, R. A. NICHOLS, AND R. M. HARDING. 1999. Minisatellite mutational processes reduce F_{st} estimates. *Human Genetics* 105:567–576.
- FRANKHAM, R. 1996. Relationship of genetic variation to population size in wildlife. *Conservation Biology* 10:1500–1508.
- FRANKHAM, R. 1997. Do island populations have less genetic variation than mainland populations? *Heredity* 78:311–327.
- FREEMAN-GALLANT, C. R. 1996. Microgeographic patterns of genetic and morphological variation in Savannah Sparrows (*Passerculus sandwichensis*). *Evolution* 50:1631–1637.
- FULLER, M. R., W. S. SEEGAR, AND L. S. SCHUECK. 1998. Routes and travel rates of migrating Peregrine Falcons *Falco peregrinus* and Swainson's Hawks *Buteo swainsoni* in the Western Hemisphere. *Journal of Avian Biology* 29:433–440.
- GILBERT, D. A., N. LEHMAN, S. J. O'BRIEN, AND R. K. WAYNE. 1990. Genetic fingerprinting reflects population differentiation in the California Channel Island fox. *Nature* 344:764–767.
- GRANT, P. R. 2002. Founder effects and silver-eyes. *Proceedings of the National Academy of Sciences USA* 99:7818–7820.
- GRANT, P. R., B. R. GRANT, AND K. PETREN. 2001. A population founded by a single pair of individuals: Establishment, expansion, and evolution. *Genetica* 112–113:359–382.
- GULLBERG, A., M. OLSSON, AND H. TEGELSTRÖM. 1999. Evolution in populations of Swedish sand lizards: Genetic differentiation and loss of variability revealed by multilocus DNA fingerprinting. *Journal of Evolutionary Biology* 12:17–26.
- JEFFREYS, A. J., V. WILSON, AND S. L. THEIN. 1985. Hypervariable 'minisatellite' regions in human DNA. *Nature* 314:67–73.

- KERLINGER, P. 1985. Water-crossing behavior of raptors during migration. *Wilson Bulletin* 97:109–113.
- LEONARD, A. C., S. E. FRANSON, V. S. HERTZBERG, M. K. SMITH, AND G. P. TOTH. 1999. Hypothesis testing with the similarity index. *Molecular Ecology* 8:2105–2114.
- LONGMIRE, J. L., A. K. LEWIS, N. C. BROWN, J. M. BUCKINGHAM, L. M. CLARK, M. D. JONES, L. J. MEINCKE, J. MEYNE, R. L. RATLIFF, F. A. RAY, AND OTHERS. 1988. Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. *Genomics* 2:14–24.
- LYNCH, M. 1988. Estimation of relatedness by DNA fingerprinting. *Molecular Biology and Evolution* 5:584–599.
- LYNCH, M. 1990. The similarity index and DNA fingerprinting. *Molecular Biology and Evolution* 7:478–484.
- LYNCH, M. 1991. Analysis of population genetic structure by DNA fingerprinting. Pages 113–126 *in* DNA Fingerprinting: Approaches and Applications (T. Burke, G. Dolf, A. J. Jeffreys, and R. Wolff, Eds.). Birkhäuser Verlag, Basel, Switzerland.
- MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27:209–220.
- MILLER, H. C., D. M. LAMBERT, C. D. MILLAR, B. C. ROBERTSON, AND E. O. MINOT. 2003. Minisatellite DNA profiling detects lineages and parentage in the endangered Kakapo (*Strigops habroptilus*) despite low microsatellite DNA variation. *Conservation Genetics* 4: 265–274.
- MORGAN, W. J. 1971. Convection plumes in the lower mantle. *Nature* 230:42–43.
- MUNDY, N. I., C. S. WINCHELL, T. BURR, AND D. S. WOODRUFF. 1997. Microsatellite variation and microevolution in the critically endangered San Clemente Island Loggerhead Shrike (*Lanius ludovicianus mearnsi*). *Proceedings of the Royal Society of London, Series B* 264:869–875.
- NEVO, E., A. BEILES, AND R. BEN-SHLOMO. 1984. The evolutionary significance of genetic diversity: Ecological, demographic and life history correlates. Pages 13–213 *in* Evolutionary Dynamics of Genetic Diversity (G. S. Mani, Ed.). Springer-Verlag, Berlin.
- NUNNEY, L. 1993. The influence of mating system and overlapping generations on effective population size. *Evolution* 47:1329–1341.
- OUBORG, N. J., Y. PIQUOT, AND J. M. VAN GROENENDAEL. 1999. Population genetics, molecular markers and the study of dispersal in plants. *Journal of Ecology* 87:551–568.
- PAETKAU, D., W. CALVERT, I. STIRLING, AND C. STROBECK. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* 4:347–354.
- PAPANGELOU, A., M. H. HARN, AND M. M. MIYAMOTO. 1998. Variation of multilocus minisatellite DNA fingerprints in avian populations. *Zoological Studies* 37:161–168.
- PARKER, P. G., AND T. A. WAITE. 1997. Mating systems, effective population size, and conservation of natural populations. Pages 244–262 *in* Behavioral Approaches to Conservation in the Wild (J. Clemmons and R. Bucholz, Eds.). Cambridge University Press, Cambridge, United Kingdom.
- PARKER, P. G., T. A. WAITE, AND M. D. DECKER. 1995. Kinship and association in communally roosting Black Vultures. *Animal Behaviour* 49:395–401.
- PARKER RABENOLD, P., K. N. RABENOLD, W. H. PIPER, M. D. DECKER, AND J. HAYDOCK. 1991. Using DNA fingerprinting to assess kinship and genetic structure in avian populations. Pages 611–620 *in* The Unity of Evolutionary Biology (E. C. Dudley, Ed.). Dioscorides, Portland, Oregon.
- RAVE, E. H. 1995. Genetic analyses of wild populations of Hawaiian Geese using DNA fingerprinting. *Condor* 97:82–90.
- RIESING, M. J., L. KRUCKENHAUSER, A. GAMAUF, AND E. HARING. 2003. Molecular phylogeny of the genus *Buteo* (Aves: Accipitridae) based on mitochondrial marker sequences. *Molecular Phylogenetics and Evolution* 27: 328–342.
- ROGSTAD, S. H., AND S. PELIKAN. 1996. GELSTATS: A computer program for population genetics analyses using VNTR multilocus probe data. *BioTechniques* 21:1128–1131.
- SLATKIN, M. 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics* 16:393–430.
- SLATKIN, M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* 47:264–279.
- TARR, C. L., AND R. C. FLEISCHER. 1999. Population boundaries and genetic diversity in the endangered Mariana Crow (*Corvus kubaryi*). *Molecular Ecology* 8:941–949.

- WERNER, R., AND K. HOERNLE. 2003. New volcanological and volatile data provide strong support for the continuous existence of Galápagos Islands over the past 17 million years. *International Journal of Earth Sciences* 92:904–911.
- WETTON, J. H., R. E. CARTER, D. T. PARKIN, AND D. WALTERS. 1987. Demographic study of a wild House Sparrow population by DNA fingerprinting. *Nature* 327:147–149.
- WHITE, W. M., A. R. MCBIRNEY, AND R. A. DUNCAN. 1993. Petrology and geochemistry of the Galápagos Islands: Portrait of a pathological mantle plume. *Journal of Geophysical Research B, Solid Earth* 98: 19533–19563.
- WILLIAMSON, M. 1981. *Island Populations*. Oxford University Press, Oxford.
- WRIGHT, S. 1951. The genetical structure of populations. *Annals of Eugenics* 15:323–354.
- WRIGHT, S. 1978. *Evolution and the Genetics of Populations*, vol. 4: Variability within and among Natural Populations. University of Chicago Press, Chicago.
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