

## DISPERSAL AND GENETIC VARIATION IN AN ENDEMIC ISLAND WOODPECKER, THE GUADELOUPE WOODPECKER (*MELANERPES HERMINIERI*)

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**Abstract:** We used mark-resight and DNA fingerprinting to investigate dispersal and genetic variation in the Guadeloupe Woodpecker (*Melanerpes herminieri*). This species is endemic to Guadeloupe, where the entire population is found on two islands: Basse-Terre and Grande-Terre. The Grande-Terre population is approximately one quarter of the total Guadeloupe Woodpecker population and the loss and fragmentation of forest on the island has resulted in some isolation from the larger Basse-Terre population. Our results suggest that dispersal and gene flow occurred between the populations, but dispersal was limited and there was a moderate degree of genetic differentiation. The Grande-Terre population had significantly higher band sharing among adults than Basse-Terre, suggesting that dispersal from Grande-Terre to Basse-Terre may be more frequent than vice versa. Band sharing between mated pairs on Grande-Terre was significantly higher than band sharing between randomized pairings of males and females, suggesting that mating was not random. Some breeding occurred between first order relatives within both island populations and one case of extra-pair fertilization was detected. Continued habitat loss and fragmentation on Grande-Terre will further reduce the total population size and may have profound effects on population persistence and the maintenance of genetic variation in the Guadeloupe Woodpecker.

**Key words:** dispersal, DNA fingerprinting, extra-pair fertilization, Guadeloupe Woodpecker, habitat loss, mark-resight, *Melanerpes herminieri*, population genetics

**Resumen:** DISPERSIÓN Y VARIACIÓN GENÉTICA EN EL CARPINTERO ENDÉMICO DE UNA ISLA, EL CARPINTERO DE GUADALUPE (*MELANERPES HERMINIERI*). Usamos las técnicas de marcaje-reavistamiento y DNA fingerprinting para investigar la dispersión y la variación genética del Carpintero de Guadalupe (*Melanerpes herminieri*). Esta especie es endémica de Guadalupe, donde toda la población se encuentra en dos islas: Basse-Terre y Grande-Terre. La población de Grande-Terre es aproximadamente un cuarto del total de la población de la especie; la pérdida y fragmentación de los bosques de la isla ha resultado en su aislamiento de la población de mayor tamaño de Basse-Terre. Nuestros resultados sugieren que hay dispersión y flujo génico entre las poblaciones, pero la dispersión fue limitada y existió un grado moderado de diferenciación genética. En la población de Grande-Terre se obtuvieron bandas significativamente más anchas compartidas entre adultos que en la población de Basse-Terre; esto sugiere que la dispersión de Grande-Terre a Basse-Terre puede ser más frecuente que viceversa. El número de bandas compartidas entre individuos formando parejas en Grande-Terre fue significativamente mayor que entre parejas aleatorias de machos y hembras; lo que sugiere que la formación de parejas no es aleatoria. Se detectaron indicios de reproducción entre parientes de primer orden dentro de las poblaciones de cada isla y un caso de fertilización extramarital. La pérdida continua de hábitat y la fragmentación de Grande-Terre reducirá el tamaño poblacional total y puede tener profundos efectos en la persistencia poblacional y mantenimiento de la variación genética en el Carpintero de Guadalupe.

**Palabras clave:** dispersión, DNA fingerprinting, fertilización extramarital, Carpintero de Guadalupe, pérdida de hábitat, marcaje-reavistamiento, *Melanerpes herminieri*, genética poblacional.

**Résumé :** DISPERSION ET VARIATION GÉNÉTIQUE CHEZ UNE ESPECE DE PIC ENDÉMIQUE ET INSULAIRE, LE PIC DE LA GUADELOUPE (*MELANERPES HERMINIERI*). Nous avons utilisé le baguage-contrôle et l'ADN (technique de fingerprinting) pour connaître la dispersion des individus et la variation génétique chez le Pic de la Guadeloupe (*Melanerpes herminieri*). Cette espèce est endémique de la Guadeloupe où la population est trouvée sur deux îles : Basse-Terre et Grande-Terre. La population de la Grande-Terre représente environ un quart de la population totale avec un certain degré d'isolement par rapport à la plus vaste population de la Basse-Terre, du à la réduction et à la fragmentation de son habitat. Nos résultats suggèrent que la dispersion des pics et donc les flux de gènes ont lieu entre les populations, mais la dispersion reste limitée avec un degré modéré de différenciation génétique. La population de la Grande-Terre avait une proportion de bandes communes considérablement plus élevée que celle de la Basse-Terre, suggérant que la dispersion de Grande-Terre vers Basse-Terre doit être plus fréquente que l'inverse. Le partage de bandes entre paires appariés sur Grande-Terre était considérablement plus élevé que celui prévu lors d'appariements au hasard, ce qui suggère que les accouplements n'étaient pas réalisés de façon aléatoire. Quelques reproductions ont eu lieu entre proches parents au sein de chacune des deux populations et nous avons aussi trouvé un cas de féconda-

fragmentation sur Grande-Terre réduiront en outre la dimension de la population totale et peuvent avoir des effets profonds sur persistance de la population et l'entretien de variation génétique dans le Pivert de Guadeloupe.

*Mots clés* : ADN fingerprinting, dispersion, fécondation extra couple, génétique de population, marquage-contrôle, *Melanerpes herminieri*, perte d'habitat, Pic de la Guadeloupe

WOODPECKERS OCCUR throughout the world, mainly in woodland and forest, and are found on islands in the Indian, Atlantic, and Pacific oceans as well as the Mediterranean and Caribbean seas (Winkler *et al.* 1995). Many of these island species are endemics, such as the Guadeloupe Woodpecker (*Melanerpes herminieri*). Habitat loss is the main reason for decline, endangerment, or extirpation of woodpecker populations, which is particularly true for island species or those that need large, undisturbed forests (Winkler *et al.* 1995). Endemic island birds in general are particularly vulnerable to extinction (Şekercioğlu *et al.* 2004), largely due to habitat loss and fragmentation, but also from the introduction of exotic predators and competitors as well as from hunting (Brook and Kikkawa 1998, Courchamp *et al.* 1999, Naka *et al.* 2002, Riley 2002).

The Guadeloupe Woodpecker populations found on Grande-Terre and Basse-Terre, the two largest islands of Guadeloupe, are the only populations of this species, with an estimated size of approximately 10,000 pairs (Villard and Rousteau 1998). The species is the only sedentary woodpecker species in the Lesser Antilles and occurs in every forested habitat found on Grande-Terre and Basse-Terre (semi-deciduous, rain, swamp, and mangrove forests) from sea level to 1000 m (Villard 1999). The Guadeloupe Woodpecker requires forest with some dead substrate in which a breeding cavity can be excavated. Currently, woodpecker habitat in forests outside of Guadeloupe National Park is disappearing through clear cutting and dead tree removal for roads and trails, agriculture, grazing, and development (Villard 1999). A pair of Guadeloupe Woodpeckers requires approximately 3 ha of forest for breeding, and in semi-open habitat with scattered fruit trees (e.g. Mango, *Mangifera* spp.), they require at least one ha of dense forest in their territory to persist (Villard 1999). It is estimated that, at present rates of deforestation, the Guadeloupe Woodpecker may soon be extirpated from Grande-Terre (Villard and Rousteau 1998). A reduction in genetic variation would result from the loss of the Grande-Terre population of woodpeckers, which comprises a large portion (approximately 23%) of the entire Guadeloupe Woodpecker population.

Multilocus DNA fingerprinting detects large amounts of genetic variation in individuals (Jeffreys *et al.* 1985), and it has often been used to study the genetic structure of populations (Gilbert *et al.* 1990, Fleischer *et al.* 1994, Arsenault *et al.* 2005). Genetics have become important in conservation biology for estimating effective dispersal and the genetic diversity of restricted populations (Rave 1995, Peacock 1997). Population bottlenecks and reduced population size can lead to the loss of genetic variation, particularly in endemic island species (Nei *et al.* 1975, Soulé and Kohn 1989, Frankham 1998). Here we used multilocus DNA fingerprinting to determine parentage, analyze mating patterns, and to assess levels of gene flow between the island populations of the Guadeloupe Woodpecker.

#### STUDY AREAS AND METHODS

Guadeloupe is located in the tropics between the Equator and Tropic of Cancer and is comprised primarily of two islands, Grande-Terre and Basse-Terre, which are separated by the 60 m wide Rivière Salée (Fig. 1). Grande-Terre (585 km<sup>2</sup>) is a flat coral island with a maximum elevation of 135 m. Basse-Terre (848 km<sup>2</sup>) is to the west, with a central mountain region averaging 500-800 m in elevation. Four forested habitat types occur on Guadeloupe, including semi-deciduous, rain, mangrove, and swamp forests.

We located woodpeckers visually and aurally during surveys of every forested habitat type throughout Basse-Terre and Grande-Terre (Villard and Rousteau 1998). Every road was driven and every forest trail was hiked at least once. A rowboat was used to survey all mangrove forest. Villard and Rousteau (1998) provide more details on survey methods. Adults were captured from 1993-1995 with mist nets at regular feeding locations and at nest sites with a mist net attached to a metal hoop on the top of a pole. Nestlings were removed from cavities by cutting a "trap door" below the entrance. Woodpeckers were banded with an aluminum ring from the Research Center on Bird Population Biology (CRBPO, Paris) on one leg and two split color plastic rings on the other. We color ringed 76 adults and 56 juveniles to evaluate site fidelity and dispersal. We collected blood (150-200 ml) from the jugu-

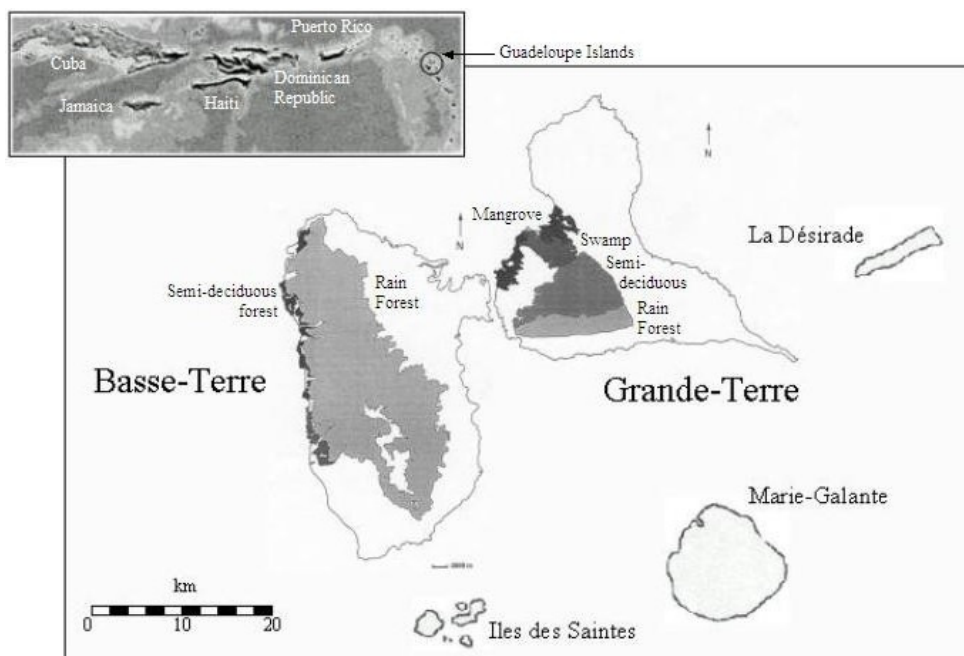


Fig. 1. The forested habitats (indicated by shades of gray), which also represent the range of the Guadeloupe Woodpecker, are restricted to the west sides of Grande-Terre and Basse Terre. Forested habitat types include mangrove forest, swamp forest, semi-deciduous forest, and rain forest. Sampling locations for genetic analysis were scattered throughout the population on both islands.

lar vein (using a syringe) or from the brachial vein (using a heparinized capillary tube) of adult ( $n = 71$ ) and juvenile ( $n = 41$ ) Guadeloupe Woodpeckers, and the blood was immediately transferred to lysis buffer.

DNA was extracted from blood samples using a standard phenol-chloroform extraction method. DNA samples were digested with *Hae* III restriction endonuclease and run on six 1% agarose gels with in-lane size standards. The Southern transfer technique was used to transfer DNA to a positively charged nylon membrane, which was hybridized with a radio-labeled DNA fingerprint probe and exposed to X-Ray film. In-lane size standards were visualized by stripping and re-probing membranes with radio-labeled lambda using the same hybridization procedure. All resolvable DNA fingerprinting bands between 20 and 2 kilobases were drawn onto transparency overlays placed over the film images by two different scorers. These images were then compared and scoring discrepancies were evaluated to increase the accuracy of the procedure. See Piper and Rabenold (1992) for additional information on lab techniques and scoring methods.

The proportion of bands shared was calculated as twice the number of shared bands over the total number of bands in both individuals (Lynch 1991). The frequency of dispersal between Basse-Terre and Grande-Terre was assessed using equations developed for multilocus data based on Wright's *F* statistics (Wright 1969, Lynch 1991). *F*<sub>st</sub> is the probability of drawing two alleles at random, which are identical by descent, from separate populations and is a measure of genetic differentiation among populations (Wright 1969). Band sharing scores were compared between the populations, between mated pairs and adults population-wide, and between mated pairs and random pairings of males and females using the nonparametric Mann-Whitney *U* test. All means are reported  $\pm$  SD.

Parentage analysis was conducted for 41 juveniles and 34 adults from 17 nests (four nests from Basse-Terre and 13 nests from Grande-Terre) by calculating band sharing scores (*D*) between juvenile nest-mates and between juveniles and the adult male and female present at the nest. A 95% confidence interval for first-order relatives was calculated from the distribution of band sharing scores between juve-

Table 1. Mark-resight results for 76 adult and 56 juvenile Guadeloupe Woodpeckers banded on Basse-Terre and Grande-Terre Islands from 1993 to 1995 and resighted in 1994, 1995, and 1997.

	Number Banded <sup>a</sup>	Number Resighted	Dispersal Distance (m)
Male	40	14 (35%)	113 ± 95 (4)
Female	36	13 (36%)	210 ± 145 (7)
Juvenile	56	2 (4%)	500 ± 424 (2)

<sup>a</sup>mark-resight data modified from Villard (1999)

niles and their parents and between siblings. Putative parents (adults at the nest) were considered the biological parents of juveniles with one, two, or three novel fragments if: (1) D values fell within the 95% CI for first order relatives and (2) the juvenile had a sibling with no novel fragments (Peacock 1997).

#### RESULTS

We resighted 36% of color-ringed adults and 4% of juveniles (Table 1). Males ( $n = 4$ ) moved 113 ± 95 m from one nest site to the next, shorter than the average distance moved by females ( $n = 7$ , 210 ± 145 m) and juveniles ( $n = 2$ , 500 ± 424 m; Table 1). Even assuming a high mortality rate for adults (50%) and juveniles (75%), individuals that were not resighted dispersed longer distances, but the distance and frequency of these events is unknown. There was a high immigration rate of new individuals into the marked population, but only a small portion of the populations on both islands was banded.

The average band sharing score between adults on Basse-Terre ( $\bar{x} = 0.34 \pm 0.12$ ; Table 2) was significantly lower than the average band sharing score between adults on Grande-Terre ( $\bar{x} = 0.43 \pm 0.11$ ; Mann Whitney  $U = 72721$ ,  $P < 0.001$ ; Table 2). The  $F_{st}$  estimate between islands was 0.07. The distribution of band sharing scores of adults compared between islands ( $\bar{x} = 0.34 \pm 0.11$ ) overlapped completely with the distribution of band sharing scores between adults on Basse-Terre (Table 2).

The average band sharing score between mated pairs was  $0.52 \pm 0.12$  (Table 2), which was in the range of first-order relatives (Table 2). However, the majority of individual scores between pairs ( $n = 31$ ) were below the lower 95% CI for first-order relatives (Table 2). A small proportion ( $n = 5$ ; 14%) of mated pairs had band sharing above the lower 95% CI for first-order relatives, indicating that

some inbreeding occurred. Furthermore, band sharing scores between mated pairs on Grande-Terre were significantly higher than band sharing scores between adults population-wide on Grande-Terre (Mann-Whitney  $U = 5111.5$ ,  $P < 0.000$ ) as well as compared to random pairings of males and females (Mann-Whitney  $U = 1935$ ,  $P < 0.000$ ), suggesting that mating may not have been random (Table 2). Band sharing scores did not fall in the lower range of the population-wide band sharing distribution (i.e.,  $< 0.30$ ), indicating that mating between individuals with the lowest levels of relatedness (low genetic similarity) did not occur (Table 2).

The adult male and female present at 16 of the 17 nests we analyzed for parentage were identified as the biological parents based on our band sharing and novel fragment analyses. The adult female at the 17th nest was determined to be the mother of the three nestlings based on band sharing scores ( $D = 0.83, 0.67, 0.68$ ), but the adult male was not the father ( $D = 0.38, 0.42, 0.42$  and six novel fragments). Based on these data, “extra-pair paternity broods” comprised 6% of the Guadeloupe Woodpecker breeding population.

#### DISCUSSION

Our results suggest that the Guadeloupe Woodpecker populations on Basse-Terre and Grande-Terre are not genetically isolated. Individuals have not been directly observed dispersing between islands, but mark-resight data indicates that individuals dispersed distances  $> 1$  km. However, the effective gene flow appears to be from Grande-Terre to Basse-Terre, which may act to maintain genetic variation and decrease the potential for inbreeding on Basse-Terre. The higher average band sharing between adults on Grande-Terre may be attributed to the smaller population size and lower rate of immigration, which could be an effect of habitat loss. Mark-resight data revealed some natal philopatry

Table 2. DNA fingerprinting results (i.e. mean, low, and high band sharing values) for 71 adults (36 male, 35 female) and 17 families (4 on Basse-Terre and 13 on Grande-Terre) with 41 nestlings in Guadeloupe.

Comparison	$n^a$	$\bar{x} \pm SD$	Low	High
Mated pairs Basse-Terre	5	0.50 $\pm$ 0.16	0.34	0.73
Mated pairs Grande-Terre	31	0.53 $\pm$ 0.11	0.30	0.79
Mated pairs both islands	36	0.52 $\pm$ 0.12	0.30	0.79
Adults within Basse-Terre	433	0.34 $\pm$ 0.12	0.06	0.73
Adults within Grande-Terre	602	0.43 $\pm$ 0.11	0.07	0.82
Adults between Basse and Grande	993	0.34 $\pm$ 0.11	0.05	0.73
Parents to nestlings	212	0.68 $\pm$ 0.10	0.41	0.93
Novel bands in nestlings	41	0.87 $\pm$ 1.10	0	6
Siblings	95	0.71 $\pm$ 0.11	0.42	0.93
First order relatives <sup>b</sup>	307	0.70 $\pm$ 0.10	0.41	0.93

<sup>a</sup>number of pairwise comparisons<sup>b</sup>95% confidence interval = 0.68-0.71

and high breeding area fidelity in the Guadeloupe Woodpecker, which may also have contributed to the observed population genetic structure.

The population on Basse-Terre is larger than Grande-Terre and had lower average band sharing, which is comparable to outbred wild populations of birds from around the world ( $\bar{x} = 0.28 \pm 0.05$ , range = 0.23 to 0.35 for six species; Piper and Rabenold 1992, Fleischer *et al.* 1994, Dickinson and Akre 1998, Haydock *et al.* 2001, Pereira and Wajntal 2001, Arsenault *et al.* 2005). The average population-wide band sharing between adults on Grande-Terre was considerably higher than what has been reported for another *Melanerpes* (0.23 for Acorn Woodpecker, *Melanerpes formicivorus*; Dickinson *et al.* 1995). The population on Grande-Terre represents approximately a quarter of the total Guadeloupe Woodpecker population. Habitat loss on Grande-Terre will certainly reduce the total population size, which was recently estimated at 2,410 pairs (Villard and Rousteau 1998). Fragmentation of the remaining habitat may have profound effects on the population's persistence and the maintenance of genetic variation.

Endemic island birds are particularly vulnerable to extinction compared to mainland birds (Brook and Kikkawa 1998), which is largely due to habitat loss and fragmentation (Naka *et al.* 2002, Riley 2002). Habitat loss is the main reason for decline, endangerment, or extirpation of woodpecker populations, which is particularly true for island species

such as the Okinawa Woodpecker (*Sapheopipo noguchii*, <100 individuals remaining) and Fernandina's Flicker (*Colaptes fernandinae*, approximately 300 pairs; Winkler *et al.* 1995). Habitat loss has contributed to the decline of the Guadeloupe Woodpecker population, and restricted dispersal between the two remaining sub-populations challenges the maintenance of genetic variation in this species. Computer simulation modeling has shown that restricted dispersal can result in increased levels of inbreeding and loss of genetic variation (Gilpin 1991). In Guadeloupe, continued loss and fragmentation of the remaining habitat could lead to extinction of the Grande-Terre population. Fortunately, much of the Basse-Terre population is protected within Guadeloupe National Park, but it is unknown if this is a large enough protected area to support the long-term persistence of the Guadeloupe Woodpecker.

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