



Small-Scale Fragmentation Effects on Local Genetic Diversity in Two Phyllostomid Bats with Different Dispersal Abilities in Panama

Christoph F. J. Meyer^{1,4}, Elisabeth K. V. Kalko^{1,2}, and Gerald Kerth³

¹Institute of Experimental Ecology, University of Ulm, Albert-Einstein Allee 11, 89069 Ulm, Germany

²Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Panama

³Department of Ecology and Evolution, University of Lausanne, Biophore, CH-1015 Lausanne, Switzerland

ABSTRACT

Habitat fragmentation is one of the greatest threats to biodiversity. Despite their importance for conservation, the genetic consequences of small-scale habitat fragmentation for bat populations are largely unknown. In this study, we linked genetic with ecological and demographic data to assess the effects of habitat fragmentation on two species of phyllostomid bats (*Uroderma bilobatum* and *Carollia perspicillata*) that differ in their dispersal abilities and demographic response to fragmentation. We hypothesized that population differentiation and the effect of habitat fragmentation on levels of genetic diversity will be a function of the species' mobility. We sequenced mtDNA from 232 bats caught on 11 islands in Gatún Lake, Panamá, isolated from the mainland for ca 90 yr, and in adjacent, continuous forest on the mainland. Populations of both species showed significant genetic differentiation (F_{ST}). Consistent with our prediction, population subdivision was lower in the highly mobile *U. bilobatum* ($F_{ST} = 0.01$) compared to the less vagile *C. perspicillata* ($F_{ST} = 0.06$), and only the latter species showed a pattern indicative of isolation by distance and, in addition, an effect of fragmentation. Genetic erosion as a result of fragmentation was also only detectable in the less mobile species, *C. perspicillata*, where haplotype diversity was lower in island compared to mainland populations. Our results suggest that some Neotropical bat species are prone to loss of genetic variation in response to anthropogenic small-scale habitat fragmentation. In this context, our findings point toward mobility as a good predictor of a species' vulnerability to fragmentation and altered population genetic structure.

Key words: Chiroptera; habitat fragmentation; isolation by distance; land-bridge islands; population genetic structure.

THE CORRELATED PROCESSES OF HABITAT LOSS AND FRAGMENTATION constitute the greatest threat to biodiversity worldwide (e.g., Diamond 1984). In tropical regions habitat loss due to deforestation is particularly severe and conversion of native forests into human-modified landscapes continues unabated (Whitmore 1997, Wright 2005), resulting in widespread habitat fragmentation (Wade *et al.* 2003). Loss of suitable habitat and fragmentation make populations more vulnerable to environmental, genetic, and demographic threats because they reduce their size and confine the remaining subpopulations to isolated patches (Lande 1993). This results in a loss of overall genetic diversity and an increase in genetic differentiation among populations due to genetic drift and reduced gene flow (Frankham 1996, Dudash & Fenster 2000, Lindenmayer & Peakall 2000).

Like many other groups of animals, bats are at risk from habitat destruction and fragmentation (Racey & Entwistle 2003), especially in tropical lowland forests where they are particularly species rich. Tropical bats are among the ecologically most diverse mammals present in local communities, filling pivotal roles as pollinators, seed dispersers, and predators (Kalko 1998, Patterson *et al.* 2003). Recent molecular studies have provided a wealth of new insights with respect to population structuring in migratory versus non-migratory species, social organization, and effects of geographical barriers on gene flow (reviewed in Burland & Worthington Wilmer 2001). At macro-geographical scales it has been shown that, with

few exceptions (e.g., Miller-Butterworth *et al.* 2003), migratory bat species typically exhibit low levels of genetic differentiation, indicating high levels of gene flow among populations (Wilkinson & Fleming 1996, Petit & Mayer 1999, Russell *et al.* 2005). In contrast, for nonmigratory species several studies have demonstrated considerable genetic population structuring (Burland *et al.* 1999, Kerth *et al.* 2000, Rossiter *et al.* 2000). Pronounced population divergence and isolation by distance in nonmigratory bat species may be the result of a variety of factors, including limited dispersal ability (Burland *et al.* 1999, Entwistle *et al.* 2000), social factors (Kerth *et al.* 2002), geographical barriers to gene flow (Castella *et al.* 2000, Carstens *et al.* 2004), and historical events (Ditchfield 2000, Burland & Worthington Wilmer 2001).

Dispersal is a fundamental life-history trait affecting gene flow, and dispersal ability has been demonstrated to be negatively correlated with genetic population structure across a range of taxonomic groups (Waser & Strobeck 1998, Bohonak 1999). At the genetic level, one could assume that bats may be relatively unaffected by local-scale habitat fragmentation because their ability to fly may allow them to move relatively easily between habitat patches. A recent study on the temperate Bechstein's bat (Kerth & Petit 2005), however, showed that forest fragmentation can have a considerable effect on the genetic population structure of bats as it creates a sex-specific barrier to gene flow, impeding colonization of empty patches by females.

We are not aware of any study assessing the effects of forest fragmentation on genetic variation in tropical bats on a microgeographic scale despite the profound impact habitat

Received 27 February 2008; revision accepted 20 May 2008.

⁴Corresponding author; e-mail: christoph.meyer@uni-ulm.de

fragmentation is likely to have on the genetic structure and persistence of populations and the importance of forests for bats. The relatively few studies assessing the genetic population structure of tropical bats mainly investigated patterns over larger spatial scales (Wilkinson & Fleming 1996, Ditchfield 2000, Carstens *et al.* 2004, Roberts 2006) or examined the genetic structure of social groups, in particular levels of colony relatedness and differentiation (McCracken & Bradbury 1977, Wilkinson 1985, Dechmann *et al.* 2007).

Mark–recapture data and radio tracking studies indicate that Neotropical bat species differ widely in their mobility (*e.g.*, Bernard & Fenton 2003, Albrecht *et al.* 2007, Bonaccorso *et al.* 2007, Meyer *et al.* 2008). We expect that species exhibiting different mobility during nightly foraging activities should also differ in their dispersal abilities when leaving their natal group. Consequently, Neotropical bats may evince different levels of genetic population structuring, as has been demonstrated for two species of nectar-feeding bats (Newton *et al.* 2003).

In this study, we linked demographic with genetic data to explore the consequences of small-scale habitat fragmentation for two syntopic species of phyllostomid bats that differ in their dispersal abilities. The two species (*U. bilobatum* and *C. perspicillata*) were sampled as part of a comprehensive project investigating fragmentation effects on Neotropical bats within a landscape of small forested islands in Gatún Lake, an artificial reservoir in central Panamá (Meyer *et al.* 2008; Meyer & Kalko 2008, in press). These islands offer unique advantages for studying the influence of fragmentation on bat population genetic structure. First, the exact date of their origin and their history in terms of land use are known. Second, the matrix around the islands (water) differs drastically from the forest habitat on the islands, enhancing the effective isolation of

the habitat patches (Ricketts 2001). Comparatively resistant matrix types, such as water, are likely to result in particularly low levels of gene flow, leading to genetic erosion in isolated populations. This scenario is reinforced by the fact that some bat species are known to be reluctant to fly over open bodies of water (*e.g.*, Albrecht *et al.* 2007).

We assessed genetic diversity and differentiation within and among island and mainland populations of the two phyllostomid bat species using mitochondrial DNA. Our aim was to infer levels of population connectedness in a landscape that had been fragmented *ca* 90 yr ago as a result of human activities. In a first step, we tested the hypothesis that genetic differentiation within and between mainland and island populations will be a function of geographical distance (isolation by distance) and/or fragmentation and that such an effect will be lower for the species with high vagility (*U. bilobatum*) than for the less mobile species (*C. perspicillata*). In a second step, we tested whether island populations differed from mainland populations with respect to genetic diversity.

METHODS

STUDY AREA.—In 1914, the impoundment of the Chagres River in central Panamá as part of the construction of the Panama Canal led to the creation of a large artificial reservoir, Gatún Lake. Lake formation isolated numerous former hilltops, resulting in over 200 forested islands ranging in size from < 1 ha to the 1560 ha Barro Colorado Island (BCI) (Adler & Seamon 1991). Together with five adjacent mainland peninsulas, BCI forms the 5400-ha Barro Colorado Nature Monument (BCNM). The BCNM is contiguous with Soberanía National Park, 22,000 ha of forest stretching along the eastern side of the canal (Fig. 1). Forests in the Panama Canal

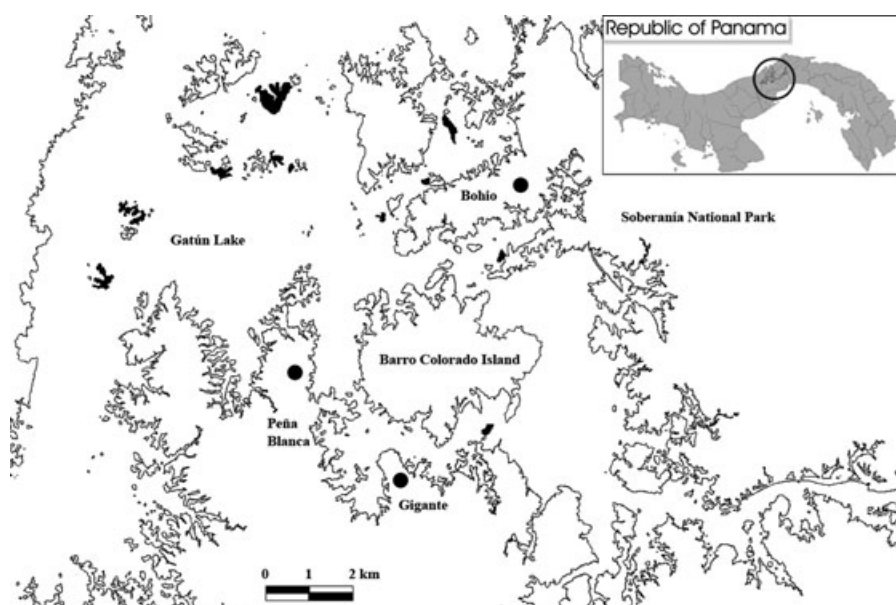


FIGURE 1. Map of the study area in the Panama Canal area in central Panamá (inset). Study islands in Gatún Lake and continuous forest sites on the peninsulas Bohío, Gigante, and Peña Blanca within the BCNM are highlighted in black.

corridor are classified as semi-deciduous, lowland tropical moist forest (Holdridge 1967). The study area experiences a strongly seasonal climate with a long rainy season punctuated by a severe dry season typically lasting from mid-December to April or May (Windsor 1990). Strong and persistent dry-season trade winds have a major impact on forest structure and dynamics particularly on exposed islands where forest is less diverse in tree species composition, typically shorter in stature and large trees are often scarce (Leigh *et al.* 1993).

STUDY SPECIES.—Choice of the two focal species was mainly based on their abundance on the study islands to obtain appropriate sample sizes and on availability of quantitative data with regard to dispersal abilities. Based on these criteria, we selected *U. bilobatum* and *C. perspicillata* for our analysis. Both species are forest-dwelling bats comparable in size (17 and 18 g, respectively) adapted to forage in cluttered situations but otherwise differ from one another in a range of ecological attributes. In previous studies (Meyer *et al.* 2008, Meyer & Kalko in press) *U. bilobatum* differed from *C. perspicillata* in its demographic response to fragmentation. While *U. bilobatum* was rare on the mainland but increased substantially in abundance on the islands, *C. perspicillata* was a common understory bat regularly captured in mainland forest but was lower in abundance on the islands.

Several lines of evidence suggest that the two species differ in their dispersal ability. Mark–recapture data indicate that *U. bilobatum* and *C. perspicillata* both fly over open water (Meyer & Kalko in press), however, *U. bilobatum* clearly is the more mobile of the two species. Its mean recapture distances are significantly larger than in *C. perspicillata*, which appears to be more reluctant to cross water (Table 1). Differential mobility in the two species at least partly reflects differences in their main diet. *Uroderma bilobatum* mostly eats fruits of figs (*Ficus* sp.) in the canopy. Fig trees produce large fruit crops but ripen asynchronously and hence constitute an ephemeral and patchily distributed food resource (*e.g.*, Wendeln *et al.* 2000), necessitating long-distance commutes and large home ranges. In contrast, understory frugivores like *C. perspicillata* primarily exploit steadily fruiting plants like *Piper* sp., a predictable resource in space and time (Fleming 1988, Thies & Kalko 2004, Bonaccorso

et al. 2007), and therefore have much smaller area requirements. *Carollia perspicillata* is an important seed disperser of pioneer plants throughout lowland Neotropical forests (Fleming 1988).

Limited foraging ranges and lower vagility in *C. perspicillata* compared to *U. bilobatum* are further supported by ecomorphological evidence as the two species differ significantly in aspect ratio and wing loading (Table 1; see also Meyer & Kalko 2008). Bats characterized by high wing loading and aspect ratio wings, such as *U. bilobatum*, are typically fast and efficient flyers while those with shorter and broader wings, such as *C. perspicillata*, have higher maneuverability in cluttered habitats but increased costs for long-distance flights (Norberg & Rayner 1987). Overall, this translates into a higher extinction risk (Jones *et al.* 2003, Safi & Kerth 2004).

SAMPLING PROCEDURE.—Genetic samples were obtained from bats captured at the same sites used for the demographic study (Fig. 1; Meyer & Kalko in press), 11 islands differing in size (2.5–50 ha) and degree of geographic isolation from the nearest mainland (0.02–3.4 km) as well as three mainland peninsulas within the BCNM (Bohio, Gigante, and Peña Blanca). For our analysis, we assumed that mainland populations were representative of prefragmentation populations and provide the source pool for rescuing or replacing island populations (*sensu* Brown & Kodric-Brown 1977) that had been reduced to low numbers or locally went extinct following inundation. Bats were captured with mist nets. Upon capture, individuals were identified, weighed, sexed, and individually marked with ball-chain necklaces prior to release (for details see Meyer & Kalko 2008). Wing tissue samples were collected using 3-mm diameter biopsy punches (Stiefel Laboratories Inc, Germany) following Worthington Wilmer and Barratt (1996). Biopsies were stored in 96 percent ethanol (VWR International Ltd., UK) until DNA extraction. Tissue samples were obtained from a total of 232 bats; the number of individuals sampled per species and the sampling locations are given in Table 2.

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING.—We extracted DNA from wing tissue samples using a salt-chloroform method (Müllenbach *et al.* 1989). Double-stranded mitochondrial

TABLE 1. Comparison of the movement capabilities of the two study species of bat (*U. bilobatum* and *C. perspicillata*) based on mark–recapture and wing morphological data. Statistical differences between species were assessed with a two-sample permutation test.

		<i>Uroderma bilobatum</i>	<i>Carollia perspicillata</i>	P
Recaptures ^a	Marked	2134	1654	
	Total recaptured	54	52	
	Same-site	17	22	
	Extra-site	37	30	
	Mean distance (km) ± SD (max)	1.40 ± 0.98 (3.51)	0.74 ± 0.60 (2.1)	0.002
Wing morphology ^b	Aspect ratio ± SD (N)	6.05 ± 0.26 (9)	5.69 ± 0.29 (21)	0.003
	Relative wing loading ± SD (N)	21.52 ± 2.44 (9)	19.93 ± 1.72 (21)	0.047

^aThis study, Kalko *et al.* 1996; E. Kalko, pers. obs.

^bMeyer *et al.* 2008, D. von Staden and E. Kalko, pers. comm.

TABLE 2. Genetic data of *U. bilobatum* and *C. perspicillata* sampled on Gatún Lake islands and on adjacent mainland peninsulas. Sample size (N bats) and, for populations with more than five individuals, local number of haplotypes (N haplotypes) and local haplotype diversity (HD) are given. For islands, size and distance to the mainland is presented (see text for further details).

Site	Island		<i>Uroderma bilobatum</i>			<i>Carollia perspicillata</i>		
	Size (ha)	Distance from mainland (m)	N bats	N haplotypes	HD	N bats	N haplotypes	HD
Cacao	12.8	155	12	6	0.88	1		
Chicha	2.8	510	10	7	0.93	0		
Guacha	7.2	2247	0			6	4	0.87
Guanábano	16.3	1420	10	7	0.93	0		
Guava	2.5	1930	17	10	0.88	2		
León	50	1544	16	13	0.97	8	5	0.86
Mona Grita	5.9	248	10	8	0.96	5	4	0.9
Pato Horqueta	11.4	3404	14	9	0.88	7	4	0.81
Piña ^a	4.4	20	13	9	0.92	1		
Tres Almendras	3.4	145	11	8	0.93	0		
Trinidad	17.3	2020	4			12	7	0.86
Mainland								
Bohio			12	9	0.96	16	15	0.99
Gigante			17	11	0.95	6	6	1
Peña Blanca			5	5	1	17	12	0.94

^aIsland #8 in Adler & Seamon (1991).

DNA from the control region (d-loop) was amplified from total cellular DNA using the polymerase chain reaction with one primer pair (primer E: 5'-CCT GAA GTA GGA ACC AGA TG-3', Wilkinson & Chapman 1991; and primer P*: 5'-CCC CAC CAT CAA CAC CCA AAG CTG A-3', Wilkinson *et al.* 1997). To obtain sequences of about 340 bp in length, 20–50 ng of mtDNA was amplified using 1 × Amplimix buffer (Microsynth; including 1.5 mM MgCl₂, and 0.2 mM dNTP mix), 0.5 units taq polymerase (Pharmacia), and 0.24 μM of each primer. All ingredients are given in final concentrations. Total reaction volume was 25.0 μL. A PTC-200 thermocycler (MJ Research) was programmed to perform 31 cycles of 94°C/30 sec, 55°C/45 sec, 72°C/60 sec after an initial 94°C/4 min step and followed by 72°C/20 min. We tested 5 μL of the PCR-product on a 1.4 percent agarose gel (1 h: 4.5 V/cm) stained with ethidium bromide. PCR products were purified using the ExoSAP-IT USB Corporation purification kit (37°C/15 min and 80°C/20 min). As a previous study on another phyllostomid bat species had confirmed the reliability of sequencing this part of the d-loop (Dechmann *et al.* 2007), we sequenced all samples in only one direction (P*) using the ABI prism Big Dye Terminator cycle sequencing ready reaction kit (Applied Biosystems). We ran the resulting PCR products on an ABI Prism 3730 48 capillary sequencer. Data were exported with Sequencing Analysis 3.4 (Applied Biosystems) and sequences were aligned and edited with Sequencher 4.1 (Gene Codes Corp).

DATA ANALYSIS.—We counted the number of haplotypes (sequences differing by their number and/or pattern of variable sites) per sampled site to quantify the genetic structure of local bat populations. The overall population structure analyses were based on an estimate of F_{ST} as implemented in FSTAT 2.9.3 (Goudet 1995). We

used a log-likelihood G -test to test for population differentiation, not assuming random mating (Goudet *et al.* 1996). To test for isolation by distance and the effect of fragmentation, we performed partial Mantel-tests. We compared matrices of pairwise F_{ST} -values to matrices coding for the geographical distances and fragmentation between the sampling sites (islands were coded as fragments [1], mainland as continuous habitat [0]; compare Kerth & Petit 2005). Based on the haplotype frequencies, we also estimated local haplotype diversity, which is defined as the likelihood that two individuals randomly chosen from a population carry different haplotypes. We then compared haplotype diversities for each species between islands and mainland sites, using a randomization test, to investigate whether island populations differed in genetic diversity from mainland populations. Only populations with at least five sampled individuals were included in calculations of F_{ST} -values and haplotype diversities. All calculations were performed using FSTAT 2.9.3. Two-sided significance levels were estimated through 10,000 permutations.

To quantify genetic distances between sequences we calculated mean pairwise differences for each species, using Arlequin 2.0 (Schneider *et al.* 2000). Deletion and transition weights were set to 1 and we allowed for 5 percent of missing data. Indels were coded as point mutations.

RESULTS

URODERMA BILOBATUM.—Among the 151 bats sequenced for 337 bp we detected 35 variable sites, resulting in a total of 43 haplotypes. The mean (\pm SD) number of pairwise distances

between haplotypes was 4.5 ± 2.3 (range: 1–11). On average, each type was present at 2.4 locations. Haplotypes were not equally distributed among the sampled sites. The same haplotype was found in a maximum of 11 sites and 23 of the 43 types were found only in a single site. The total population ($N = 12$ sites with at least five bats sampled) showed a low F_{ST} -value (0.01) but was significantly differentiated (G -test, $P < 0.05$). The differentiation was very similar among the three mainland sites and across the nine islands (F_{ST} : 0.01 vs. 0.01; $P = 0.98$) and we found neither a significant effect of isolation by distance ($P = 0.89$) nor of fragmentation ($P = 0.86$). Haplotype diversity was lower in the island populations (0.92) than in the mainland populations (0.96), however, this difference was not significant ($P = 0.11$; Fig. 2).

CAROLLIA PERSPICILLATA.—We detected 51 variable sites among the 81 bats sequenced for 337 bp, resulting in a total of 41 haplotypes. The mean number of pairwise distances between haplotypes (11.1 ± 5.4 ; range: 1–26) was higher than in *U. bilobatum*. The different haplotypes were rather equally distributed among the sampled sites. On average, each type was present in 1.5 locations. The same haplotype was found in a maximum of four sites and 29 of the 41 haplotypes were found only in a single site. The population ($N = 8$ sites) was significantly differentiated ($F_{ST} = 0.06$, $P < 0.02$), with island populations being significantly more differentiated ($F_{ST} = 0.10$) than mainland populations ($F_{ST} = 0.00$; $P < 0.02$). Moreover, we found a significant effect of both, isolation by distance ($P < 0.05$) and fragmentation ($P < 0.02$). Finally, island populations had significantly lower haplotype diversities (0.86) than mainland populations (0.97; $P < 0.02$; Fig. 2).

DISCUSSION

The idea that population structure in bats may be associated with species' intrinsic characteristics such as mobility, reflected by wing morphology, was first discussed for the nonmigratory long-eared bat, *Plecotus auritus* (Burland *et al.* 1999, Entwistle *et al.* 2000). Since then evidence for it has been found in three migratory bats (Miller-Butterworth *et al.* 2003, Newton *et al.* 2003). Our results corroborate these findings for nonmigratory Neotropical bats and suggest that, as advocated by Burland and Worthington Wilmer (2001), explicitly linking intrinsic attributes to population structure may generally serve as a useful predictive framework for population genetic analyses. Although populations of both species exhibited significant mtDNA haplotype divergence and even though our sample sizes were in part rather limited, the relative estimates of genetic differentiation based on F_{ST} were consistent with our prediction and matched the relative movement ability of the two species estimated on the basis of mark–recapture and wing morphological data (Table 1). Populations of the canopy frugivore *U. bilobatum* were overall only weakly differentiated ($F_{ST} = 0.01$) while genetic subdivision was higher in the understory frugivore *C. perspicillata* ($F_{ST} = 0.06$). The relatively low levels of genetic differentiation suggest that there is regular exchange of individuals of *U. bilobatum* and, although probably to a much lesser extent, of *C. perspicillata*,

between islands. The interpretation of more restricted inter-island dispersal in *C. perspicillata* compared to *U. bilobatum* is supported by the significant pattern of isolation by distance observed only in the former species.

While significant population differentiation and genetic isolation by distance has been documented for several tropical bat species at larger geographic scales (Maharadatunkamsi *et al.* 2000, Newton *et al.* 2003), to our knowledge, only two studies on the temperate zone bats, *P. auritus* (Burland *et al.* 1999) and *Myotis bechsteinii* (Kerth & Petit 2005), have described isolation by distance and significant population differentiation at a microgeographical scale comparable to that of our study. For other groups of vertebrates such as birds (Bates 2002, Brown *et al.* 2004) and small nonvolant mammals (Gaines *et al.* 1997), studies of habitat fragmentation have also mainly focused on geographic areas much larger than the scale of our study, typically reporting significant levels of population subdivision. However, some recent studies on small mammals (Lindenmayer & Peakall 2000, Mossman & Waser 2001), discovered significant interpopulation differentiation at a scale comparable to our study.

Levels of population genetic differentiation in our study species were proportionate to the respective species' dispersal ability and such an effect was also evident for the reduction of genetic diversity on islands (Fig. 2). Although haplotype diversity on islands compared to continuous forest was also somewhat lower in *U. bilobatum*, this effect was only significant in the less mobile *C. perspicillata*. Moreover, only in *C. perspicillata* did we detect significantly higher levels of population structuring among island compared to mainland populations. Together with the observed lower genetic diversities in island than in mainland populations (Fig. 2), this finding is suggestive of an isolation effect caused by the formation of the islands. We are aware that our sample size for *C. perspicillata* is small due to the low number of captures of this species on the

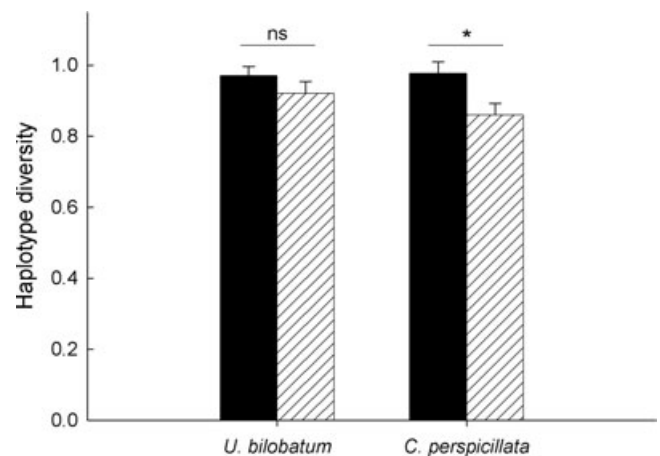


FIGURE 2. Comparison of haplotype diversities (mean \pm SD) between mainland (full bars) and island (striped bars) populations for the two study species. Significant differences (randomization test) are indicated by an asterisk ($*P < 0.05$, ns = nonsignificant).

islands and that our results should therefore be interpreted with caution. Nonetheless, the genetic effects observed in *C. perspicillata* follow a clear trend and appear strong enough that they are likely to hold also with larger sample sizes for this species. This is suggested by very similar haplotype diversities observed in better-sampled island populations such as the one on Trinidad ($N = 12$) compared to islands like Guacha for which sample sizes were low ($N = 6$; Table 2). It is further supported by a general lack of a significant correlation between haplotype diversity and sample size ($r_s = 0.036$, $P = 0.93$).

Our choice of genetic marker (mtDNA) does not allow us to explore the potential reasons for the indicated fragmentation effect but our data are consistent with at least two scenarios: (1) Temporal population reductions of prelake populations shortly after the fragmentation event may have resulted in reduced genetic variability in the surviving island populations because of genetic drift; (2) founder effects due to the colonization of islands, where no prelake populations had survived, by a limited number of individuals would also explain lower genetic diversities in island populations. A follow-up study using genetic markers with a higher temporal resolution, such as nuclear microsatellites, and preferably involving larger sample sizes could provide more insight concerning the question of what caused the observed lower genetic diversity on islands. Moreover, the use of microsatellites, which are biparentally inherited, would give a more complete and unbiased view of gene flow compared to mtDNA, which due to its maternal inheritance, has the limitation to provide only information on female-mediated gene flow.

It is increasingly being advocated to jointly consider genetic and demographic data to fully unravel species' responses to fragmentation (Lindenmayer & Peakall 2000, Srikwan & Woodruff 2000, Tallmon *et al.* 2002). Srikwan and Woodruff (2000), studying genetic erosion in nonvolant small mammal populations on land-bridge islands in Thailand, reported genetic erosion for a species that was favored by fragmentation and showed no signs of demographic decline. Although not significant, we also found slightly reduced haplotype diversity in island compared to mainland populations for *U. bilobatum*, a species that increased in abundance following fragmentation. Significant loss of genetic diversity was, however, most evident in *C. perspicillata*, which was characterized by a negative demographic response to fragmentation in our study system (Meyer *et al.* 2008). Interestingly, higher abundances for this species are observed in fragmented landscapes where forest remnants are surrounded by forest regrowth (*Piper*, *Vismia*) that provides additional food resources (*e.g.*, Faria 2006).

Our findings therefore suggest that, in fragmented landscapes with a high degree of fragment to matrix contrast like in our study (land to water), bat species with limited dispersal capacity like *C. perspicillata* and that evince a pronounced demographic decline may experience a considerable loss of genetic diversity. Although this remains to be tested in future studies, similar effects could also be envisaged for systems with a terrestrial but similarly high-contrast matrix as in our study, for instance in fragmented landscapes where small forest fragments are embedded in a matrix of crop monocultures (*e.g.*, soy, corn, sugarcane) or vast stretches of pasture without any shrubs or trees, situations that are becoming increasingly

common in many tropical regions. Because neither of these types of matrix offers bats any resources or shelter, they come close to the characteristics of a water matrix, particularly in terms of their effective isolation. From a conservation viewpoint, negative genetic and demographic effects in such terrestrial high-contrast systems could be mitigated through management efforts that promote vegetation regrowth along forest edges. This would decrease the effective isolation of habitat remnants, enhance landscape connectivity, and ensure maintenance of species numbers and also continued functioning of the ecosystem services provided by bats, in particular seed dispersal (Meyer *et al.* 2008).

In conclusion, we found that in spite of their mobility, differences in vagility among species may render less mobile species of Neotropical bats susceptible to loss of genetic variation in response to habitat fragmentation already on a local scale. Such genetic erosion can apparently manifest itself even after fairly short periods of time following fragmentation. In accordance with previous findings from comparative studies (*e.g.*, Safi & Kerth 2004), our results suggest that a bat species' dispersal ability can serve as a good predictor of fragmentation-related genetic effects and population genetic differentiation. Further comparative studies across a range of bat species focusing on local geographic scales are undoubtedly needed to broaden our knowledge as to the genetic consequences of habitat fragmentation for bat populations and are a prerequisite for the formulation of broad-scale conservation strategies for bats.

ACKNOWLEDGMENTS

We are grateful to L. Berset-Brändli, T. Broquet, J. Jacquiéry, N. Perrin, B. Fenton, B. Patterson, and two anonymous reviewers for helpful comments on the manuscript. We cordially thank J. Garbely for the genetic lab work. We thank the Smithsonian Tropical Research Institute for logistical support and the Autoridad del Canal de Panamá for permission to work on the islands in Gatún Lake. We would further like to thank the following people for help with fieldwork: A. Bravo, K. Bürger, S. Estrada Villegas, J. Fründ, I. Geipel, N. Herdina, A. Lang, J. Nagel, A. Reside, R. Rodriguez, A. Sjollem, C. Stubenrauch, and C. Weise. Financial support was provided by a grant from the German Academic Exchange Service (DAAD) to CFJM and two grants from the German Science Foundation (DFG) to EKVK and GK, respectively.

LITERATURE CITED

- ADLER, G. H., AND J. O. SEAMON. 1991. Distribution and abundance of a tropical rodent, the spiny rat, on islands in Panama. *J. Trop. Ecol.* 7: 349–360.
- ALBRECHT, L., C. F. J. MEYER, AND E. K. V. KALKO. 2007. Differential mobility in two small phyllostomid bats, *Artibeus watsoni* and *Micronycteris microtis*, in a fragmented Neotropical landscape. *Acta Theriol.* 52: 141–149.
- BATES, J. M. 2002. The genetic effects of forest fragmentation on five species of Amazonian birds. *J. Avian Biol.* 33: 276–294.
- BERNARD, E., AND M. B. FENTON. 2003. Bat mobility and roosts in a fragmented landscape in Central Amazonia, Brazil. *Biotropica* 35: 262–277.

- BOHONAK, A. J. 1999. Dispersal, gene flow, and population structure. *Quart. Rev. Biol.* 74: 21–45.
- BONACCORSO, F. J., J. R. WINKELMANN, D. SHIN, C. I. AGRAWAL, N. ASLAMI, C. BONNEY, A. HSU, P. E. JEKIELEK, A. K. KNOX, S. J. KOPACH, T. D. JENNINGS, J. R. LASKY, S. A. MENESALE, J. H. RICHARDS, J. A. RUTLAND, A. K. SESSA, L. ZHAUROVA, AND T. H. KUNZ. 2007. Evidence for exploitative competition: Comparative foraging behavior and roosting ecology of short-tailed fruit bats (Phyllostomidae). *Biotropica* 39: 249–256.
- BROWN, J. H., AND A. KODRIC-BROWN. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* 58: 445–449.
- BROWN, L. M., R. R. RAMEY, B. TAMBURINI, AND T. A. GAVIN. 2004. Population structure and mitochondrial DNA variation in sedentary Neotropical birds isolated by forest fragmentation. *Conserv. Gen.* 5: 743–757.
- BURLAND, T. M., AND J. WORTHINGTON WILMER. 2001. Seeing in the dark: Molecular approaches to the study of bat populations. *Biol. Rev.* 76: 389–409.
- BURLAND, T. M., E. M. BARRATT, M. A. BEAUMONT, AND P. A. RACEY. 1999. Population genetic structure and gene flow in a gleaning bat, *Plecotus auritus*. *Proc. R. Soc. Lond. B* 266: 975–980.
- CARSTENS, B. C., J. SULLIVAN, L. M. DAVALOS, P. A. LARSEN, AND S. C. PEDERSEN. 2004. Exploring population genetic structure in three species of Lesser Antillean bats. *Mol. Ecol.* 13: 2557–2566.
- CASTELLA, V., M. RUEDI, L. EXCOFFIER, C. IBÁÑEZ, R. ARLETTAZ, AND J. HAUSSE. 2000. Is the Gibraltar Strait a barrier to gene flow for the bat *Myotis myotis* (Chiroptera: Vespertilionidae)? *Mol. Ecol.* 9: 1761–1772.
- DECHMANN, D. K. N., E. K. V. KALKO, AND G. KERTH. 2007. All-offspring dispersal in a tropical mammal with resource defense polygyny. *Behav. Ecol. Sociobiol.* 61: 1219–1228.
- DIAMOND, J. M. 1984. “Normal” extinctions of isolated populations. *In* M. H. Nitecki (Ed.). *Extinctions*, pp. 191–246. University of Chicago Press, Chicago, Illinois.
- DITCHFIELD, A. D. 2000. The comparative phylogeography of Neotropical mammals: Patterns of intraspecific mitochondrial DNA variation among bats contrasted to nonvolant small mammals. *Mol. Ecol.* 9: 1307–1318.
- DUDASH, M. R., AND C. B. FENSTER. 2000. Inbreeding and outbreeding depression in fragmented populations. *Conserv. Biol.* 4: 35–53.
- ENTWISTLE, A. C., P. A. RACEY, AND J. R. SPEAKMAN. 2000. Social and population structure of a gleaning bat, *Plecotus auritus*. *J. Zool.* 252: 11–17.
- FARIA, D. 2006. Phyllostomid bats of a fragmented landscape in the north-eastern Atlantic forest. *J. Trop. Ecol.* 22: 531–542.
- FLEMING, T. H. 1988. *The short-tailed fruit bat: A study in plant-animal interactions*. University of Chicago Press, Chicago, Illinois.
- FRANKHAM, R. 1996. Relationship of genetic variation to population size in wildlife. *Conserv. Biol.* 10: 1500–1508.
- GAINES, M. S., J. E. DIFFENDORFER, R. H. TAMARIN, AND T. S. WHITTAM. 1997. The effects of habitat fragmentation on the genetic structure of small mammal populations. *J. Heredity* 88: 294–304.
- GOUDET, J. 1995. FSTAT (Version 1.2): A computer program to calculate F-statistics. *J. Heredity* 86: 485–486.
- GOUDET, J., M. RAYMOND, T. DE MEEUS, AND F. ROUSSET. 1996. Testing differentiation in diploid populations. *Genetics* 144: 1933–1940.
- HOLDRIDGE, L. R. 1967. Life zone ecology. *Occasional Papers of the Tropical Science Center, San José, Costa Rica*.
- JONES, K. E., A. PURVIS, AND J. L. GITTLEMAN. 2003. Biological correlates of extinction risk in bats. *Am. Nat.* 161: 601–614.
- KALKO, E. K. V. 1998. Organisation and diversity of tropical bat communities through space and time. *Zoology* 101: 281–297.
- KALKO, E. K. V., C. O. HANDLEY, JR., AND D. HANDLEY. 1996. Organization, diversity and long-term dynamics of a Neotropical bat community. *In* M. L. Cody and J. Smallwood (Eds.). *Long-term studies in vertebrate communities*, pp. 503–553. Academic Press, Los Angeles, California.
- KERTH, G., F. MAYER, AND B. KÖNIG. 2000. Mitochondrial DNA (mtDNA) reveals that female Bechstein’s bats live in closed societies. *Mol. Ecol.* 9: 793–800.
- KERTH, G., AND E. PETTIT. 2005. Colonization and dispersal in a social species, the Bechstein’s bat (*Myotis bechsteinii*). *Mol. Ecol.* 14: 3943–3950.
- KERTH, G., F. MAYER, AND E. PETTIT. 2002. Extreme sex-biased dispersal in the communally breeding, nonmigratory Bechstein’s bat (*Myotis bechsteinii*). *Mol. Ecol.* 11: 1491–1498.
- LANDE, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* 142: 911–927.
- LEIGH, E. G. JR., S. J. WRIGHT, AND E. A. HERRE. 1993. The decline of tree diversity on newly isolated tropical islands: A test of a null hypothesis and some implications. *Evol. Ecol.* 7: 76–102.
- LINDENMAYER, D., AND R. PEAKALL. 2000. The Tumut experiment—integrating demographic and genetic studies to unravel fragmentation effects: A case study of the native bush rat. *In* A. G. Young and G. M. Clarke (Eds.). *Genetics, demography and viability of fragmented populations*, pp. 173–201. Cambridge University Press, Cambridge, UK.
- MAHARADATUNKAMSI, H. S., D. J. KITCHENER, AND L. H. SCHMITT. 2000. Genetic and morphometric diversity in Wallacea: Geographical patterning in the horse shoe bat, *Rhinolophus affinis*. *J. Biogeogr.* 27: 193–201.
- MCCRACKEN, G. F., AND J. W. BRADBURY. 1977. Paternity and genetic heterogeneity in the polygynous bat, *Phyllostomus hastatus*. *Science* 198: 303–306.
- MEYER, C. F. J., AND E. K. V. KALKO. 2008. Bat assemblages on Neotropical landbridge islands: Nested subsets and null model analyses of species co-occurrence patterns. *Divers. Distrib.* 14: 644–654.
- MEYER, C. F. J., AND E. K. V. KALKO. 2008. Assemblage-level responses of phyllostomid bats to tropical forest fragmentation: Land-bridge islands as a model system. *J. Biogeogr.* doi: 10.1111/j.1365-2699.2008.01916.x.
- MEYER, C. F. J., J. FRÜND, W. PINEDA LIZANO, AND E. K. V. KALKO. 2008. Ecological correlates of vulnerability to fragmentation in Neotropical bats. *J. Appl. Ecol.* 45: 381–391.
- MILLER-BUTTERWORTH, C. M., D. S. JACOBS, AND E. H. HARLEY. 2003. Strong population substructure is correlated with morphology and ecology in a migratory bat. *Nature* 424: 187–191.
- MOSSMAN, C. A., AND P. M. WASER. 2001. Effects of habitat fragmentation on population genetic structure in the white-footed mouse (*Peromyscus leucopus*). *Can. J. Zool.* 79: 285–295.
- MÜLLENBACH, R., P. J. L. LAGODA, AND C. WELTER. 1989. An efficient salt-chloroform extraction of DNA from blood and tissues. *Trends Genet.* 5: 391–391.
- NEWTON, L. R., J. M. NASSAR, AND T. H. FLEMING. 2003. Genetic population structure and mobility of two nectar-feeding bats from Venezuelan deserts: Inferences from mitochondrial DNA. *Mol. Ecol.* 12: 3191–3198.
- NORBERG, U. M., AND J. M. V. RAYNER. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. *Philos. Trans. R. Soc. Lond. B* 316: 335–427.
- PATTERSON, B. D., M. R. WILLIG, AND R. D. STEVENS. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. *In* T. H. Kunz and M. B. Fenton (Eds.). *Bat ecology*, pp. 536–579. University of Chicago Press, Chicago, Illinois.
- PETTIT, E., AND F. MAYER. 1999. Male dispersal in the noctule bat (*Nyctalus noctula*): Where are the limits? *Proc. R. Soc. Lond. B* 266: 1717–1722.
- RACEY, P. A., AND A. C. ENTWISTLE. 2003. Conservation ecology of bats. *In* T. H. Kunz and M. B. Fenton (Eds.). *Bat ecology*, pp. 680–743. University of Chicago Press, Chicago, Illinois.
- RICKETTS, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. *Am. Nat.* 158: 87–99.
- ROBERTS, T. E. 2006. History, ocean channels, and distance determine phylogeographic patterns in three widespread Philippine fruit bats (Pteropodidae). *Mol. Ecol.* 15: 2183–2199.
- ROSSITER, S. J., G. JONES, R. D. RANSOME, AND E. M. BARRATT. 2000. Genetic variation and population structure in the endangered greater horseshoe bat *Rhinolophus ferrumequinum*. *Mol. Ecol.* 9: 1131–1135.

- RUSSELL, A. L., R. A. MEDELLÍN, AND G. F. MCCrackEN. 2005. Genetic variation and migration in the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*). *Mol. Ecol.* 14: 2207–2222.
- SAFI, K., AND G. KERth. 2004. A comparative analysis of specialization and extinction risk in temperate-zone bats. *Conserv. Biol.* 18: 1293–1303.
- SCHNEIDER, S., D. ROESSLI, AND L. EXCOFFIER. 2000. Arlequin ver. 2.000: A software for population genetics data analysis. Genetics and Biometry Laboratory, University of Geneva, Geneva, Switzerland.
- SRIKWAN, S., AND D. S. WOODRUFF. 2000. Genetic erosion in isolated small-mammal populations following rainforest fragmentation. In A. G. Young and G. M. Clarke (Eds.), *Genetics, demography and viability of fragmented populations*, pp. 149–172. Cambridge University Press, Cambridge, UK.
- TALLMON, D. A., H. M. DRAHEIM, L. SCOTT MILLS, AND F. W. ALLENDORF. 2002. Insights into recently fragmented vole populations from combined genetic and demographic data. *Mol. Ecol.* 11: 699–709.
- THIES, W., AND E. K. V. KALKO. 2004. Phenology of Neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). *Oikos* 104: 362–376.
- WADE, T. G., K. H. RIITERS, J. D. WICKHAM, AND K. B. JONES. 2003. Distribution and causes of global forest fragmentation. *Conserv. Ecol.* 7: 7.
- WASER, P., AND C. STROBECK. 1998. Genetic signatures of interpopulation dispersal. *Trends Ecol. Evol.* 13: 43–44.
- WENDELN, M. C., J. R. RUNKLE, AND E. K. V. KALKO. 2000. Nutritional values of 14 fig species and bat feeding preferences in Panama. *Biotropica* 32: 489–501.
- WHITMORE, T. C. 1997. Tropical forest disturbance, disappearance, and species loss. In W. F. Laurance and R. O. Bierregaard Jr. (Eds.), *Tropical forest remnants: Ecology, management, and conservation of fragmented communities*, pp. 3–12. University of Chicago Press, Chicago, Illinois.
- WILKINSON, G. S. 1985. The social organization of the common vampire bat. II. Mating system, genetic structure, and relatedness. *Behav. Ecol. Sociobiol.* 17: 123–134.
- WILKINSON, G. S., AND A. CHAPMAN. 1991. Length and sequence variation in evening bat D-loop mt DNA. *Genetics* 128: 607–617.
- WILKINSON, G. S., AND T. H. FLEMING. 1996. Migration and evolution of lesser long-nosed bats *Leptonycteris curasoae*, inferred from mitochondrial DNA. *Mol. Ecol.* 5: 329–339.
- WILKINSON, G. S., F. MAYER, G. KERth, AND B. PETRI. 1997. Evolution of repeated sequence arrays in the D-loop region of bat mtDNA. *Genetics* 146: 1035–1048.
- WINDSOR, D. M. 1990. Climate and moisture variability in a tropical forest: Long-term records from Barro Colorado Island, Panama. *Smith. Contr. Earth Sci.* 29: 1–145.
- WORTHINGTON WILMER, J., AND E. BARRATT. 1996. A non-lethal method of tissue-sampling for genetic studies of chiropterans. *Bat Res. News* 37: 1–3.
- WRIGHT, S. J. 2005. Tropical forests in a changing environment. *Trends Ecol. Evol.* 20: 553–560.