

4-2015

Historical and contemporary demography of leaf-toed geckos (Phyllodactylidae: Phyllodactylus) in the Mexican dry forest

Christopher Blair
CUNY New York City College of Technology


Victor H. Jiménez Arcos
Universidad Nacional Autónoma de México

Fausto R. Méndez de la Cruz
Universidad Nacional Autónoma de México

Robert W. Murphy
University of Toronto

How does access to this work benefit you? Let us know!

Follow this and additional works at: https://academicworks.cuny.edu/ny_pubs

 Part of the [Biodiversity Commons](#), [Molecular Genetics Commons](#), [Other Animal Sciences Commons](#), and the [Zoology Commons](#)

Recommended Citation

Blair C, Jimenez-Arcos VH, Mendez de la Cruz, FR, Murphy RW. 2014. Historical and contemporary demography of leaf-toed geckos (Phyllodactylidae: Phyllodactylus) in the Mexican dry forest. *Conservation Genetics* 16:419-429.

This Article is brought to you for free and open access by the New York City College of Technology at CUNY Academic Works. It has been accepted for inclusion in Publications and Research by an authorized administrator of CUNY Academic Works. For more information, please contact AcademicWorks@cuny.edu.

1 **Historical and contemporary demography of leaf-toed geckos**
2 **(Phyllodactylidae: *Phyllodactylus*) in the Mexican dry forest**

3
4 CHRISTOPHER BLAIR^{*,†}, VICTOR H. JIMÉNEZ ARCOS[‡], FAUSTO R. MÉNDEZ DE LA CRUZ[‡], ROBERT
5 W. MURPHY^{*,†}

6
7 **Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street,*
8 *Toronto, ON, M5S 3B2, Canada.*

9 *†Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, ON, M5S*
10 *2C6, Canada.*

11 *‡Laboratorio de Herpetología, Instituto de Biología, Universidad Nacional Autónoma de*
12 *México, A.P. 70-153. C.P. 04510, México*

13
14 Corresponding author and present address: Christopher Blair, Department of Biology, Duke
15 University, Box 90338, BioSci 130 Science Drive, Durham, NC 20098, USA.

16
17 Running Head: Gene flow in *Phyllodactylus* geckos

18

19

20 Abstract

21 Disentangling the relative influence of historical versus contemporary processes shaping the
22 spatial distribution of genetic variation is critical if we are to effectively mitigate key biodiversity
23 issues. We utilize a comprehensive approach based on different molecular marker types and
24 analytical methods to understand the demographic consequences of recent habitat fragmentation
25 in a spatially explicit context. We focus our efforts on native leaf-toed geckos (*Phyllodactylus*
26 *tuberculosis saxatilis*) throughout fragmented habitat in the tropical dry forest of northern
27 Mexico. Recent evidence suggests that geographic ranges for these species may be much smaller
28 than currently realized and no data are available regarding recent shifts in demographic trends
29 and how these trends may correspond with recent fragmentation and introductions of non-native
30 gecko species (*Hemidactylus*). Mitochondrial DNA sequences reveal substantial historical
31 genetic divergence over a small geographic area (<40 km). We find evidence for an increase in
32 contemporary versus historical migration rates based on 10 microsatellite loci, but evidence that
33 many populations suffer from recent reductions in effective population sizes. Landscape genetic
34 analyses find stronger correlations between landscape structure and contemporary versus
35 historical migration or mtDNA divergence, suggesting that individuals have altered their
36 dispersal routes in response to recent habitat changes. Taken together, this study suggests that
37 long-term female philopatry, recent habitat fragmentation, and possibly introductions of non-
38 native gecko species all contribute to the demographic patterns and the high degree of
39 differentiation observed over fine-spatial scales in Mexican leaf-toed geckos.

40

41 *Key Words:* Alamos; gecko; migration; mtDNA; Sonora; tropical dry forest

42

43

44 **Introduction**

45 Evidence continues to accumulate showing that rates and patterns of dispersal and gene flow can
46 be influenced by a variety of intrinsic and extrinsic factors (Ricketts 2001; Manel et al. 2003;
47 Storfer et al. 2010). Habitat fragmentation and loss due to both natural and anthropogenic forces
48 can represent a substantial threat to the maintenance and connectivity of populations (Sanderson
49 et al. 2002; Ewers and Didham 2005). Maintaining genetic connectivity is essential to allow the
50 free exchange of beneficial neutral and adaptive alleles between demes. Processes that disrupt or
51 prevent dispersal and gene flow could lead to inbreeding depression, the accumulation of
52 deleterious alleles, reduced adaptive potential, and local extinction (Fahrig 2003; Crispo et al.
53 2011).

54 With the advent and continued interest in the field of landscape genetics, there has been a
55 renewed interest in understanding the contemporary ecological processes influencing the genetic
56 structure of natural populations (see Sork and Waits 2010; Storfer et al. 2010 for review).

57 Although many of these studies have had a profound impact on what we now understand about
58 the spatial distribution of genetic variation in nature, many of these studies fail to examine the
59 influence of historical demographic processes on contemporary genetic structure (e.g. Spear et
60 al. 2005; Vignieri 2005; Wang 2009; Goldberg and Waits 2010, but see Vandergast et al. 2007;
61 Zellmer and Knowles 2009; Dyer et al. 2010). Historical demographic patterns can be examined
62 through multiple mechanisms including using historical landscape layers (Vandergast et al.
63 2007), different molecular marker types (Wang 2011), and different analytical methods
64 (Andersen et al. 2009; Schmidt et al. 2009; Chiuicchi and Gibbs 2010).

65 The tropical deciduous or dry forests (TDF) of western Mexico are home to an enormous
66 diversity of species, several of which are endemic (Robichaux and Yetman 2000; Myska 2007).
67 Dry forests are characterized by distinct wet/dry seasons, with the latter lasting up to 10 months
68 in some regions (Murphy and Lugo 1996; Robichaux and Yetman 2000). Prior to recent
69 fragmentation, Mexican TDF was a predominant ecosystem in Mexico spanning most of the
70 Pacific versant of the Sierra Madre Occidental and Sierra Madre del Sur (Robichaux and Yetman
71 2000; Becerra 2005; Cartron et al. 2005). Although the floral and faunal diversity within these
72 forests is immense, conservation efforts have historically emphasized tropical rain forests and
73 high elevation pine and pine/oak habitats, specifically throughout areas of the Mexican Volcanic
74 Belt (Pennington et al. 2000; Robichaux and Yetman 2000; García 2006). This is problematic, as
75 the annual deforestation rate for Mexican TDF is estimated at up to 1.4–2%, with approximately
76 73% of the biome altered due to agriculture and livestock (Trejo and Dirzo 2000). Indeed, some
77 authorities have concluded that TDF is one of Earth's most threatened ecosystems (Janzen 1988).

78 Leaf-toed geckos, (*Phyllodactylus*, Phyllodactylidae; Gamble et al. 2008) encompass
79 approximately 50 species distributed throughout arid and semi-arid forests of the New World
80 Tropics (Dixon 1964). In Mexico, their distribution mirrors that of TDF, making them suitable
81 models to test ecological and evolutionary hypotheses in this system. Recent work on the genus
82 has documented the presence of substantial cryptic diversity, diagnosable only with a careful
83 selection of molecular and morphological characters (Blair et al. 2009; Castiglia et al. 2009;
84 Murphy et al. 2009). There is also evidence that species that were once considered widespread
85 are actually composed of several species exhibiting limited geographic ranges (Blair et al.

86 unpublished data). Further, recent introductions of non-native gecko species of the genus
87 *Hemidactylus* also appear to directly compete with and displace leaf-toed geckos (pers. obs.).
88 These factors make leaf-toed geckos an ideal system for conservation genetics-based studies to
89 ascertain the demographic consequences of recent habitat alteration and ecosystem functioning
90 within TDF.

91 A recent landscape genetic study of *P. tuberculosus saxatilis* near Alamos, Sonora finds
92 that patterns of gene flow are correlated with multiple landscape variables including the amount
93 of undisturbed habitat (Blair et al. 2013). However, this study did not examine how demographic
94 parameters such as effective population size (N_e) and migration rates vary through time. In this
95 study we use microsatellite and mtDNA data to compare spatially explicit historical and
96 contemporary demographic parameters for leaf-toed geckos. Because of its relatively slow rate
97 of evolution, mtDNA is an ideal marker for examining the genetic consequences of evolutionary
98 processes occurring over geologic time, but may not be useful to infer complex landscape-
99 genetic relationships (Wang 2010). We specifically address the following questions: (i) How is
100 mtDNA diversity spatially structured? (ii) How do historical demographic parameters compare
101 to contemporary parameters? (iii) Do populations show evidence of recent bottlenecks? (iv) How
102 does landscape structure correlate with contemporary migration, historical migration and
103 mtDNA divergence?

104

105 **Materials and methods**

106 *Study site and tissue sampling*

107 All sampling localities were mapped in Figure 1. Microsatellite data (10 loci) for 336 individuals
108 (mean=28 individuals per locality) were obtained from a previous study (Blair et al. 2013;
109 DRYAD). Previous analyses showed no significant deviations from Hardy-Weinberg
110 expectations or linkage disequilibrium and an estimated genotyping error rate of <1% based on
111 re-running 10% of all PCRs (Blair et al. 2013). We also screened 77 individuals from 11
112 populations for mtDNA polymorphism to assess fine-scale patterns of deep lineage divergence
113 (Fig. 1; Supplementary Table S1). Individuals were captured by hand during chance encounters
114 on public, private, and protected land following permit guidelines. All tissues were preserved in
115 the field in 95% ethanol following approved animal use protocols from the Royal Ontario
116 Museum. Vouchers were fixed in the field with 10% formalin, transferred to 70% ethanol and
117 deposited in the Laboratorio de Herpetologia, Instituto de Biología, Universidad Nacional
118 Autónoma de México. Fieldwork was conducted during the summers of 2007 and 2008. DNA
119 sequences were obtained from *P. xanti* (Blair et al. 2009) and *P. homolepidurus* (this study) to
120 root all mtDNA networks. For all demographic analyses we defined a ‘population’ based on
121 collection locality.

122

123 *DNA extraction, amplification and sequencing*

124 Total genomic DNA was digested and extracted from liver or muscle tissue using standard
125 proteinase K and phenol–chloroform protocols. We amplified and sequenced 2400 base pairs
126 (bp) of mtDNA encompassing partial sequences of cytochrome *c* oxidase subunit I (COI),
127 NADH dehydrogenase subunit 4 (ND4) and adjacent tRNAs, and 16S rRNA. In addition,

128 sequences were obtained for the entire NADH dehydrogenase subunit I (NDI) gene and flanking
129 tRNAs. Amplified gene fragments, number of corresponding bp, primer sequences, and
130 references were presented in Supplementary Table S2. All PCR and sequencing conditions
131 followed Blair et al. (2009).

132
133 *mtDNA analysis*

134 Detailed analysis of the mtDNA data can be found in the Online Supplementary Materials. In
135 brief, mtDNA sequences were edited and aligned in BIOEDIT 5.0.6 (Hall 1999). Genealogical
136 relationships among individuals were assessed using both maximum parsimony (MP) and
137 Bayesian inference (BI). DNASP v.5.0 (Rozas et al. 2003) was used to calculate standard
138 diversity statistics and divergence among lineages. Isolation by distance (IBD) was assessed
139 using the Isolation By Distance Web Service (IBDWS) v.3.16 (Jensen et al. 2005).

140

141 *Historical and contemporary migration rates*

142 We used the program MIGRATE 3.2.16 (Beerli and Felsenstein 2001; Beerli 2006) to estimate
143 historical N_e and asymmetric migration rates between populations based on the microsatellite
144 data. MIGRATE uses the coalescent in a Bayesian or maximum likelihood framework to calculate
145 two parameters from the data, θ and M , where θ represents effective population size ($4N_e\mu$ for
146 nuclear DNA) and M represents the mutation-scaled immigration rate (m/μ). This coalescent-
147 based approach is most suitable for detecting migration rates over thousands of years or
148 approximately $4N_e$ generations in the past (Beerli 2008). The data were assumed to follow a
149 Brownian motion mutation model. We used the F_{ST} calculation method to generate starting values
150 for both θ and M . We specified uniform priors for both parameters with a minimum of 0, mean

151 of 50, maximum of 100, and a delta of 10. We then implemented the Bayesian method to infer Θ
152 and M , specifying two independent runs, static heating with four chains (temperatures: 1, 1.5,
153 3.0, 10,000.0), a sampling increment of 200, 5,000 recorded steps, and a burn-in of 100,000.
154 Convergence was assessed by examination of ESS values with a target of at least 1,000. We also
155 ran the program multiple times to make sure the algorithm was reaching the same posterior
156 distribution of parameter estimates. We also used MIGRATE to estimate Θ and M based on the
157 mtDNA data. Two independent Bayesian searches were performed with the same number of
158 chains and heating scheme as the microsatellite analysis. Default priors were used for Θ and a
159 uniform prior (minimum = 0, mean = 1000, maximum = 4000, delta = 400) was used for M .
160 Each independent run used 5,000 steps and a sampling increment of 500.

161 We used the Bayesian method implemented in BAYESASS EDITION 3.0 (Wilson and
162 Rannala 2003) to estimate contemporary migration rates between populations. Unlike MIGRATE,
163 BAYESASS does not assume genetic equilibrium and is therefore more suitable for inferring
164 contemporary (over the past few generations) processes. The model in BAYESASS assumes
165 linkage equilibrium between loci, but allows for deviations in Hardy-Weinberg proportions by
166 introducing an additional inbreeding (F) parameter. We ran BAYESASS for 30 million generations
167 with a burn-in of 3 million and a sampling interval of 300. We modified the MCMC mixing
168 parameters to obtain the target values recommended by the program authors. We ran the program
169 multiple times starting from a different random number seed in order to make sure that the chain
170 was converging adequately. We also examined the raw trace files in the program TRACER V1.6.1
171 (Rambaut and Drummond 2007) to assess convergence.

172 Migration estimates obtained from MIGRATE were based on the mutation-scaled
173 immigration rate M (m/μ) whereas BAYESASS returned the immigration rate m . Thus, to obtain

174 estimates of m from MIGRATE we multiplied all M -values by an estimated mutation rate of $5 \times$
175 10^{-4} (Garza and Williamson 2001; Waples and Do 2010). To statistically quantify the
176 relationship between historical and contemporary migration rates we implemented a Mantel test
177 (Mantel 1967) in the R package ECODIST (Goslee and Urban 2008) using 10,000 permutations.

178 *Historical and contemporary effective population sizes*

179 Historical N_e was estimated in MIGRATE. To estimate contemporary N_e we used the linkage
180 disequilibrium method (Hill 1981) in the program LDNE v. 1.3.1, which implemented separate
181 bias correction factors for sample sizes greater than or less than 30 individuals (Waples 2006;
182 Waples and Do 2008). We specified a random mating model with default critical values for allele
183 frequencies. Jackknife 95% confidence intervals were used as a measure of variance and
184 negative values were interpreted as infinity (Waples and Do 2008).

185 We used the program BOTTLENECK v 1.2.02 (Piry et al. 1999) to compare estimates of
186 observed heterozygosity to number of alleles at each locus. Following a population bottleneck,
187 the number of alleles is reduced faster than heterozygosity, resulting in an observed
188 heterozygosity larger than would be expected if the locus were at mutation-drift equilibrium
189 (Cornuet and Luikart 1996). This test is useful for tracking bottlenecks occurring over the last
190 $0.2-4.0N_e$ generations (Cornuet and Luikart 1996). Heterozygosity excess was tested using the
191 infinite allele mutation model (IAM) with 1,000 iterations. Although microsatellites were
192 traditionally assumed to follow an approximate SMM model (Di Rienzo et al. 1994, Piry et al.
193 1999), more recent evidence suggests that recent bottlenecks may be better detected under an
194 IAM (Cristescu et al. 2010). Significance was assessed using the Wilcoxon signed rank test

195 (Cornuet and Luikart 1996). Second, we examined allele frequency distributions for each locus
196 and population. Populations in mutation-drift equilibrium tend to show L-shaped distributions
197 representing a large proportion of alleles at low frequency (<0.1 ; Luikart et al. 1998). In contrast,
198 recently bottlenecked populations tend to show a mode-shift in allele frequency distribution
199 because low frequency alleles are lost more quickly versus alleles present in high frequency.
200 This test is most suitable for detecting bottlenecks occurring relatively recently (i.e. a few
201 generations ago; Luikart et al. 1998).

202

203 *Landscape genetics*

204 We adopted a landscape genetic approach to understand the relationship between landscape
205 structure, historical migration, contemporary migration and mtDNA divergence. We first created
206 resistance surfaces in ARCMAP 10 (ESRI) based on landscape variables shown to be important in
207 shaping functional connectivity for this species (see Blair et al., 2013 for details). Next, we used
208 CIRCUITSCAPE 3.5.7 (Shah and McRae 2008) to calculate pairwise resistance distances between
209 populations based on each resistance surface. We then used a matrix regression approach
210 (Legendre et al. 1994; Lichstein 2007) to correlate resistance distance with both historical and
211 contemporary migration rates. Because MIGRATE and BAYESASS produced asymmetrical
212 pairwise rates, we averaged both values to obtain a single rate between populations. Although
213 averaging rates potentially discarded valuable information regarding source-sink dynamics, it
214 was a necessary step to correlate these values with resistance distance between populations. We
215 assumed that if recent fragmentation was altering dispersal routes then we would observe a

216 higher correlation between contemporary migration and landscape versus historical migration
217 and landscape. All regression analyses were conducted in ECODIST. As a second measure of
218 historical migration we correlated resistance distances with pairwise mtDNA sequence
219 divergence (D_{xy}). We did not perform regressions using migration rate estimates based on the
220 mtDNA data because of difficulty in parameter estimation (see Results).

221

222 **Results**

223 *mtDNA diversity and phylogenetic analysis*

224 We recovered 2400 bp of mtDNA sequence data for 77 individuals from 11 populations
225 distributed throughout the immediate area surrounding Alamos. The total number of bp per
226 partition, the proportion of potentially phylogenetically informative characters, and selected
227 models of sequence evolution were shown in Supplementary Table S3. Bayes Factors suggested
228 the most heavily partitioned dataset (by gene and codon position) to be the most efficient
229 (Supplementary Table S4). Thus, all Bayesian analyses were based on this partitioning strategy.
230 MP analysis resulted in eight most parsimonious trees (MPTs) of 723 steps. Both MP and BI
231 resulted in a highly supported genealogical hypothesis comprised of four mitochondrial lineages
232 differing up to 6% (uncorrected p -distances; Fig. 2). Lineage A was the most divergent and was
233 comprised solely of individuals from Choquincahui. This population was sister to the remaining
234 populations with strong statistical support from both MP bootstrap proportions (BSP = 99) and
235 Bayesian posterior probabilities (BPP = 1.0). The remaining three lineages were also supported
236 by moderate to high statistical support from both inference methods (Lineage B = 53/0.80;

237 Lineage C = 96/1.0; Lineage D = 100/1.0) and showed east-to-west geographic structuring.
238 Populations central to our study area served as a secondary contact zone for multiple divergent
239 mitochondrial lineages, whereas no haplotypes were shared among eastern and western
240 populations (Fig. 2). Sequence divergence between Lineages B, C, and D approached 3%
241 uncorrected p -distances.

242
243 *Population genetic analysis of mtDNA*

244 Standard nucleotide diversity statistics for nine populations sampled for mtDNA polymorphism
245 were presented in Supplementary Table S5. As expected, genetic diversity was greater for
246 populations composed of haplotypes from multiple lineages (e.g. $\pi = 0.0147$ vs. 0.0032).
247 Haplotype diversity was high in all populations, with a value of 1.0 recovered for several
248 populations. Significant population differentiation was present throughout the region
249 (Supplementary Table S5). Choquincahui, on average, differed from all other populations by
250 106.0525 substitutions or 0.0588 substitutions per site. Individuals from the Alamos population
251 were more similar genetically to the populations west of Alamos versus populations east of
252 Alamos. Rio Cuchujaqui differed from western populations by approximately 29.059 changes or
253 0.0239 substitutions per site. The results of the Mantel and reduced major axis regression (RMA)
254 tests showed a significantly positive relationship between geographic distance (km) and mtDNA
255 genetic distance ($Z = 5314.0176$; $r = 0.5007$; $P = 0.0002$). Model estimates for the RMA analysis
256 included an intercept of -6.435 , a slope of 0.4518, and an R^2 value of 0.251.

257 *Historical and contemporary migration rates*

258 Multiple runs of BAYESASS and MIGRATE for the microsatellite data gave consistent results
259 within each program, indicating that the MCMC chains were mixing well and adequately
260 sampling from the posterior distribution. Contemporary migration rates estimated from
261 BAYESASS (i.e. proportion of migrants per generation) were generally low to moderate and for
262 most population pairs 95% confidence intervals included zero (Supplementary Table S7).
263 However, some pairs show signs of exchanging a relatively high number of migrants per
264 generation. For example, migration rates from Aduana to the Road to Navojoa population were
265 0.155, and rates from El Quintero to Choquincahui were 0.256. Conversely, rates from
266 Choquincahui to El Quintero and from the Road to Navojoa to Aduana were much lower (0.008
267 and 0.012 respectively). The fraction of non-migrants per generation ranged from 0.675 in
268 Choquincahui to 0.940 in Rio Cuchujaqui. Estimates of M obtained from MIGRATE also
269 suggested little migration between populations (Supplementary Table S7). We used M to
270 calculate the number of migrants per generation (N_m) using the formula $N_m = (M\theta)/4$. Many of
271 these values were less than one indicating little historical migration between populations. Mean
272 historical estimates of m were approximately one-tenth the size of contemporary m (Fig. 3) with
273 no significant correlation detected (Mantel $r = 0.2592$, $p = 0.055$). We could not obtain reliable
274 parameter estimates using the mtDNA data in MIGRATE (results not shown). This was the case
275 even after altering priors, increasing chain length and decreasing the number of populations.
276 Therefore, these analyses were not pursued further.

277

278 *Historical and contemporary effective population sizes*

279 For estimates of contemporary N_e , we focused our results based on a P_{crit} value of 0.02 as this
280 value was shown to be an adequate choice to minimize bias and maximize precision in most
281 situations (Waples and Do 2010). Estimates for Road to Navojoa 1, Arroyo Tabela, and
282 Mocuzari showed relatively small sizes in comparison to all remaining populations (Table 1).
283 Point estimates from Aduana and El Quintero were negative. Although 95% confidence intervals
284 were broad, estimates of historical N_e were generally greater than contemporary estimates (Table
285 1). Tests for recent population bottlenecks using the excess heterozygosity method showed recent
286 reductions in N_e for all populations except La Sierrita (Table 2). Tests for mode-shifts in allele
287 frequency distribution showed an L-shaped curve for all populations except for the Road to
288 Navojoa 1 population, which showed a shifted distribution.
289

290

291 *Landscape genetics*

292 Results from the regression analyses indicated significant correlations between landscape
293 resistance and contemporary migration rates in comparison to historical rates and mtDNA
294 divergence (Table 3). There was no significant correlation between Euclidean distance and
295 historical migration rates. Slope was the only variable to show a significant correlation with
296 historical rates. Coefficient of determination (R^2) values in the historical models ranged from
297 0.0073 to 0.1145 (mean=0.0551), whereas correlations in contemporary models ranged from
298 0.0214 for slope to 0.1994 for Euclidean distance (mean= 0.1268). Euclidean distance was the
299 only variable significantly correlated with mtDNA divergence.

300

301 **Discussion**

302 Disentangling the relative influence of historical and contemporary processes in shaping the
303 spatial distribution of genetic variation is currently a major research focus of landscape genetics
304 (Vandergast et al. 2007; Spear and Storfer 2008; Anderson et al. 2010; Burbrink 2010; Dyer et
305 al. 2010; Wang 2010). We expand upon previous studies (e.g. Chiucchi and Gibbs 2010)
306 utilizing a spatially explicit approach to understand the temporal dynamics of demographic
307 processes. We demonstrate high levels of lineage divergence over small spatial scales, consistent
308 with high female philopatry and low levels of historical gene flow. In contrast to our
309 expectations, we find an increase in contemporary versus historical migration rates, but find
310 evidence that landscape heterogeneity better correlates with contemporary gene flow versus
311 historical estimates. We also find evidence for recent reductions in N_e for many populations.
312 Below we extrapolate on these major findings and discuss the utility of adopting similar multi-
313 tiered approaches to understand the demographic consequences of recent habitat modification.

314

315 *Sequence divergence and mitochondrial genealogy*

316 We find substantial lineage divergence among populations of leaf-toed geckos with divergence
317 values approaching 6%. If we assume the widely used vertebrate mtDNA divergence rate of 2%
318 per million years, divergence between lineages occurred at least 3 million years ago illustrating
319 the influence of historical processes. As no major biogeographic barrier separates these deep
320 lineages, these results suggest a high degree of female philopatry through evolutionary history.
321 Substantial geographic structure and significant IBD are detected with an apparent east-west
322 pattern (Fig. 2). Further, several populations central to the study area show signs of sympatric
323 lineages. It is possible that these sites are composed of hybrids of eastern and western
324 populations. For example, Blair et al. (2013) find evidence of substantial admixture within

325 geckos from many of these areas. Additional taxonomic work is needed to clarify the specific
326 status of these individuals. However, combining our mtDNA results (>6% sequence divergence)
327 with previous nuclear DNA evidence (Blair et al. 2013) suggests that geckos from Choquincahui
328 and El Quintero are not exchanging genetic information with other populations and should be
329 recognized as a distinct species. In addition, the fact that no haplotypes are shared among the
330 most eastern and western populations suggests the notion that home range sizes of these lizards
331 are small and dispersal capabilities are limited to <20 km (Fig. 2). These results are consistent
332 with previous studies and provide further evidence that many gecko species possess small home-
333 range sizes (Gübitz et al. 2000; Kaspidis et al. 2005; Rato et al. 2011).

334

335 *Historical and contemporary demography*

336 To date, only a small handful of studies have simultaneously tested for similarities in historical
337 and contemporary demographic parameters with the majority focusing on temperate species (e.g.
338 Ross et al. 2007; Andersen et al. 2009; Schmidt et al. 2009; Muscarella et al. 2011). This is
339 problematic, as tropical regions are generally considered to be global hotspots of biodiversity
340 (Myers et al. 2000). In addition, tropical ecosystems (and TDF in particular) continue to suffer
341 from high rates of habitat fragmentation (Janzen 1988; Trejo and Dirzo 2000). Thus, from a
342 conservation perspective, additional studies are needed to quantify temporal dynamics in key
343 demographic parameters in species distributed throughout these ecosystems.

344 We find weak evidence for a reduction in contemporary versus historical migration rates.
345 Conversely, our results suggest that contemporary migration rates may be an order of magnitude
346 higher in many cases. Further, our Mantel test shows no significant correlation between these
347 two estimates. This suggests that recent habitat fragmentation is not impacting the ability of

348 individuals to disperse. These conclusions are based on an estimated microsatellite mutation rate
349 of 5×10^{-4} recommended by previous studies (e.g. Garza and Williamson 2001; Waples and Do
350 2010). Although a range of microsatellite mutation rates have been estimated for humans
351 (Ellegren 2004), an unrealistically high value of 0.01 would need to be assumed to yield
352 comparable historical and contemporary migration rates in these geckos. Thus, these results
353 provide strong evidence for recent increases in pairwise migration rates.

354 Although a direct explanation for higher contemporary migration rates is presently
355 untenable, it is possible that these results are a due to anthropogenic influence. It is well-known
356 that gecko species are commonly encountered in and around human settlements. Thus, it is
357 possible that the relatively recent colonization of humans in the area has increased migration
358 rates via hitchhiking. Additional studies conducted on gecko species will be useful to determine
359 if similar patterns occur in other taxa distributed in areas with varying anthropogenic influence.

360 Acknowledging the large confidence intervals recovered in our analyses, historical N_e
361 estimates for several populations are generally larger than contemporary estimates, suggesting
362 that recent habitat fragmentation and/or introduction of competing species (*Hemidactylus*) has
363 reduced N_e in these areas irrespective of an increase in overall migration rate. Further, the
364 majority of populations show signs of a recent bottleneck. A finding of recent bottlenecks and
365 reduced contemporary N_e in a region of relatively intact Mexican TDF (Fig. 2) suggests that
366 similar studies are needed for other less-common TDF taxa inhabiting even more fragmented
367 forest patches through western Mexico. Quantifying the demographic consequences of habitat
368 fragmentation in diverse taxa is imperative if adequate conservation measures are to be
369 implemented throughout Mexican TDF.

370

371 *Landscape genetics*

372 There has been considerable recent debate as to the utility of different molecular marker types
373 and analytical methods for landscape genetic inference (Manel et al. 2003; Vandergast et al.
374 2007; Storfer et al. 2010; Wang 2010,2011; Bohonak and Vandergast 2011). To date, most
375 landscape genetic studies correlate different effective distances with genetic distance using an
376 F_{ST} -like metric based on microsatellite loci. Here, we use different molecular markers and
377 analytical methods to test if correlations between the landscape and population connectivity are
378 larger when using estimates of contemporary population genetic metrics (e.g. contemporary
379 migration). Our results suggest that the landscape is significantly more correlated with
380 contemporary versus historical migration rates, as would be expected if populations are altering
381 dispersal routes in response to recent habitat changes.

382 Correlations between landscape structure and mtDNA divergence contrast sharply with
383 those based on contemporary migration rate. Although landscape genetic studies continue to rely
384 predominantly on microsatellites (Storfer et al. 2010), a handful of studies have relied solely on
385 mtDNA to infer contemporary ecological and evolutionary processes (e.g. Vandergast et al.
386 2007; Kosciński et al. 2009). We assume that the choice of mtDNA as a marker for many of
387 these studies is partly a factor of cost and ease of data collection. However, sole reliance on
388 mtDNA comes with issues that must be acknowledged including the stochasticity of the lineage
389 sorting process, relatively slow mutation rates and the fact that mtDNA is maternally inherited
390 (Wang 2010). The fact that we obtain drastically different correlations when using mtDNA
391 versus microsatellites raises the question as to the utility of mtDNA for inferring contemporary
392 ecological processes. Although mtDNA may be adequate for testing simple barrier hypotheses
393 using binary matrices (e.g. Vandergast et al. 2007), landscape-genetic relationships are often

394 more complex and require the use of more sophisticated spatial analysis and molecular markers
395 powerful enough to give adequate resolution at the spatial and temporal scale under investigation
396 (Cushman et al. 2006). Our results suggest that though mtDNA may be an acceptable marker to
397 test hypotheses in deep time, it may not be the ideal marker for modeling complex landscape-
398 genetic relationships. We agree with Wang (2010) that researchers should be explicit about their
399 hypotheses and the timeframe under consideration as to avoid erroneous conclusions regarding
400 landscape influences on genetic divergence.

401

402 *Conclusions*

403 Our results suggest a complex demographic history in leaf-toed geckos and that studies that
404 simultaneously examine historical and contemporary demographic parameters can serve as a
405 powerful tool to understand the population genetic consequences or recent habitat fragmentation.
406 We find high levels of mtDNA divergence over small spatial scales and evidence for recent
407 reductions in N_e for several populations. Although our results suggest relatively high levels of
408 contemporary migration, landscape genetic analyses suggest that geckos are altering dispersal
409 routes in response to habitat changes. Finally, our results suggest that mtDNA is poor marker for
410 inferring contemporary landscape genetic relationships, presumably due to its slow mutation rate
411 and stochasticity associated with the coalescent process. As TDF contains an extraordinary
412 diversity of species (Robichaux and Yetman 2000), yet remains a conservation concern (Trejo
413 and Dirzo 2000), additional molecular genetic studies are needed to assess recent demographic
414 changes in the native flora and fauna. Only then will conservation initiatives be most effective.

415 Acknowledgments

416 We would like to thank A. Ngo, D. Dewsbury, I. Conflitti, and C. Davy for providing insightful
417 comments on previous drafts of the manuscript. This research was supported by a discovery
418 grant from the Natural Sciences and Engineering Research Council of Canada and by the Royal
419 Ontario Museum Board of Governors to RWM. Support was also provided from a Theodore
420 Roosevelt Memorial grant through the American Museum of Natural History (CB). Invaluable
421 field assistance was provided by Martin G. Figueroa, Norberto Martinez Mendez, Rafael Lara
422 Resendiz and Arabel Escalona López. Fieldwork in reserves was conducted under the permit
423 issued to Dr. Francisco Molina Freaner. Stephanie A. Meyer provided invaluable advice and
424 field logistics. All research was conducted using approved Animal Use Protocols. All necessary
425 permits (SGPA/DGVS/1995/08, SGPA/DGVS/01493/09, SGPA/DGVS/3220/10) were obtained
426 from SEMARNAT through the Universidad Nacional Autónoma de México (UNAM).

427 **References**

- 428 Andersen LW, Born EW, Doidge DW, Gjertz I, Wiig Ø, Waples RS (2009) Genetic signals of
429 historic and recent migration between sub-populations of Atlantic walrus *Odobenus*
430 *rosmarus rosmarus* west and east of Greenland. *Endan Species Res* 9:197–211.
- 431 Anderson CD, Epperson BK, Fortin MJ *et al.* (2010) Considering spatial and temporal scale in
432 landscape-genetic studies of gene flow. *Mol Ecol* 19:3565–3575.
- 433 Becerra JX (2005) Timing the origin and expansion of the Mexican tropical dry forest. *Proc Natl*
434 *Acad Sci USA* 102:10919–10923.
- 435 Beerli P (2006) Comparison of Bayesian and maximum likelihood inference of population
436 genetic parameters. *Bioinformatics* 22:341–345.
- 437 Beerli P (2008) MIGRATE documentation (version 3.0). Technical Report.
438 <http://popgen.sc.fsu.edu>.
- 439 Beerli P, Felsenstein J (2001) Maximum likelihood estimation of a migration matrix and effective
440 population sizes in n subpopulations by using a coalescent approach. *Proc Natl Acad Sci*
441 *USA* 98:4563–4568.
- 442 Blair C, Méndez de la Cruz FR, Ngo A, Lindell J, Lathrop A, Murphy RW (2009) Molecular
443 phylogenetics and taxonomy of leaf-toed geckos (Phyllodactylidae: *Phyllodactylus*)
444 inhabiting the peninsula of Baja California. *Zootaxa* 2027:28–42.
- 445 Blair C, Jiménez-Arcos VH, Méndez de la Cruz FR, Murphy RW (2013) Landscape genetics of
446 leaf-toed geckos in the tropical dry forest of northern Mexico. *PLoS One* 8:e57433.
- 447 Bohonak AJ, Vandergast AG (2011) The value of DNA sequence data for studying landscape
448 genetics. *Mol Ecol* 20:2477–2479.

- 449 Burbrink FT (2010) Historical versus contemporary migration in fragmented populations. *Mol*
450 *Ecol* 19:5321–5323.
- 451 Cartron JE, Ceballos G, Felger RS (2005) *Biodiversity, Ecosystems, and Conservation in*
452 *Northern Mexico*. New York, New York: Oxford University Press.
- 453 Castiglia R, García A, Bezerra AMR, Flores-Villela O, Gornung E (2009) Karyotypic
454 diversification due to Robertsonian rearrangements in *Phyllodactylus lanei* Smith, 1935
455 (Squamata, Gekkonidae) from Mexico. *Rendiconti Lincei* 20:77–82.
- 456 Chiuichi JE, Gibbs HL (2010) Similarity of contemporary and historical gene flow among highly
457 fragmented populations of an endangered rattlesnake. *Mol Ecol* 19:5345–5358.
- 458 Cornuet JM, Luikart G (1996) Description and power analysis of two tests for detecting recent
459 population bottlenecks from allele frequency data. *Genetics* 144:2001–2014.
- 460 Crispo E, Moore JS, Lee-Yaw JA, Gray SM, Haller BC (2011) Broken barriers: human-induced
461 changes to gene flow and introgression in animals. *BioEssays* 33:508–518.
- 462 Cristescu R, Sherwin WB, Handasyde K, Cahill V, Cooper DW (2010) Detecting bottlenecks
463 using Bottleneck 1.2.02 in wild populations: the importance of the microsatellite structure.
464 *Conserv Genet* 11:1043–1049.
- 465 Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex landscapes:
466 testing multiple hypotheses with causal modeling. *Am Nat* 168:486–499.
- 467 Di Rienzo A, Peterson AC, Garza JC et al. (1994) Mutational processes of simple-sequence
468 repeat loci in human populations. *Proc Natl Acad Sci USA* 91:3166–3170.
- 469 Dixon JR (1964) The systematics and distribution of lizards of the genus *Phyllodactylus* in North
470 and Central America. New Mexico State University Research Center, Scientific Bulletin,
471 64–1:1–139.

- 472 Dyer RJ, Nason JD, Garrick RC (2010) Landscape modeling of gene flow: improved power using
473 conditional genetic distance derived from the topology of population networks. *Mol Ecol*
474 19:3746–3759.
- 475 Ellegren H (2004) Microsatellites: simple sequences with complex evolution. *Nat Rev Genet*
476 5:435–445.
- 477 Ewers RM, Didham RK (2005) Confounding factors in the detection of species responses to
478 habitat fragmentation. *Biol Rev* 81:117–142.
- 479 Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Syst* 34:487–
480 515.
- 481 Gamble T, Bauer AM, Greenbaum E, Jackman TR (2008) Out of the blue: a novel, trans-Atlantic
482 clade of geckos (Gekkota, Squamata). *Zool Scripta* 37:355–366.
- 483 García A (2006) Using ecological niche modeling to identify diversity hotspots for the
484 herpetofauna of Pacific lowlands and adjacent interior valleys of Mexico. *Biol Conserv*
485 130:25–46.
- 486 Garza JC, Williamson EG (2001) Detection of reduction in population size using data from
487 microsatellite loci. *Mol Ecol* 10:305–318.
- 488 Goldberg CS, Waits LP (2010) Comparative landscape genetics of two pond-breeding amphibian
489 species in a highly modified agricultural landscape. *Mol Ecol* 19:3650–3663.
- 490 Goslee S, Urban D (2008) *Dissimilarity-Based Functions for Ecological Analysis*. CRAN
491 repository. Available from <http://cran.r-project.org/web/packages/ecodist/>.
- 492 Gübitz T, Thorpe RS, Malhotra A (2000) Phylogeography and natural selection in the Tanerife
493 gecko *Tarentola delalandii*: testing historical and adaptive hypotheses. *Mol Ecol* 9:1213–
494 1221.

- 495 Hall TA (1999) BIOEDIT: a user-friendly biological sequence alignment editor and analysis
496 program for Windows 95/98/NT. *Nucleic Acids Symp Ser* 41:95–98.
- 497 Hill WG (1981) Estimation of effective population size from data on linkage disequilibrium.
498 *Genet Res* 38:209–216.
- 499 Janzen DH (1988) Tropical dry forests: the most endangered major tropical ecosystem. In:
500 Wilson EO (Ed.) *Biodiversity*. National Academy Press, Washington, pp 130–137.
- 501 Jensen JL, Bohonak AJ, Kelley ST (2005) Isolation by distance, web service. *BMC Genet* 6:13.
502 v.3.16 <http://ibdws.sdsu.edu/>.
- 503 Kosciński D, Yates AG, Handford P, Lougheed SC (2009) Effects of landscape and history on
504 diversification of a montane, stream-breeding amphibian. *J Biogeography* 36:255–265.
- 505 Legendre P, Lapointe FJ, Casgrain P (1994) Modeling brain evolution from behaviour: a
506 permutational regression approach. *Evolution* 48:1487–1499.
- 507 Lichstein JW (2007) Multiple regression on distance matrices: a multivariate spatial analysis tool.
508 *Plant Ecol* 188:117–131.
- 509 Luikart G, Allendorf FW, Cornuet JM *et al.* (1998) Distortion of allele frequency distributions
510 provides a test for recent population bottlenecks. *J Hered* 89:238–247.
- 511 Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape
512 ecology and population genetics. *Trends Ecol Evol* 18:189–197.
- 513 Murphy PG, Lugo AE (1996) Ecology of tropical dry forest. *Ann Rev Ecol Syst* 17:67–88.
- 514 Murphy RW, Blair C, Méndez de la Cruz FR (2009) A new species of leaf-toed gecko, genus
515 *Phyllodactylus* (Squamata: Gekkota: Phyllodactylidae) from Guerrero, Mexico. *S Am J*
516 *Herpetol* 4:17–24.

- 517 Muscarella RA, Murray KL, Ortt D, Russell AL, Fleming TH (2011) Exploring demographic,
518 physical, and historical explanations for the genetic structure of two lineages of Greater
519 Antillean bats. PLoS One 6:e17704.
- 520 Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity
521 hotspots for conservation priorities. Nature 409:853–858.
- 522 Myska P (2007) *Viva Natura. Field Guide to the Amphibians, Reptiles, Birds, and Mammals of*
523 *Western Mexico*. Peter Myska, Viva natura.
- 524 Pennington TR, Prado DE, Pendry CA (2000) Neotropical seasonally dry forests and Quaternary
525 vegetation changes. J Biogeography 27:261–273.
- 526 Piry S, Luikart G, Cornuet JM (1999) BOTTLENECK: a computer program for detecting recent
527 reductions in effective population size using allele frequency data. J Hered 90:502–503.
- 528 Rambaut A, Drummond AJ (2007) Tracer v1.6.1. Available
529 from <http://beast.bio.ed.ac.uk/Tracer>.
- 530 Rato C, Carranza S, Harris DJ (2011) When selection deceives phylogeographic interpretation:
531 the case of the Mediterranean house gecko, *Hemidactylus turcius* (Linnaeus, 1758). Mol
532 Phylogenet Evol 58:365–373.
- 533 Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. Am Nat
534 158:87–99.
- 535 Robichaux RH, Yetman DA (2000) *The Tropical Deciduous Forest of Alamos. Biodiversity of a*
536 *Threatened Ecosystem in Mexico*. Tucson: The University of Arizona Press.
- 537 Ross, KG, Krieger MJB, Keller L, Shoemaker DD (2007) Genetic variation and structure in
538 native populations of the fire ant *Solenopsis invicta*: evolutionary and demographic
539 implications. Biol J Linnean Soc 92:541–560.

- 540 Rozas J, Sanchez-Delbarrio JC, Messeguer X, Rozas R (2003) DNASP, DNA polymorphism
541 analyses by the coalescent and other methods. *Bioinformatics* 19:2496–2497.
- 542 Sanderson EW, Jaiteh M, Levy MA, *et al.* (2002) The human footprint and the last of the wild.
543 *Bioscience* 52:891–904.
- 544 Schmidt JI, Hundertmark KJ, Bowyer TR, McCracken KG (2009) Population structure and
545 genetic diversity of moose in Alaska. *J Hered* 100:170–180.
- 546 Shah VB, McRae BH (2008) CIRCUITSCAPE: a tool for landscape ecology. In: Varoquaux G,
547 Vaught T, Millman J (eds). *Proceedings of the 7th Python in Science Conference (SciPy*
548 *2008)*, pp. 62–66.
- 549 Sork VL, Waits LP (2010) Contributions of landscape genetics—approaches, insights, and future
550 potential. *Mol Ecol* 19:3489–3495.
- 551 Spear SF, Storfer A (2008) Landscape genetic structure of coastal tailed frogs (*Ascaphus truei*) in
552 protected vs. managed forests. *Mol Ecol* 17:4642–4656.
- 553 Spear SF, Peterson CR, Matocq M, Storfer A (2005) Landscape genetics of the blotched tiger
554 salamander (*Ambystoma tigrinum melanostictum*). *Mol Ecol* 14:2553–2564.
- 555 Storfer A, Murphy MA, Spear SP, Holderegger R, Waits LP (2010) Landscape genetics: where
556 are we now? *Mol Ecol* 19:3496–3514.
- 557 Trejo I, Dirzo R (2000) Deforestation of seasonally dry tropical forest: a national and local
558 analysis in Mexico. *Biol Conserv* 94:133–142.
- 559 Vandergast AG, Bohonak AJ, Weissman DB, Fisher RN (2007) Understanding the genetic
560 effects of recent habitat fragmentation in the context of evolutionary history:
561 phylogeography and landscape genetics of a southern California endemic Jerusalem
562 cricket (Orthoptera: Stenopelmatidae: *Stenopelmatus*). *Mol Ecol* 16:977–992.

- 563 Vignieri SN (2005) Streams over mountains: influence of riparian connectivity on gene flow in
564 the Pacific jumping mouse (*Zapus trinotatus*). *Mol Ecol* 14:1925–1937.
- 565 Wang IJ (2010) Recognizing the temporal distinctions between landscape genetics and
566 phylogeography. *Mol Ecol* 19:2605–2608.
- 567 Wang IJ (2011) Choosing appropriate genetic markers and analytical methods for testing
568 landscape genetic hypotheses. *Mol Ecol* 20:2480–2482.
- 569 Wang IJ, Savage WK, Shaffer BH (2009) Landscape genetics and least-cost path analysis reveal
570 unexpected dispersal routes in the California tiger salamander (*Ambystoma californiense*).
571 *Mol Ecol* 18:1365–1374.
- 572 Waples RS (2006) A bias correction for estimates of effective population size based on linkage
573 disequilibrium at unlinked gene loci. *Conserv Genet* 7:167–184.
- 574 Waples RS, Do C (2008) LDNE: a program for estimating effective population size from data on
575 linkage disequilibrium. *Mol Ecol Resour* 8:753–756.
- 576 Waples RS, Do C (2010) Linkage disequilibrium estimates of contemporary N_e using highly
577 variable genetic markers: a largely untapped resource for applied conservation and
578 evolution. *Evol Appl* 3:244–262.
- 579 Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus
580 genotypes. *Genetics* 163:1177–1191.
- 581 Zellmer AJ, Knowles LL (2009) Disentangling the effects of historic vs. contemporary landscape
582 structure on population genetic divergence. *Mol Ecol* 18:3593–3602.
- 583
- 584
- 585
- 586

Table 1. Estimates of contemporary and historical effective population sizes (N_e). Contemporary N_e was estimated in the program LDNe using a P_{crit} value of 0.02 (Waples and Do 2010). Historical N_e was calculated from theta estimated in MIGRATE and assuming a microsatellite mutation rate of 5×10^{-4} (Garza and Williamson 2001; Waples and Do 2010). Values in parentheses represent 95% confidence intervals.

Locality	n	Contemporary N_e	Historical N_e
Road to Navojoa 1	10	25.4 (15.5–56.0)	483.355 (0–1333)
Alamos	36	464.1 (104.8–infinity)	749.5 (0–1566)
Arroyo Tabelo	57	36.4 (28.1–48.7)	703.34 (0–1500)
Aduana	17	-331 (74.1–infinity)	501.685 (0–1333)
Rio Cuchujaqui	72	636.7 (225.3–infinity)	1456.435 (466–2400)
Sierrita	38	142.9 (65.2–infinity)	668.235 (0–1500)
Mocuzari	30	29.2 (21.0–43.9)	272.6 (0–1066)
El Quintero	30	-865.0 (110.9–infinity)	432.8 (0–1266)
Choquincahui	31	121.3 (43.9–infinity)	296.295 (0–1100)
San Antonio	15	224.4 (45.2–infinity)	323.865 (0–1133)

Table 2. Results of tests for population bottlenecks performed using the software BOTTLENECK. Wilcoxon IAM represents P-values based on the Infinite Allele Mutation model. Allelic distribution represents the test for a shift in the relative abundance of alleles at different frequencies.

Locality	n	Wilcoxon IAM	Allelic Distribution
Road to Navojoa 1	10	0.042	Shifted
Alamos	36	0.001	Normal
Arroyo Tabelo	57	0.001	Normal
Aduana	17	0.001	Normal
Rio Cuchujaqui	72	0.001	Normal
La Sierrita	38	0.065	Normal
Mocuzari	30	0.001	Normal
El Quintero	30	0.005	Normal
Choquincahui	31	0.001	Normal
San Antonio	15	0.002	Normal

Table 3. Regression on distance matrices results showing the relationships between landscape resistance and historical migration, contemporary migration, and mtDNA sequence divergence (D_{xy}). Model M = MIGRATE; Model B = BAYESASS; Model MtDNA = mtDNA divergence. Models in italics significant at an alpha = 0.05.

Model	Variables	β	Model R^2	P
M1	Euclidean	-8.2E-09	0.0337	0.231
M2	Temp	-1.3E-05	0.0742	0.0795
M3	Forest	-2.3E-05	0.0514	0.1447
M4	Stream	-4E-05	0.0497	0.1578
M5	Anthropogenic	-3.1E-06	0.0073	0.6023
<i>M6</i>	<i>Slope</i>	<i>-1.3E-05</i>	<i>0.1145</i>	<i>0.0217</i>
<i>B1</i>	<i>Euclidean</i>	<i>-8.1E-07</i>	<i>0.1994</i>	<i>0.0016</i>
B2	Temp	-0.0005	0.0587	0.0656
<i>B3</i>	<i>Forest</i>	<i>-0.0017</i>	<i>0.1768</i>	<i>0.0077</i>
<i>B4</i>	<i>Stream</i>	<i>-0.0027</i>	<i>0.1342</i>	<i>0.008</i>
<i>B5</i>	<i>Anthropogenic</i>	<i>-0.0006</i>	<i>0.1703</i>	<i>0.002</i>
B6	Slope	-0.0002	0.0214	0.2446
<i>Mt1</i>	<i>Euclidean</i>	<i>1.78E-06</i>	<i>0.6235</i>	<i>0.0193</i>
Mt2	Temp	0.002	0.558	0.1135
Mt3	Forest	0.003	0.3978	0.0724
Mt4	Stream	0.003	0.1159	0.5357
Mt5	Anthropogenic	0.0001	0.0029	0.8827
<i>Mt6</i>	<i>Slope</i>	<i>0.001</i>	<i>0.5219</i>	<i>0.1012</i>

589 **Figure Legends**

590 **Fig. 1.** Map of the Alamos region of Sonora showing sampling locality information for all
591 *Phyllodactylus tuberculosus saxatilis* included in this study. Gray shading represents the current
592 distribution of tropical dry forest throughout the landscape. Lines represent stream, rivers and
593 arroyos throughout the study area. Triangles = sites that were assayed for mtDNA polymorphism;
594 circles = sites assayed for microsatellite DNA polymorphism (Blair et al. 2013); squares = sites
595 assayed for both mtDNA and microsatellite polymorphism. Populations targeted for mtDNA
596 sequencing were based on genetic results from previous studies (Blair et al. 2013). Values in
597 parentheses adjacent to site names represent sample sizes (mtDNA, microsatellite DNA). Inset
598 shows the general area of Alamos, Sonora within Mexico.

599

600 **Fig. 2.** Bayesian majority rule phylogram resulting from the optimal partitioning strategy of gene
601 + codon position. Numbers above nodes represent 10,000 nonparametric bootstrap proportions
602 using maximum parsimony. Numbers below nodes represent Bayesian posterior probabilities
603 sampled from the posterior distribution of trees. Gray shading represents the current distribution
604 of tropical dry forest throughout the landscape. Lines represent stream, rivers and arroyos
605 throughout the study area. Colored pies represent the mtDNA lineages represented at specific
606 sites.

607

608 **Fig. 3.** A) Kernel density plot of historical migration rates (m) estimated from MIGRATE. B)
609 Kernel density plot of contemporary migration rates (m) estimated from BAYESASS.