

APPLICATION OF JOHNSON ET AL.'S SPECIATION THRESHOLD MODEL TO APPARENT COLONIZATION TIMES OF ISLAND BIOTAS

ROBERT E. RICKLEFS¹ AND ELDRIDGE BERMINGHAM²

¹*Department of Biology, University of Missouri-St. Louis, 8001 Natural Bridge Road, St. Louis, Missouri 63121-4499*
E-mail: ricklefs@umsl.edu

²*Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, Panama*
E-mail: eb@stri.org, eb@naos.si.edu

Abstract.—Understanding patterns of diversity can be furthered by analysis of the dynamics of colonization, speciation, and extinction on islands using historical information provided by molecular phylogeography. The land birds of the Lesser Antilles are one of the most thoroughly described regional faunas in this context. In an analysis of colonization times, Ricklefs and Bermingham (2001) found that the cumulative distribution of lineages with respect to increasing time since colonization exhibits a striking change in slope at a genetic distance of about 2% mitochondrial DNA sequence divergence (about one million years). They further showed how this heterogeneity could be explained by either an abrupt increase in colonization rates or a mass extinction event. Cherry et al. (2002), referring to a model developed by Johnson et al. (2000), argued instead that the pattern resulted from a speciation threshold for reproductive isolation of island populations from their continental source populations. Prior to this threshold, genetic divergence is slowed by migration from the source, and species of varying age accumulate at a low genetic distance. After the threshold is reached, source and island populations diverge more rapidly, creating heterogeneity in the distribution of apparent ages of island taxa. We simulated of Johnson et al.'s speciation-threshold model, incorporating genetic divergence at rate k and fixation at rate M of genes that have migrated between the source and the island population. Fixation resets the divergence clock to zero. The speciation-threshold model fits the distribution of divergence times of Lesser Antillean birds well with biologically plausible parameter estimates. Application of the model to the Hawaiian avifauna, which does not exhibit marked heterogeneity of genetic divergence, and the West Indian herpetofauna, which does, required unreasonably high migration-fixation rates, several orders of magnitude greater than the colonization rate. However, the plausibility of the speciation-divergence model for Lesser Antillean birds emphasizes the importance of further investigation of historical biogeography on a regional scale for whole biotas, as well as the migration of genes between populations on long time scales and the achievement of reproductive isolation.

Key words.—Colonization, genetic divergence, Hawaiian Islands, migration, speciation, speciation-threshold model, West Indies.

Received July 30, 2003. Accepted May 4, 2004.

Species richness in island biotas represents a history of colonization, radiation, and extinction of taxa. Understanding the dynamics of community assembly depends on estimating the rates of each of these processes and their variation over time. Molecular assessments of genetic distance between populations provide estimates of colonization times of island populations from their continental source populations. Ricklefs and Bermingham (2001) showed that the dynamics of colonization and extinction could be explored by analyzing the distribution of colonization times of extant island lineages. Cherry et al. (2002) have cautioned, however, that genetic distance does not reveal the history of a particular population on an island when continuing gene flow from the source prevents genetic divergence. Only after a speciation threshold of genetic divergence has been reached do source and island populations diverge at a rate determined by independent evolutionary change in both (Johnson et al. 2000). The degree to which the speciation threshold masks the history of colonization is a matter of concern for understanding both the history of island biotas and the dynamics of colonization and gene flow between source and island populations. In this study, we fit a simple speciation-threshold model to the distribution of genetic distances between source and island populations in three systems for which data are available for most of the island lineages: land birds of the Lesser Antilles, reptiles and amphibians of the West Indies, primarily the Greater Antilles, and birds of the Hawaiian archipelago. We then discuss whether the fitted parameters de-

scribing rates of colonization, extinction, migration, and the speciation threshold are biologically realistic, focusing primarily on the land birds of the Lesser Antilles.

Ricklefs and Bermingham (2001) examined the accumulation of lineages of land birds in the Lesser Antilles as a function of increasing relative age of colonization, which they inferred from genetic divergence between Lesser Antillean lineages and South American or Greater Antillean sources. When probabilities of colonization and extinction are constant over time and homogeneous over lineages, the accumulation curve increases exponentially toward an equilibrium value. Ricklefs and Bermingham (2001) found instead that the accumulation curve did not reach equilibrium and that its slope changed abruptly at a mitochondrial DNA (mtDNA) genetic distance (d) of about 0.02 (2% sequence divergence).

As Cherry et al. (2002) pointed out, however, the non-homogeneity in the lineage accumulation curve could also be explained by the speciation-threshold model developed by Johnson et al. (2000). Accordingly, following initial colonization of an island, genes carried by individuals continuing to arrive from the source would occasionally become fixed in the gene pool of the island population by drift or selection. Such a migration-fixation event would eliminate any divergence between the mainland and island populations and set the divergence clock back to zero. Thus, the apparent rate of divergence among recent colonists would be low due to migration, and seemingly new colonist populations would ac-

cumulate at low genetic distances from source populations. Once a speciation threshold of genetic distance had been achieved, however, migrant alleles could no longer become fixed in the island population and divergence would proceed at a more rapid pace determined by independent evolutionary change in each population. Thus, the distribution of genetic divergence values in an island biota with continuous colonization and migration would exhibit a high density prior to the speciation threshold and a sparser distribution over a wider range of divergence values above that threshold. The slope of the curve relating the cumulative number of species as a function of increasing genetic divergence, which was the basis of analyses by Ricklefs and Bermingham (2001), would appear to change abruptly at the speciation threshold.

Assuming that the model of Johnson et al. (2000) could replicate the observed lineage accumulation curve, testing the model as a viable alternative to heterogeneous colonization and extinction would depend on (1) the plausibility of the particular parameters in the successful model, (2) whether the threshold genetic divergence for speciation corresponds to a level that is reasonable for species-level distinction, and (3) whether geographic patterns of genetic variation are consistent with predictions of the model. This last point arises because Johnson et al.'s speciation-divergence model should apply to relations between island populations within archipelagoes as well as to relations between the archipelago and the source areas. Specifically, and depending on the distances involved, genetic divergence between island populations should sometimes exceed the genetic divergence between any island and the source (Ricklefs and Bermingham 2002).

Regardless of whether Johnson et al.'s speciation-divergence model applies in the end, we have found it useful to evaluate parameters of the model that provide a close fit to data. We have tried to determine whether these parameters are consistent with other information on colonization, divergence between populations in allopatry, and geographic structure in the distribution of genetic variation within lineages distributed over archipelagoes, particularly the Lesser Antilles. In this analysis, we construct a simple simulation of the Johnson et al. model and examine the sensitivity of the model's output to variation in migration rates and the genetic divergence required for speciation.

MODELS OF COLONIZATION TIME DISTRIBUTIONS

The Speciation-Threshold Model

We consider lineages present in a source area that colonize a single island. Our simulation follows the fate of 1000 lineages (biological species) over 10,000 time steps. The fate of each lineage is independent of all others in the simulation; that is, there are no competitive or precedence effects. Probabilities of genetic divergence and migration are constant over the course of the simulation. We found that it was unnecessary to include background extinction to provide adequate fits of the model to the data examined in this analysis.

For each lineage, the time of initial colonization of the island was drawn from a random uniform distribution over the 10,000 time steps in the simulation in one set of simulations, and it was the initial time step in another set of simulations. For convenience, we considered nucleotide sub-

stitutions in a 1000 base-pair sequence of mtDNA. Substitutions were additive, as in an infinite alleles model. At each time step, the model determined whether initial colonization occurred by comparing a uniform random variate to the probability of initial colonization during a single time step (0.0001). Following colonization of the island by each lineage, at each subsequent time step we determined whether either a nucleotide substitution or a migration-fixation event occurred. Substitutions were assumed to be neutral. Mutation events (probability μ) were based on the probability of a single mutation over the entire mtDNA sequence; the mutation rate was low enough that the probability of multiple mutations was close to zero. Nucleotide substitutions were accumulated over time to determine sequence divergence (d), which occurred at an average rate of $k = 2\mu$. A migration-fixation event (probability M) resulted in the fixation of the source haplotype in the island population, which reset genetic divergence between the source and island population to zero.

Speciation occurred when the number of nucleotide substitutions exceeded a threshold. The probability of speciation (p_s) remained at zero until the number of substitutions (n) had accumulated to a minimum required for reproductive isolation (the speciation threshold, n_s), after which it increased, approaching one exponentially according to

$$\begin{aligned} p_s &= 0 && \text{when } n < n_s \text{ and} \\ p_s &= [1 - e^{-b_s(n-n_s)}] && \text{when } n \geq n_s, \end{aligned} \quad (1)$$

where b_s is a scaling parameter that determines the rate at which p_s approaches one. When $b_s = 0.25$, which was the typical value in our simulations, p_s exceeded 0.5 after $n_s + 3$ nucleotide substitutions and it exceeded 0.9 after $n_s + 10$ nucleotide substitutions. The model of speciation employed by Johnson et al. (2000) is more complex than this, but produces a similar exponential approach to a speciation probability of one.

For each simulation, we recorded the proportion of lineages that had achieved species status by the 10,000 time steps, the colonization time of lineages that had become new species (differentiated) and those that had not (undifferentiated), the average time to speciation among those lineages that had become new species, and the nucleotide divergence (n) between source and island populations for both sets of lineages. Because we simulated a 1000-nucleotide sequence, $d = n/1000$. We also produced a plot of the cumulative number of lineages as a function of genetic divergence to compare with the observed data.

The Homogeneous Colonization-Extinction Model

When the arrival of new species on an island is constant at rate C per unit time (t) and resident island species go extinct at rate E per species per unit time, that is, species survival $S = \exp(-Et)$, the cumulative number of species (S) with colonization times up to t is $S = (C/E)(1 - \exp[-Et])$ (Ricklefs and Bermingham 2001). Thus, S exponentially approaches an asymptotic equilibrium number of species (C/E) with increasingly older colonists included in the sample. We fitted this model to the cumulative species curves by nonlinear regression (SAS Proc NLIN).

The Mass Extinction Model

The mass extinction model is identical to the homogeneous colonization-extinction model except that a mass extinction event survived by proportion S of the resident biota occurs at time t_S in the past. The consequence of this event is that the rate of accumulation of extant lineages colonizing the island prior to t_S is proportion S of the rate determined by the balance of C and E . Fits of this model to data were obtained by nonlinear regression. The mass extinction model is identical to a model with an increase in colonization at t_M by a factor of $1/S$ or a decrease in extinction rate by proportion $(1 - S)$.

All simulations and statistical analyses were carried out with the Statistical Analysis System, version 8.12 (SAS Institute, Cary, NC).

EMPIRICAL DATA

Land Birds of the Lesser Antilles

The observed data were the mtDNA genetic distances between source and Lesser Antillean populations of 38 lineages of small land birds. A 39th lineage, representing the endemic Antillean crested hummingbird *Orthorhynchus cristatus* was not included because we were unsure of its source taxon, hence the genetic distance to the source population representing its initial entry into the Lesser Antilles. Observed genetic distances were based on 842 bp of the overlapping ATPase 6 and ATPase 8 protein-coding mitochondrial gene regions. We used the Tamura-Nei model of nucleotide substitution (Tamura and Nei 1993) to calculate genetic distances. These distances are corrected for multiple substitutions and are therefore comparable to the additive distances produced by the simulation. The observed lineage accumulation curve is linear over the range of genetic divergence (d) between approximately 0.025 (2.5%) and the maximum value of 0.174 (17.4%) in our sample (Ricklefs and Bermingham 2001). Accordingly, we chose $0.025 \times 1000 = 25$ as the minimum number of nucleotide substitutions (n_s) for speciation to occur with probability $p_s > 0$ (eq. 1).

Among the observed data, 21 of 38 Lesser Antillean lineages (55%) had mtDNA nucleotide divergence values under $d = 0.025$. Thus, one benchmark for judging the fit of a simulation to the observed data was the approximately 55% of lineages that had not achieved species-level differentiation. In comparing the overall fit graphically, the cumulative number of lineages in the simulation was multiplied by $38/1000 = 0.038$ to make the output comparable to the observed data.

The Hawaiian Avifauna

Fleischer and McIntosh (2001) summarized what is known about genetic divergence between Hawaiian taxa and their continental sister taxa. Of 22 avian lineages that colonized the Hawaiian Islands, genetic divergences based on varying amounts of mtDNA sequence have been estimated for 13 lineages. Fleischer and McIntosh assumed that three additional lineages (*Fulica alai*, *Gallinula chloropus sandvicensis*, *Nycticorax nycticorax hoactii*) were recent colonists based on their lack of differentiation in the Hawaiian Islands, and we arbitrarily set their sequence divergence at 1%. Of the re-

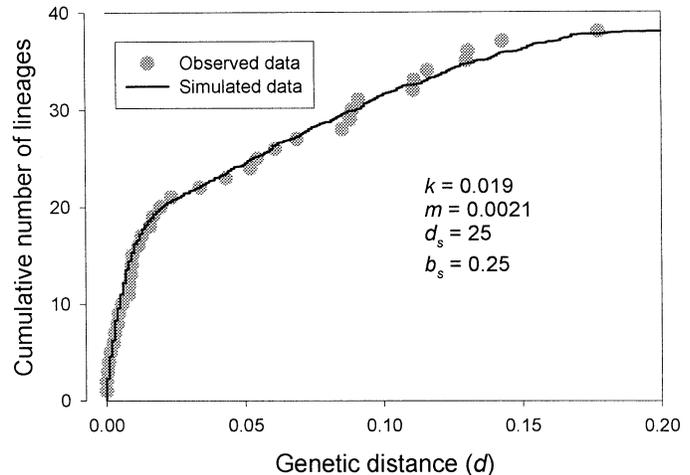


FIG. 1. The speciation-divergence model fits the observed cumulative distribution of genetic divergence values of land birds in the Lesser Antilles closely when the divergence rate $k = 0.019$ and the migration-fixation rate $M = 0.0021$. Simulated data are based on 1000 lineages over 10,000 time steps.

maining six lineages, one (*Asio flammeus sandwichensis*) is almost certainly a recent colonist and the other five (*Circus dosseus*[†], *Grallistrix* sp.[†], *Acrocephalus familiaris*, *Chasiempis sandwichensis*, *Moho* [*Chaetoptila*][†]) are well differentiated but of unknown age ([†] indicates extinct). We analyzed the relationship between colonization time and the species accumulation curve both without these species ($n = 16$), and with estimates of genetic differentiation of 1% for subspecific distinction (*Asio*), 5% for specific distinction (*Circus*, *Acrocephalus*), and 10% for generic distinction (*Grallistrix*, *Chasiempis*, *Moho*) ($n = 22$).

The West Indian Herpetofauna

Hedges (1996) estimated colonization times in millions of years (my) for 38 of 42 endemic lineages of reptiles and amphibians of the West Indies, primarily the Greater Antilles, based on immunological distance. In many cases these estimates were presented as ranges, often very broad, from which we chose the midpoint. We arbitrarily set the colonization times of 35 nonendemic lineages at 1 my, but spreading these colonization times over 5 my did not substantially affect the fitted constants in the model. Although immunological distance provides a scale of relative age (Prager 1993), the accuracy and applicability of this approach to the West Indian herpetofauna are not uniformly agreed upon (Crother and Guyer 1996; Hedges 1996).

RESULTS

Lesser Antillean Land Birds

For our initial simulations, we used $b_s = 0.25$ as the exponential rate of approach to complete speciation and a speciation threshold (d_s) of 0.025 ($n_s = 25$ nucleotide substitutions). Using a systematic search over the potential parameter space, we determined that a divergence rate of $k = 0.019$ and a migration-fixation rate of $M = 0.0021$ produced an output that described the observed data well (Fig. 1).

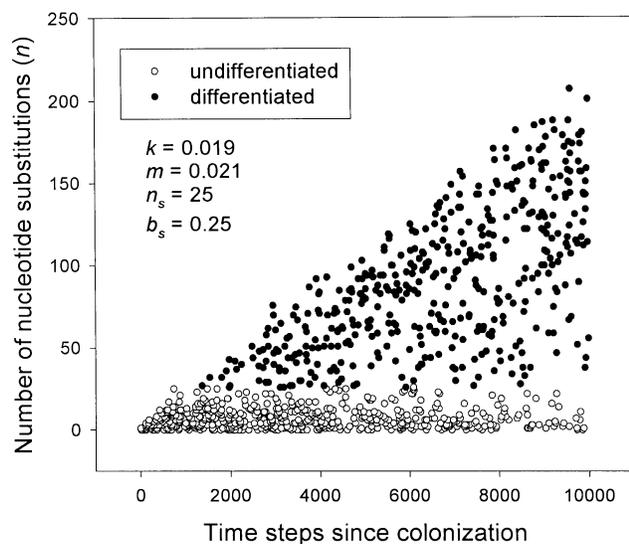


FIG. 2. Genetic divergence (number of nucleotide substitutions) as a function of colonization time. Differentiated lineages are represented by solid circles. Simulation parameters as indicated in Figure 1.

This simulation produced 560 (56%) undifferentiated lineages, with an average of $n = 7.4 \pm 6.2$ SD nucleotide substitutions (0.74% sequence divergence), and 440 differentiated lineages, with an average of 92.4 ± 45.5 SD nucleotide substitutions (9.2% sequence divergence). The average age of colonization events was 3843 ± 2751 time steps for undifferentiated lineages and 6670 ± 2353 time steps for those that had achieved species status. Finally, the average time to speciation following colonization was 3190 ± 1905 SD time steps. Fig. 2 shows the relationship between speciation status, genetic divergence, and time since colonization.

We explored the effect of varying the migration-fixation rate (M) on the proportion of lineages that had not achieved species status, keeping the remaining parameters constant. As expected, the proportion of such lineages increases with M (Fig. 3). It has a minimum value of about 15% at $M = 0$ because a proportion of lineages colonized the island too recently to diverge genetically to the speciation threshold of $n_s = 25$. At a divergence rate of $k = 0.019$, achieving the minimum speciation threshold would require an average of $25/0.019 = 1316$ time steps, which is 13% of the total period over which colonization times are uniformly distributed in this simulation. The proportion of lineages not having achieved species status increases asymptotically to 100% as migration rate increases, reaching 90% at a migration rate (0.004), which is about double the fitted value of $M = 0.0021$.

Over the same range of increasing M , the average age of undifferentiated lineages increases and the average genetic divergence decreases (Table 1). Among lineages that become new species, the average time since colonization increased moderately, the average time to species formation increased more dramatically, and the average divergence decreased concomitantly.

The proportion of undifferentiated lineages appears to be insensitive to the rate of exponential increase (b_s) with genetic divergence (n) in the probability of speciation. For our ‘‘stan-

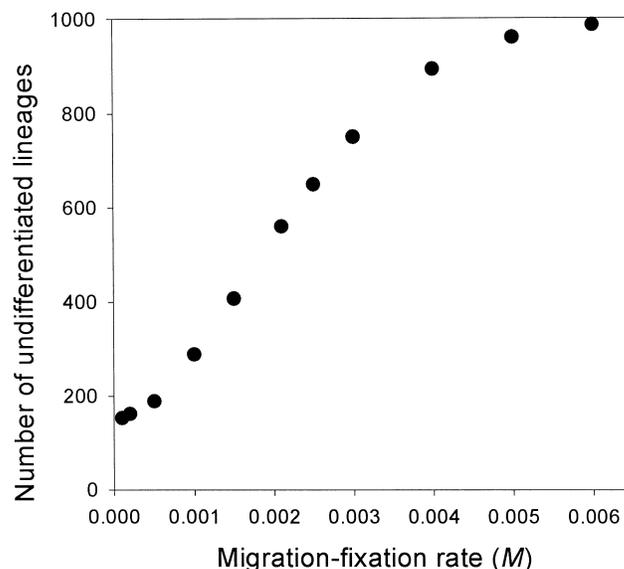


FIG. 3. Number of undifferentiated lineages per 1000 as a function of the migration-fixation rate (M). All other parameters as in Figure 1.

ard’’ simulation with parameters $M = 0.0021$, $k = 0.019$, $n_s = 25$, the number of undifferentiated lineages out of 1000 varied between 558 for $b_s = 0.0625$ and 546 for $b_s = 1$. Over the same range, the number of nucleotide substitutions at achieving 90% probability of speciation (n_{90}) varied between 28 ($n_{90} = 25 + 3$) for $b_s = 1$ and 62 ($n_{90} = 25 + 37$) for $b_s = 0.0625$, as shown in Table 2. Thus, the important step toward speciation is reaching the minimum genetic divergence for speciation rather than the rate at which the probability of speciation increases with further genetic divergence.

The proportion of undifferentiated lineages clearly reflects the interaction between the speciation threshold and the rates of migration and genetic divergence. As the speciation threshold decreases, all other parameters remaining equal, the proportion of undifferentiated lineages decreases. Thus, to obtain the observed level of undifferentiated lineages (55%) in simulations with different speciation thresholds, the rate of migration must be increased as the speciation threshold is decreased (Table 3). Accordingly, we obtained reasonable fits to observed data over a large portion of the parameter space.

The foregoing simulations were based on initial colonization times distributed uniformly over 10,000 time steps. In another version of the speciation-divergence model, all lineages colonized the island at the first time step. In this simulation, the observed data were matched closely for $n_s = 25$ and $b_s = 0.25$ when $k = 0.013$ and $M = 0.0018$ (Table 4 and Fig. 4). These parameters do not differ substantially from the fit of $k = 0.019$ and $M = 0.0021$ in the case of uniformly distributed colonization times. Thus, the speciation-divergence model appears to be relatively insensitive to the distribution of colonization times.

The Hawaiian Avifauna

The colonization-extinction model with unchanging rates and the speciation-divergence model fit the observed distri-

TABLE 1. Variation in number of undifferentiated lineages $N(NS)$, average age (t_i) of lineages that have or have not achieved species status, average time to speciation (t_s), and average genetic divergence (n) as a function of the migration-fixation rate M , with other parameters in the simulation held constant at $k = 0.019$, $n_s = 25$, and $b_s = 0.25$. The simulations included 1000 independent lineages and 10,000 time steps.

M	0.0001	0.0002	0.0005	0.0010	0.0015	0.0021	0.0025	0.003	0.004	0.005	0.006
$N(NS)$	153	162	189	289	407	560	650	751	893	960	986
Species status not achieved											
t_i	831	926	1255	1889	2918	3843	3952	4364	4840	3836	4984
SD	571	719	1014	1681	2306	2751	2704	2810	2927	2911	2904
n	12.31	12.35	11.56	9.99	8.21	7.41	6.44	5.90	4.50	3.63	3.03
SD	7.28	7.51	6.97	7.51	6.80	6.24	5.91	5.55	4.66	3.96	3.37
Species status achieved											
t_i	5800	5702	5811	6286	6237	6670	6758	6737	6723	6791	6868
SD	2497	2408	2408	2340	2353	2350	2220	2101	2150	2334	1801
t_s	1460	1483	1824	2314	2853	3190	3478	3722	3529	3586	4025
SD	429	486	824	1319	1677	1905	1971	1936	2117	1793	1627
n	109.0	106.0	102.0	101.6	90.4	92.42	88.1	84.1	87.34	85.85	78.79
SD	48.49	46.44	46.85	45.69	42.97	45.47	43.89	41.66	42.57	42.27	33.38

TABLE 2. The effect of varying the exponential rate of approach (b_s) to a speciation probability (p_s) of 1 on the time to $p_s = 0.90$ and the proportion of undifferentiated lineages in simulations with $k = 0.019$, $n_s = 25$, and $b_s = 0.25$. The simulations included 1000 individuals and 10,000 time steps. n_{90} is the genetic divergence at which the speciation probability reaches 90%.

b_s	$N(NS)$	n_{90}
0.0625	558	62
0.125	556	44
0.25	560	35
0.5	583	30
1	546	28

bution of colonization times well (Fig. 5). We do not report the results of fitting a mass-extinction model because the data did not indicate such an event. With 16 species, nonlinear least squares regression fitting of the homogeneous colonization-extinction model provides parameter estimates of colonization rate (C) of 386 ± 38 SE (95% CI, 305–468) and extinction rate (E) of 22.6 ± 4.0 (14.1–31.1). The units are the probability of a colonization event in the archipelago, and the probability that a resident lineage in the archipelago will become extinct, per unit (100%) of mtDNA sequence divergence. Assuming approximately 2% sequence divergence per 1 million years, these estimates divided by 50 are equivalent to rates per million years, that is, $C = 7.7$ and $E = 0.45$ per million years. With all 22 species included in the analysis, estimates were $C = 388 \pm 29$ (327–449) and $E = 15.1 \pm 2.4$ (10.1–20.1), or 7.8 and 0.3 per million years, respectively. The ratio C/E defines the number of lineages at the colonization-extinction equilibrium. These ratios were 17.1 and 25.7, respectively, which indicates that the lineage diversity of the islands is close to the colonization-extinction equilibrium. The colonization rate is much lower than the value of 1600–1700 per unit mtDNA sequence divergence estimated for the subset of land birds in the Lesser Antilles (Ricklefs and Bermingham 2001).

The observed colonization times for Hawaiian island birds also conform closely to a speciation-threshold model (Fig. 5). With all 22 lineages included, the data are modeled over 10,000 time steps with rates per time step for divergence of $k = 0.011$ and migration-fixation of $M = 0.00045$, setting the speciation threshold at 25 nucleotide substitutions with $b_s = 0.25$. The statistics for lineages are shown in Table 5.

The West Indian Herpetofauna

The cumulative distribution of colonization times for reptiles and amphibians within the West Indies as a whole re-

TABLE 3. Fitted values of M that produce about 55% undifferentiated lineages when the speciation threshold (n_s) was varied between 15 and 30 (1.5 and 3.0% sequence divergence). For these simulations, $k = 0.019$ and $b_s = 0.25$.

n_s	M
15	0.0046
20	0.0030
25	0.0021
30	0.0015

TABLE 4. Statistics for the case in which all lineages colonize the island from the source at the beginning of the simulation period. t_i , age of lineages (time steps since colonization); t_s , time steps to speciation; n , genetic divergence between island and source populations (number of nucleotide substitutions).

	Lineages	t_i	t_s	SD	n	SD
Undifferentiated	530	10,000			6.29	5.95
Differentiated	470	10,000	5216.5	2512.5	88.24	33.16

sembles the distribution for birds of the Lesser Antilles (Fig. 6). Accordingly, a homogeneous colonization-extinction model would not provide a good fit to the data. We fitted a mass-extinction model with homogenous rates of colonization (C) and background extinction (E) overlaid by a mass extinction event at 2 my survived by proportion S of lineages. The close fit (Fig. 6) provides parameter estimates of $C = 19.6 \pm 0.9$ (95% CI, 17.7–21.5), $E = 0.027 \pm 0.014$ (–0.001–0.054), and $S = 0.062 \pm 0.020$ (0.021–0.103). Background extinction for reptiles and amphibians is close to zero, with an estimated average persistence time of lineages of almost 40 my, and the contemporary (post mass extinction) rate of colonization in the herpetofauna as a whole is about 20 lineages per my. This colonization rate estimated under a mass-extinction model is not substantially less than that estimated for birds in the Lesser Antilles (about 32–34 my⁻¹).

Hedges (1996) estimated the oldest lineages of West Indian reptiles and amphibians to be 70 my, which corresponds approximately to the Cretaceous-Tertiary boundary. For simulations of the speciation-threshold model, we set the time scale to 0.0065 my per time step, which gives an estimated time over 10,000 time steps of 65 my. The model provides a close fit to the data with the following variables: divergence rate $k = 0.0065$ my per time step, migration-fixation rate $M = 0.03$ per time step, speciation threshold $d_s = 2.4$ my, and $b_s = 0.25$ (Fig. 6). The estimated frequency of migration-fixation is equivalent to $M = 4.6$ per my, or a migration-fixation event within each island resident population every 0.22 my. Statistics for the lineages that had and had not achieved species status are presented in Table 6. Divergence

(d) is expressed in my and the times are expressed in number of time steps, as in related tables.

When the colonization times of the nonendemic lineages were spread uniformly over 5 my, a reasonable fit to the data was obtained with fitted parameters $d_s = 10$, $b_s = 0.25$, $k = 0.0065$, and $M = 0.0022$ (results not shown). In this case, the predicted curve initially rises more steeply than the data. The fit is improved by increasing d_s to 20 ($k = 0.0065$, $M = 0.00085$) but, as a result, many endemics are classified as undifferentiated (73% of all lineages).

DISCUSSION

For the land birds of the Lesser Antilles, the models proposed by Ricklefs and Bermingham (2001) employed change in colonization or extinction rates, or a mass extinction event, to explain the abrupt change in the lineage accumulation rate prior to a genetic distance of 2.5% mtDNA sequence divergence. Thus, the heterogeneity in the lineage accumulation curve was caused by changes in external environmental factors. The model of Johnson et al. (2000) differs in that neither changes in rates nor a transient event is required to account for the apparent heterogeneity in the lineage accumulation rate. This is produced in their model by an internal factor: a speciation threshold that separates lineages in two groups, one of which diverges slowly (before speciation) and the other rapidly (after speciation) from source populations. Because the different models fit the observed data equally well, evaluating the applicability of the models will depend on how well the fitted parameters conform to other information about rates of migration and divergence and the genetic dis-

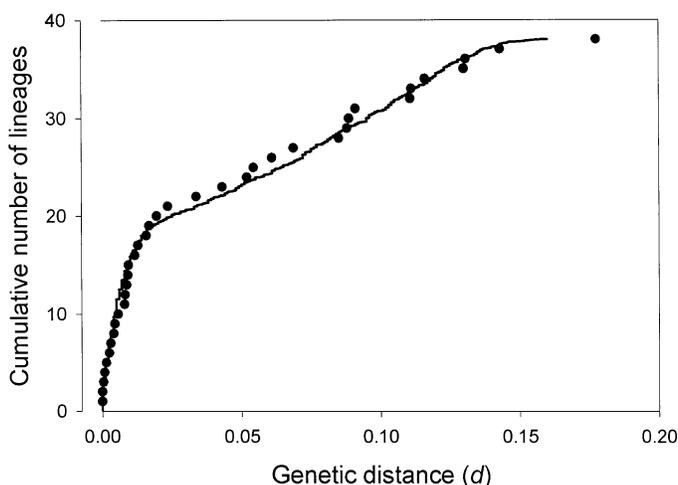


FIG. 4. The fit of the simulated lineage accumulation curve to the observed data for land birds of the Lesser Antilles when all lineages colonize at time 0 and $k = 0.013$ and $M = 0.0018$. Other parameters as in Figure 1 ($n_s = 25$, $b_s = 0.25$).

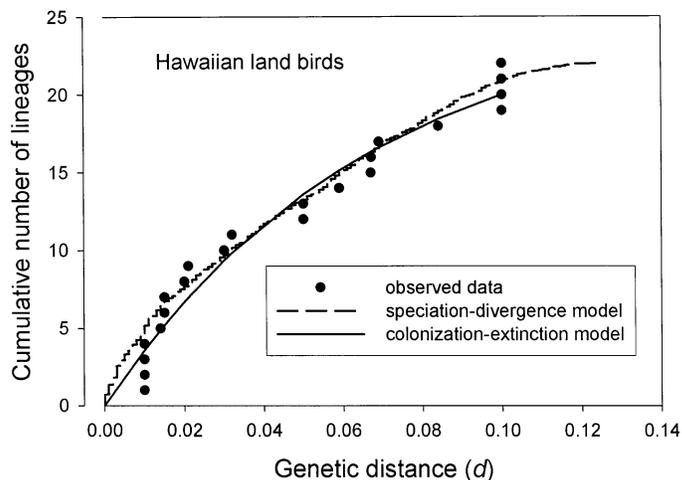


FIG. 5. Three models fit to the lineage accumulation with genetic distance in Hawaiian birds. Data from Fleischer and McIntosh (2001); see text for explanation and fitted constants.

TABLE 5. Simulation statistics for a speciation-divergence model of colonization times of birds of the Hawaiian Islands. Colonization times are drawn from a uniform random distribution over the 10,000 time steps of the simulation. t_i , age of lineages (time steps since colonization); t_s , time steps to speciation; n , genetic divergence between island and source populations (number of nucleotide substitutions).

	Lineages	t_i	SD	t_s	SD	n	SD
Undifferentiated	399	2730	2210			9.7	7.4
Differentiated	601	6785	2131	3295	1536	63.9	24.3

tance associated with species formation. The land birds of the Lesser Antilles are particularly well suited for comparing these models in that they offer additional predictions concerning the geographic structure of genetic variation among islands within the archipelago. We shall return to this property below.

The Migration-Fixation Rate

For the land birds of the Lesser Antilles, we ask whether the fitted migration-fixation rate of $M = 0.0021$ per time step is reasonable in the context of what we know about the colonization of islands and the genetic relationships among island populations in the Lesser Antilles. When we equate the time step in our simulations to 1000 years, the rate of genetic divergence over 1000 nucleotides of mtDNA sequence is equivalent to genetic divergence at a rate of 1.9% per my. This value is similar to estimates based on calibrations for birds (Shields and Wilson 1987; Klicka and Zink 1997; Fleischer et al. 1998; Lovette 2004) and suggests that a 10 million-year simulation period reasonably approximates the history of the contemporary Lesser Antillean avifauna. Accordingly, a rate of $M = 0.0021$ per time step (1000 years) would be equivalent to the fixation of continental nucleotide substitutions in an island population at a rate of 2.1 events per my and an average waiting time between successful migration-fixation events of about 0.48 my.

The fitted migration-fixation interval of 0.48 my implies that the accumulation of nucleotide differences over the average interval between migration events would be $0.48 \text{ my} \times 0.019$ substitutions per nucleotide per my $\times 1000$ nucle-

otides = 9.05 substitutions. In addition, the simulations indicate that at this rate about 44% of the lineages will cross the speciation threshold within the 10^7 years of the simulation interval, with a mean time to speciation of about 3.2 my (i.e., six migration-fixation intervals; see Table 1 for simulation results).

For an island population of N females, the probability that the mtDNA haplotype of a single female colonist will become fixed in the population by drift is $1/N$, and the average time in generations required for fixation (the coalescence time) is N (Hartl and Clark 1997). For example, for a population size of $N = 10,000$ females, the probability of fixation of a single mtDNA haplotype is 0.0001 (10^{-4}) per generation. Thus, to achieve a rate of migration-fixation of $M = 2.1 \times 10^{-6}$, females from the source population would have to immigrate to an island population at a rate of $m = 2.1$ per hundred years, assuming one year per generation.

This rate of migration is consistent with the rapid spread of several species (shiny cowbird *Molothrus bonairiensis* and bare-eyed thrush *Turdus nudigenis*) through the Lesser Antilles during the 1900s (Bond 1956) and the continuous distributions without genetic differentiation of many recent colonists across the islands (Raffaele et al. 1998; Ricklefs and Bermingham 1999). However, it is not consistent with gaps in the distributions of older (>1 my) lineages (Ricklefs and Cox 1972; Ricklefs and Bermingham 1999), implying that migration rates do not remain constant through time, particularly up to the average time to speciation of 3.2 my indicated by our simulations. Nor is it consistent with the absence of multiple colonization events to single islands in the archipelago following achievement of the speciation threshold.

The oldest colonization times in the Hawaiian avifauna occur at $d = 0.10$, which we presume corresponds to about 5 my, close to the age of the oldest of the present-day large islands (Kauai, 5.1 my; Wagner and Funk 1995). Thus, a convenient calibration in our 10,000-step simulation model is 2000 time steps per my (my^{-1}), and the fitted constants are thus equivalent to a nucleotide divergence rate of $2.2\% \text{ my}^{-1}$ and a migration-fixation rate (M) of 0.9 my^{-1} . The migration-fixation rate seems unrealistically high in this case. The average mtDNA sequence divergence of Hawaiian land bird lineages is 4.7%, which corresponds to about 2.35 my, or an average colonization rate (inverse of the waiting time to colonization) among successful colonists of 0.42 my^{-1} . Because migration-fixation rates for neutral alleles by genetic drift are on the order of the migration (\approx colonization) rate (m) divided by population size, a migration-fixation rate within even several orders of magnitude of the estimated colonization rate is unrealistic. Thus, although a speciation-divergence model fits the observed data closely, the model probably is not applicable. This is not surprising for such a

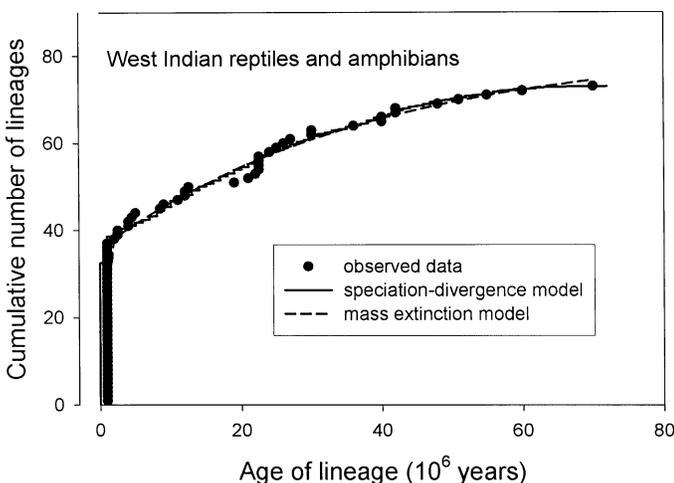


FIG. 6. Speciation-divergence and mass-extinction models fitted to the cumulative distribution of lineages with respect to age in the West Indian herpetofauna, based on data in Hedges (1996).

TABLE 6. Simulation statistics for a speciation-divergence model of colonization times of reptiles and amphibians of the West Indies. Colonization times are drawn from a uniform random distribution over the 10,000 time steps of the simulation. t_i , age of lineages (time steps since colonization); t_s , time steps to speciation; d , the divergence time in my.

	Lineages	t_i	SD	t_s	SD	d	SD
Undifferentiated	540	3931	2757			0.20	0.45
Differentiated	460	6416	2445	2941	2229	25.4	15.9

remote island group that receives potential colonists at very long intervals. However, the same inconsistency applies to the birds of the Lesser Antilles.

The estimated colonization rate in a mass-extinction model for the Lesser Antilles was 33 species my^{-1} years (Ricklefs and Bermingham 2001). If the 21 species having divergence times less than 0.025 represented the entire source pool for recent colonization, the colonization rate per species would be about 1.5 my^{-1} , and less if the source pool were larger. Thus, the migration-fixation rate of 2.1 my^{-1} years is too high by comparison. The only way to reconcile this discrepancy in the speciation-divergence model is to assume very high rates of migration, with most species reaching the archipelago soon after islands were available for colonization (e.g., Fig. 4). Of course, this does not explain the absence from the archipelago of so many of the source-area species or gaps in the distribution of older Lesser Antillean endemics.

The estimated migration-fixation rate under the speciation-threshold model for the West Indian herpetofauna also seems very high. The colonization rate in the herpetofauna as a whole (73 endemic lineages over 65 my) is close to one per my, and the colonization rate per lineage is probably on the order of 0.01–0.1 my^{-1} , which makes a migration-fixation rate of 4.6 my^{-1} several orders of magnitude too high, especially considering that populations of many reptiles and amphibians on the larger islands might number in the tens of millions (Ricklefs and Lovette 1999). Even when the colonization of nonendemic lineages is spread over 5 my, and the speciation threshold (d_s) is increased from 2.4 to 10 or 20 my, the estimated migration-fixation rates of 0.34 and 0.13, respectively, are still high and the speciation threshold is unrealistically long. Although dispersal of individuals (m) to an established island population of size N is undoubtedly much more likely than an initial colonization event, it is unlikely that m/N , the estimated probability of fixation of a migrant mitochondrial allele, would approach the migration-fixation rates estimated under any of these sets of parameter values.

The Speciation Threshold

Although the speciation-threshold model can approximate a particular distribution of divergence values, the threshold value itself must also be realistic. Where the distribution of genetic divergence values show an obvious break, as in the case of the Lesser Antillean land birds, the model speciation threshold is clearly defined and offers little room for adjustment. Does an mtDNA distance of 0.025 (2.5%) represent enough genetic divergence to prevent reproduction through either pre-mating or post-mating mechanisms? Differences between populations of the same “species” on different islands range up to 7%. We surveyed 32 monophyletic lineages of

passerine birds within the Lesser Antilles, 30 of which were represented by two or more island populations (Ricklefs and Bermingham 2001). Of these, 19 exhibited Tamura-Nei distances greater than 0.5% ($d = 0.005$) between at least one pair of islands, which exceeds more than 97% of within-population genetic distances. Twelve species had interisland divergences exceeding 1%, and 8 exceeded 2%.

Genetic divergence between geographically distinct populations within continental species (incipient species, perhaps) ranged up to 8.5% (average $2.5 \pm 2.1\%$ SD, $n = 26$; Avise and Walker 1998). Between continental “species” in the same genus, many of them sympatric, surveys of mtDNA genetic distances have shown ranges between 1.6 and 7.3% ($4.4 \pm 1.9\%$ SD, $n = 11$; Seutin et al. 1993) and between 0.4 and 10.9% ($5.1 \pm 3.0\%$ SD, $n = 35$; Klicka and Zink 1997). Among allopatric “species” of the thrasher genus *Toxostoma*, genetic distances averaged 5.2% (3.1 SD, $n = 11$ pairwise comparisons), and among sympatric species, d averaged 9.3% (1.1 SD, $n = 6$; Zink et al. 1999).

Darwin’s finches (Geospizinae) of the Galapagos Islands exhibit smaller genetic distances between sympatric species ($<0.7\%$ within *Geospiza*, $n = 5$; $<1\%$ within *Camarhynchus*, $n = 4$; Sato et al. 1999). Indeed, Zink (2002) seriously suggested that patterns of genetic variation do not reject the hypothesis that all *Geospiza* belong to a single species. Even between recognized genera, however, genetic distances are modest (*Platyspiza-Certhidia*, 3.9%; *Camarhynchus-Platyspiza*, 2.6%). The Darwin’s finches are exceptional in that many species hybridize readily (P. R. Grant and B. R. Grant 1996, 1997a; B. R. Grant and P. R. Grant 1998); reproductive isolation is effected by song discrimination rather than relying on genetic incompatibility (B. R. Grant and P. R. Grant 1996; P. R. Grant and B. R. Grant 1997b).

The data generally suggest that genetic distances between full species average about twice the speciation threshold of 2.5% mtDNA sequence divergence used to fit the speciation-divergence model to birds of the Lesser Antilles. However, genetic distance varies considerably among named species and some exhibit genetic distances of 2% or even less. In addition, the accumulation of neutral mitochondrial nucleotide substitutions at the point of reproductive isolation might be lower among island populations where selection for ecological and behavioral diversification in species-poor faunas could be strong. This is implied by the rapid morphological diversification of some bird lineages in the Galapagos and Hawaiian Islands (e.g., Lovette et al. 2002), which appears to be associated with secondary sympatry of sister species with relatively little genetic divergence (Grant 1998).

If speciation of Lesser Antillean populations from source populations were prevented by a high rate of migration, one would expect secondary invasions of islands following spe-

ciation events that did occur. However, there are no cases in the Lesser Antilles of two or more closely related species of colonists on any single island that were sequentially derived from the same source population (Raffaele et al. 1998, E. Bermingham and R. E. Ricklefs, unpubl. data). Two cases might represent multiple invasions of distinct genetic haplotypes of the same species from one source to a single island, but these require further investigation. The population of the house wren (*Troglodytes aedon*) on Grenada harbors two mtDNA haplotypes differing by 4.1% and <0.1% from populations in Venezuela and Trinidad (E. Bermingham and R. E. Ricklefs, unpubl. data). However, the two mainland reference sequences came from different localities, and so they may represent different source populations, as we have seen in the Caribbean grackle (*Quiscalus lugubris*). Nonetheless, it would appear that an mtDNA genetic distance of 4.1% was below the speciation threshold in this case, unless two cryptic species of house wrens occur on Grenada.

The population of the yellow-bellied elaenia (*Elaenia flavogaster*) on Grenada has two haplotypes that are 0.1 and 0.7% distant from contemporary haplotypes in the source population on Trinidad. The higher level of genetic divergence occasionally occurs within populations and we do not know whether additional sampling of the Trinidad population might reveal the more distant haplotypes there as well. Regardless of these details, the high colonization rates required by the speciation-divergence model should be accompanied by frequent multiple colonization of islands from the source and a rapid buildup of sympatric species through adaptive radiation within the archipelago. Except for the endemic radiation of four species of thrashers (Mimidae; Hunt et al. 2001: minimum genetic divergence = 0.104) and two hummingbirds of the genus *Eulampis* (genetic divergence = 0.069), this has not happened in the Lesser Antilles. Indeed, the endemic radiations suggest a higher speciation threshold than 0.025.

Geographic Structure

With respect to archipelagoes such as the Lesser Antilles, the speciation-divergence model also predicts that islands closest to the source would be most similar genetically to the source population when the migration rate is high. If time has been sufficient for speciation between the first island and the source population, there should also have been enough time for speciation between the second island and the first. In the present model, colonization, which is likely to be governed by the migration rate m , is rapid compared to the rate of differentiation. Thus, all ecologically suitable islands would have populations soon after the colonization process begins, as observed in several recent cases and inferred from the lack of genetic differentiation among many widespread species. Because migration, divergence, and speciation occur independently across each gap in the distribution of a species, deep genetic divergence is as likely to arise between two islands as between the first island and the mainland source of colonists. This never happens. There is not a single case in the Lesser Antilles in which the divergence between two islands is greater than that between any one island and the source population. Reconciling this observation with the speciation-divergence model requires a much higher rate of mi-

gration between islands than between the continent and the first island in the chain. This might be the case in the Lesser Antilles because the islands are closer to each other than the first and last islands in the archipelago are to either the South American continent or the Greater Antilles, and because island populations tend to have higher densities in a broader range of habitats (Ricklefs and Bermingham 1999), potentially making dispersal to other islands more likely. However, the implied high rate of interisland movement is not consistent with the genetic divergence of island populations and gaps in the distributions of many species across the archipelago.

Conclusions

The data and model fits presented in this analysis do not provide a clear choice between models for the accumulation of species of small land birds in the Lesser Antilles. Speciation-divergence, heterogeneous colonization, and mass-extinction models all provide excellent fits to the data. However, a speciation threshold of 2.5% mtDNA sequence divergence is probably too low for birds in reasonably diverse avifaunas. Variation in the speciation threshold itself would reduce the abruptness of the change in slope of the species accumulation curve, contrary to the pattern observed in the data and reproduced by a mass-extinction model. The strongest points of evidence disfavoring the speciation-divergence model for Lesser Antillean birds are (1) the lack of multiple colonization events where island species have passed the speciation threshold, (2) the absence of species in which island-island genetic distances exceed the source-archipelago distance, and (3) the extinction of island populations without recolonization from within the archipelago or the source population. Infrequent phases of secondary expansion of taxa within the Lesser Antilles (Ricklefs and Bermingham 2001) suggest that high colonization rates are transient and therefore inconsistent with the continued migration presumed by the speciation-threshold model.

Any ambiguity concerning mechanism represented by the lineage accumulation curve for the Lesser Antillean avifauna disappears in cases where colonization potential is considerably reduced, as in remote islands or groups with poor dispersal ability. When there is little potential for migration to prevent divergence, one does not expect a heterogeneous distribution of genetic divergence values between source and island populations. In this context, we examined data for the avifauna of the remote Hawaiian Islands and the herpetofauna of the West Indies, the latter presumably built up through infrequent colonization by rafting. Moreover, migration-fixation rates in the West Indian herpetofauna should be particularly low owing to the large population sizes of reptiles and amphibians on islands in the Greater Antilles.

In both cases, the estimated rates of migration for the speciation-divergence model are too large, by several orders of magnitude, to be plausible. The Hawaiian avifauna does not exhibit marked heterogeneity of genetic divergence values, and a simple colonization-extinction model described the data adequately, as did a mass-extinction model with a moderate-sized event ($S = 0.40$ at $d = 0.02$ mtDNA sequence divergence). The West Indian herpetofauna exhibits a striking

change in the slope of the lineage accumulation curve caused by assigning a young age to the large number of undifferentiated taxa in the islands. It is unlikely that improved genetic resolution of the relative colonization times would change the pattern markedly or that the fitted migration-fixation constant of the speciation-threshold model would become more acceptable.

Because the speciation-divergence hypothesis remains marginally plausible for birds of the Lesser Antilles, additional studies on species formation and on the more detailed phylogeographic history of the avifauna are priorities. In particular, both high and low source-island divergence values among independent molecular markers within populations would be expected of the speciation-divergence model, whereas uniformly low divergence in recent colonists would favor transient phases of colonization followed by rapid genetic isolation of island populations.

One conclusion from the analyses presented here, which is independent of the particular model adopted, is that barring mass extinctions the background extinction rate of lineages in archipelagoes is very low. In all cases, in the absence of mass extinctions, estimated average persistence times of lineages are at least half the total span represented by the range of colonization times. As a result, a substantial portion of the total colonization history of a group within a region is preserved in the living descendants of the original colonists. This means that much of the material needed to evaluate historical hypotheses concerning the accumulation and maintenance of diversity on islands is available.

ACKNOWLEDGMENTS

K. Johnson, J. Lichstein, T. Simons, two anonymous reviewers, and Associate Editor G. Wallis provided valuable comments on the manuscript. Our research on birds in the West Indies was supported generously by the Smithsonian Institution, the National Geographic Society, and the National Science Foundation, as well as by laboratory and field assistance of G. Seutin and I. Lovette, among others. Fieldwork would not have been possible without the permission, cooperation, and support of many government agencies and individuals throughout the West Indies.

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