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MORPHOLOGICAL EVOLUTION OF BIRDS RECENTLY INTRODUCED TO ISLANDS: PATTERNS OF DIVERSIFICATION

By

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ABSTRACT OF THE DISSERTATION

Morphological evolution of birds recently introduced to islands: patterns of

diversification

by BLAKE MATHYS

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Evolution was originally considered to be observable only over geological time scales. It

has recently become apparent that evolutionary changes can be detected over

contemporary time periods. Exotic species often experience intense selection, making

them good model systems for investigating evolutionary changes over contemporary

time. We often know details of the introductions, such as exact time, location of the

source population, founding propagule size, and establishment history. These details

allow us to formulate hypotheses concerning the evolutionary changes expected in these

species' exotic ranges.

I examined contemporary morphological evolution of passerine birds introduced to islands. Passerine birds have been introduced to many islands world-wide, making them conducive for examining patterns of insular evolution. In chapters one and two, I evaluated whether these species conform to the Island Rule, an ecogeographic rule based on the study of native insular species. It states that, on islands, small species should increase in body size while large species should decrease body size. All of the species I studied are small, therefore they were expected to increase in body size. I found equivocal results concerning the Island Rule. In chapter one, I found that the great kiskadee (*Pitangus sulphuratus*) follows the Island Rule, as it is larger in its exotic island range than in the native source range. However, in chapter two, I found no clear Island Rule pattern examining 39 insular populations. However, I did find a clear pattern of decrease in wing length and increase in tail length. Although these populations may not be following an overall Island Rule pattern, they are still adapting to their exotic environments. In chapter three, I evaluated among-island diversification of six passerine species introduced to the Hawaiian archipelago. Five of these six species show some morphological differentiation between islands, and at least some of this differentiation cannot be accounted for by genetic drift.

The results of this dissertation provide further support for the idea that evolutionary divergence can happen over contemporary time scales. The passerine bird populations examined in these chapters have adapted to local conditions, giving us insights into the genesis of evolutionary diversity.

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INTRODUCTION

Species that experience novel environments are subjected to selection pressures that are entirely new or of a different magnitude than previously encountered. Novelty may arise due to colonization of new areas, climatic changes, or arrival or extirpation of ecologically relevant competitors, predators, or prey. These new selection regimes have the ability to cause evolutionary changes. If selection is strong and consistent, these changes may occur over contemporary time scales (Stockwell *et al.*, 2003). One example of this is Darwin's finches on the Galapagos Islands; they have been shown to evolve in one generation due to extreme climatic selection pressures (Grant & Grant, 1993). Species that arrive in new areas, either naturally or through human-mediated introductions, will often experience very different environments than those found in their native range. If the selective pressures are significantly different and very strong, they will often prevent the successful establishment of the colonizing species (Brooke *et al.*, 1995). However, if a species possesses the necessary evolutionary flexibility, it will be able to adapt to the novel selection pressures and establish a self-sustaining population in the new range. This new population may be quite different from the original source population, dependent on the amount of evolutionary change during and after colonization. This process of differentiation in new ranges is difficult to study in naturally colonizing species, as the original propagule is often not noticed until a self-sustaining population has already established. Further, it is often not known from where the propagule originated. Finally, many natural colonizations have happened in historical times, therefore all that is left to observe are the evolutionary consequences (Grant, 1998). Inferences can be made concerning the evolutionary trajectories that led to modern taxa, but there is no possibility to observe these changes occurring in real time.

Species that have been introduced by humans are conducive to examining the genesis of evolutionary divergence patterns, as most have been introduced in recent times (Sax *et al.,* 2005, 2007). These human-mediated introductions differ from natural colonizations in that we often know details concerning the geographic origin of the original propagule. Also, the exact timing and sequence of introduction events are recorded. These data allow us to determine the rate of evolutionary change as well as observe the differentiation occurring over contemporary time periods.

Birds are especially appropriate for such investigations, as their introductions were often very well documented. Birds were commonly introduced by private individuals or by acclimatization societies for aesthetic or sentimental reasons. Acclimatization societies often kept detailed records, and some, like the Hui Manu in Hawaii (Dillingham, 1936), published newsletters documenting their activities. Other exotic birds were translocated for biocontrol purposes. These introductions were generally carried out by government agencies, which also documented their efforts. These data make exotic birds very useful model systems for examining evolutionary changes (Long, 1981).

Birds have been preferentially introduced to islands (Blackburn *et al.*, 2009). Islands are very amenable to examinations of evolution, as they are simplified systems that have fewer confounding factors (such as lower overall species richness and habitat diversity) than mainland areas. The reduction of these factors makes it easier to assign mechanisms to observed evolutionary changes, as the number of variables is smaller than in continental habitats (Vitousek, 2002). The combination of the large number of exotic birds on islands as well as the simpler nature of islands makes study of exotic insular

birds an especially appropriate group for observing evolutionary divergence over contemporary time periods.

There is some evidence of exotic taxa evincing evolutionary change that is consistent with classic biogeographical theory (Johnston & Selander, 1971; Huey et al., 2000); however, most exotic species are not examined in this manner, therefore it is not known how commonly adaptive evolution occurs in introduced taxa.

The Island Rule is one biogeographical pattern that lends itself to examination using exotic birds. The Island Rule states that species will change in body size after establishing island populations. It was originally envisioned as a taxonomically dependent pattern, positing that some taxa (e.g., Artiodactyla) will become smaller in body after establishing an insular population (Foster, 1962, 1965). Conversely, it was proposed that other taxa (e.g. Rodentia) on islands would increase in body size. Later, the Island Rule in mammals was said to "have fewer exceptions than any other ecotypic rule in animals" (Van Valen, 1973), and was eventually modified to be dependent on size instead of taxonomy (Lomolino, 1985). In subsequent years, the Island Rule has been generalized to many non-mammalian taxa (Lomolino, 2005), including birds (Clegg & Owens, 2002).

In my first chapter, "Rapid evolution of great kiskadees on Bermuda: an assessment of the ability of the Island Rule to predict the direction of contemporary evolution in exotic vertebrates", I use a single human-introduced population to determine whether the Island Rule is operating over a contemporary time scale. The great kiskadee, a passerine bird in the New World flycatcher family (Tyrannidae), was introduced to

Bermuda for biocontrol purposes. This introduction event was well-documented with regard to source population, propagule size, and time of introduction, therefore I am able determine whether differences found are attributable to genetic drift or adaptive selection needs to be invoked. In order to compare the morphology of kiskadees in the exotic and the native source range (Trinidad), I traveled to these two locations and captured individuals to measure. These measurements were compared between locations to determine whether any morphological differentiation has occurred in the time since this species was introduced to Bermuda, and whether the observed differentiation follows an Island Rule pattern.

My second chapter is titled "Contemporary evolution of exotic bird morphology in response to insularization: does the Island Rule hold for exotic passerines?" This chapter continues my examination of the Island Rule, examining many species introduced to various islands. The methodology for chapter two is similar to chapter one, in that I obtained morphological measurements of exotic birds within several non-native island populations. However, unlike the kiskadee study, information on morphological dimensions in the native range was obtained from museum specimens. In addition, some data concerning exotic populations was also taken from museum collections. This allowed me to test a much broader range of species originating from diverse geographical areas. I collected field data in Bermuda, Puerto Rico, and Hawaii. I visited museums in Bermuda, Hawaii, the United Kingdom, and the United States to obtain museum measurements. These comparisons allowed me to determine whether an Island Rule pattern was in evidence across many species on multiple islands. I also examined change

of individual morphological characters (as opposed to overall body size metrics as I did for the Island Rule analysis) for these same populations.

In my final chapter, "Contemporary morphological diversification of passerine birds introduced to the Hawaiian archipelago", I used data from the second chapter to determine whether the species that have been introduced to Hawaii have differentiated among islands. This analysis was different from the first two chapters, in that it used data only from the introduced populations. I used these data to compare conspecific island populations in order to determine whether they differ in morphology. I also evaluated whether these morphological differences were likely due to genetic drift or are the result of adaptive evolution.

All three chapters were written with my advisor, Dr. Julie L. Lockwood. The first chapter is formatted for the *Journal of Biogeography* and was published there (Mathys & Lockwood, 2009). The second chapter is formatted for *Global Ecology & Biogeography*, and will be submitted to that journal. Chapter three is formatted for *Proceedings of the Royal Society B: Biological Sciences*, and will be submitted there.

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Chapter 1

Article Type: Original Article

Article Title: Rapid evolution of great kiskadees on Bermuda: an assessment of the ability of the Island Rule to predict the direction of contemporary evolution in exotic vertebrates

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Running head: Rapid morphological evolution in an exotic bird population

ABSTRACT

Aim To determine whether an exotic bird species, the great kiskadee (*Pitangus sulphuratus*), has diverged in morphology from its native source population, and if so, has done so in a manner predicted by the Island Rule. The Island Rule predicts that insular vertebrates will tend towards dwarfism or gigantism when isolated on islands, depending on their body size. For birds, the Island Rule predicts that species with body sizes below 70 to 120 g should increase in size. The great kiskadee has a mean mass of ~60 g in its native range; therefore, we predicted that it would increase in size within the exotic, and more insular, Bermuda range.

Location The islands of Bermuda (exotic population) and Trinidad (native source population).

Methods We took eight morphological measurements on 84 individuals captured in the exotic (Bermuda) population and 62 individuals captured in the native source (Trinidad) population. We compared morphological metrics between populations using univariate and principal component analyses. We assessed whether the effects of genetic drift could explain observed differences in morphology. We calculated divergence rates in haldanes and darwins for comparison with published examples of contemporary evolution. Finally, we used mark–recapture analysis to determine the effects of the measured morphological characters on survivorship within the exotic Bermuda population.

Results Individuals in the exotic Bermuda population have larger morphological dimensions than individuals in the native source population on Trinidad. The degree of divergence in body mass (g) and bill width (mm) is probably not due to genetic drift. This rate of divergence is nearly equal to that observed amongst well-documented examples of contemporary bird evolution, and is within the mid-range of rates reported across taxa. There is no clear effect of body size on survivorship, as only one character (bill width) was found to have an influence on individual survivorship.

Main conclusions Exotic species provide useful systems for examining evolutionary predictions over contemporary time-scales. We found that divergence between the exotic and native populations of this bird species occurred over approximately 17 generations, and was in the direction predicted by the Island Rule, a principle based on the study of native species.

INTRODUCTION

Although evolutionary processes were originally envisioned to occur over thousands of generations (Darwin, 1859), over the last few decades it has become clear that significant divergence can occur over contemporary time-scales (Thompson, 1998; Stockwell *et al.,* 2003). Much of this evidence comes from exotic species that have evolved novel morphologies or life history traits in response to the conditions they experienced in their non-native range (Johnston & Selander, 1971; St. Louis & Barlow, 1988; Gilchrist *et al.,* 2004; Maron *et al.,* 2004; Amiot *et al.,* 2007). These studies add to our overall understanding of evolution via the unprecedented information available concerning their date of initial isolation from the native population, propagule geographical origin, and number of founding individuals; all of these are typically unavailable for natural colonization events. More broadly, the evolution of exotic species allows us the opportunity to observe in real time the production of large-scale biogeographical patterns such as body size clines in response to climate (Huey *et al.,* 2005; Lomolino *et al.,* 2006; Blackburn *et al.,* 2009). In this sense, the study of exotic species can serve as an 'experimental arm' of biogeography (Sax *et al.,* 2005, 2007).

Islands have historically been an epicentre for the study of evolution and biogeography. They provide simplified systems where effects can be more clearly ascertained due to the reduction of confounding variables as compared to mainland areas (Vitousek, 2002). Islands tend to be depauperate in species and often less geographically diverse than comparable mainland regions. This trend is also manifest across islands of various sizes, such that smaller more isolated islands are less biologically and physically diverse than larger well-connected ones. More recently, islands have figured prominently

in studies of contemporary evolution in birds (Boag & Grant, 1981; Grant & Grant, 1993, 2002, Frentiu *et al.*, 2007). Indeed, birds provide a unique opportunity to explore the prevalence of contemporary evolution of exotic species because they have been preferentially introduced to islands world-wide (Blackburn & Duncan, 2001). As a result, there are now dozens of established exotic bird populations across islands such as Hawaii, New Zealand, Tahiti, Puerto Rico and Bermuda (Blackburn & Duncan, 2001; Blackburn *et al.,* 2009). Nearly all of the exotic bird species established on islands are native to a mainland region, thus they also collectively provide an unprecedented opportunity to explore contemporary evolution of exotic species in response to recent insularization.

Many birds were introduced to islands by acclimatization societies or private individuals for aesthetic or sentimental reasons (Blackburn *et al.,* 2009). These entities kept detailed records on the year in which an exotic bird was introduced, the number of individuals of each species released, and the native source population for each species introduced. This information allows for the unbiased quantification of divergence rates, and for a way to assess the role of genetic drift in accounting for observed changes. Such information is rarely available for other exotic taxa, much less for colonizations by native species.

If we accept that these island-dwelling exotic birds have the potential to evolve in the time since they became established, we can then refer to well-accepted biogeographical theories to generate *a priori* expectations as to how evolution should proceed (Lomolino *et al.,* 2006). In the case of islands, their broad-scale and consistent characteristics have led to a clear trend in body size evolution among (native) vertebrates,

which was first recognized by Foster (1964, 1965). This trend was originally described for mammals, and predicted that certain orders (e.g., Artiodactyla and Carnivora) evolve to smaller size on islands, while others (Rodentia, Lagomorpha) display the opposite pattern. No discernible trend was found for some mammalian taxa (e.g., Insectivora). Van Valen (1973) first used the term 'Island Rule' to describe this pattern and suggested that it was more consistent than any other ecogeographical rule. Lomolino (1985) modified the Island Rule to be size-based instead of taxon-dependent. He suggested that large mammals evolve to get smaller on islands whereas small mammals evolve to get larger. Recently, Lomolino (2005) generalized the rule to a variety of taxa. The Island Rule predicts a middle-point where no change is expected, although this 'tipping point' changes according to taxon (Brown *et al.,* 1993). Clegg & Owens (2002) and Lomolino (2005) demonstrated that phenotypic evolution of island birds follows the Island Rule, and that the tipping point for change is between 70 and 120 g. We should thus expect nearly all exotic birds established on islands to increase in size (most weigh <70 g; Dunning, 1992).

We address the ability of the Island Rule to predict morphological shifts in the great kiskadee (*Pitangus sulphuratus* L.) between an exotic population on Bermuda and its native population of origin on Trinidad. The great kiskadee is a passerine bird from the New World flycatcher family (Tyrannidae), with a native range spanning from southern Texas to central Argentina and including the island of Trinidad. Its average mass ranges from 55 to 74 g over its large native range (Brush & Fitzpatrick, 2002). The kiskadee is a very catholic forager, and because of its habit of eating lizards, was introduced to Bermuda in 1957. The Commonwealth Institute of Biological Control hoped that the

kiskadee would consume the three exotic *Anolis* lizard species, especially *Anolis grahami*, resulting in a trophic cascade eventually benefiting an endemic tree, the Bermuda cedar (*Juniperus bermudiana*) (Wingate, 1957, 1973; Long, 1981). A total of 200 individuals from the Port of Spain area of Trinidad were released on Bermuda. The population quickly spread to all parts of the islands. The population was estimated to have reached 60,000 by 1976 (Crowell & Crowell, 1976). Due to the kiskadee's quite varied diet, the hoped for control of the *Anolis* lizards was never realized; however, the kiskadee population continued to grow. It is now the third most abundant bird on the island (Long, 1981).

Although the great kiskadee was moved from one island to another, these two islands (Bermuda and Trinidad) are quite disparate. Bermuda is smaller in area, geographically more isolated, and biologically depauperate as compared to Trinidad (Fig. 1). The lack of any geographically close populations of kiskadees means that the exotic Bermuda population is completely genetically isolated from its source (native) population, and from all other native populations. In contrast, the Trinidad population of great kiskadees (native) probably experiences considerable gene flow with the (native) South American population. The kiskadee population on Bermuda may experience reduced competition for available resources due to overall decreased species diversity. The Bermuda kiskadee population is certainly subject to substantially lower predation pressure (Fig. 1). All of these differences are supposed drivers in the production of the Island Rule for native species (Lomolino, 2005). We should thus expect that the kiskadee's release from competitors and predators on Bermuda would allow it to attain comparatively large densities, which serves to intensify intraspecific competition for

available resources. Each of these factors should lead to evolution towards larger body size, assuming enough time has passed for such a change to occur.

MATERIALS AND METHODS

In order to determine whether any morphological divergence has occurred in the Bermuda population, it is necessary to capture and measure kiskadees from the exotic (Bermuda) population and the native (Trinidad) source population. Capture–recapture information also allows us to measure survivorship in Bermuda kiskadees in order to determine whether body size has an impact on survivorship.

We caught and measured great kiskadees on Bermuda on the grounds of the Bermuda Institute of Ocean Sciences in May and June of 2005–2008, and in Trinidad at Arima and at the Emperor Valley Zoo in Port of Spain in 2005 and 2006. The habitats were similar, consisting of open grassy areas with medium to large trees providing perches. We placed mist nets in areas of high kiskadee activity. We did not use lures or attractants in the capture process, as these would have created gender ratio bias in our capture information. We used identical methods in Trinidad, allowing comparison of measurements between the two islands. We used only adult measurements because juvenile birds do not attain full size for all morphological characters until after their first year.

We measured the following characteristics on each individual captured: body mass (in grams), wing chord, head length (from back of head to tip of culmen), culmen length (from base to tip of bill), tarsus length, tail length, bill depth, and bill width – the

latter two at the anterior margin of the nares. We chose these characters based on their well-known relationships to overall body size (i.e., mass, wing chord and tarsus length) and trophic apparatus (i.e., all bill dimensions). We judged these factors as important in niche breadth and life history and thus their divergence between populations should reflect the suspected differences in selection pressures between Bermuda and Trinidad. Mass was determined with an Ohaus CS200 compact scale (Ohaus Corporation, Pine Brook, NJ, USA) with one-tenth of a gram precision. Morphometrics were measured to the nearest hundredth of a millimetre with a Mitutoyo dial calliper (Mitutoyo America Corporation, Aurora, IL, USA).

We initially computed Pearson product–moment correlations for all morphological data to ascertain the degree to which these characters were intercorrelated. We found tail length to be highly correlated with wing chord, and culmen length and head length were also highly correlated, with correlation coefficients greater than 0.6 in both cases. Due to inter-year differences in measuring technique, culmen length was removed from the analysis. Wing chord is a more informative character than tail length, and was retained for further analyses.

We used principal components analysis (PCA) to condense the six morphological characters into uncorrelated orthogonal axes. PCA has been extensively used for birds, and the meaning of the first two components is well understood (Rising & Somers, 1989). The first principal component is a measure of overall body size, while the second component reflects the shape and proportions of the bill relative to body size dimensions. We performed PCA on the correlation matrix of the log-transformed data, with unrotated axes. As expected based on previously published PCAs on bird morphology, the first two

axes accounted for > 60% of the overall variance in the raw morphological scores. We compared PCI and PCII between populations with *t*-tests to determine if overall body size or proportion differences exist between the Bermuda and Trinidad kiskadees. In order to better understand specific differences between populations, we also retained the original univariate morphological measures and evaluated the differences in mean values across populations using t-tests with sequential Bonferroni correction (Rice, 1989).

Lande (1976) provides a calculation for N_e^*, which is the maximum founding population size that would have allowed an observed phenotypic differential to originate solely by drift. That is to say, if the founding population size is larger than this value, then the observed difference is not likely to have originated by drift (Lande, 1976). In our case, the original founding population size is known with certainty (200) because this was recorded during the original introduction, with the effective population size very likely close to the total number of individuals taken to Bermuda. Great kiskadees increased to an estimated 60,000 individuals within 19 years after introduction, thus providing no evidence of a lag period that may have resulted in a skewed gender ratio or population bottleneck (Crowell & Crowell, 1976). This information on founding population size thus allows us to determine whether drift is a likely explanation for observed character differences, or whether some other mechanism, for example selection, can be invoked.

We used Lande's equation, $N_e^* = \dfrac{(1.96)^2 h^2 t}{\left(\dfrac{z}{\sigma}\right)^2}$, where h^2 is the narrow sense heritability of the trait, t is the number of generations since the population was founded, z

is the mean morphological shift observed in that trait, and σ is the standard deviation of the trait in the founded population (in our case, the Bermuda kiskadee population). Unfortunately, demography and life-history are not well-studied for the great kiskadee, leaving the heritability and generation time variables unknown. We thus estimated generation time in the same manner as Saether *et al.* (2005), using $T = \alpha + \dfrac{s}{1-s}$, where T is generation time, α is age at maturity, and *s* is annual adult survival rate. We estimated adult survival rate as 0.65 using mark – recapture data derived from the Bermuda population (see Results below). We estimated age at maturity as 1 year, as there is no reason to suspect delayed breeding in this species (Brush & Fitzpatrick, 2002). These estimates yielded a generation time, *T*, of 2.88 years. We used a range of values for heritability similar to those reported in Clegg *et al.* (2002; range = 0.2 to 0.6) as these were calculated for similarly sized birds and for approximately the same suite of morphological characters.

We calculated haldanes and darwins, which are metrics describing rates of evolutionary divergence over time, from the kiskadee morphological data obtained in Bermuda and Trinidad. We divided the number of years since introduction (i.e., 51) by *T*, the generation time calculated above, to obtain the number of generations. The calculation of darwins is based on absolute time and not generations. Darwins, *d*, are calculated with the following equation, $d = \dfrac{\ln X_2 - \ln X_1}{t_2 - t_1}$, where $\ln X_2$ is the mean of natural log measurements from the Bermuda population, $\ln X_1$ is the mean of natural log measurements from Trinidad, and t_1 and t_2 are the dates of introduction (1957) and sampling (2008) respectively, measured in millions of years (Haldane, 1949). Haldanes,

H, are calculated based on generation times, $\quad H = \dfrac{\dfrac{\ln X_2 - \ln X_1}{S_{\ln x}}}{t_2 - t_1}$, where $\ln X_2$ and $\ln X_1$

are the same as in the previous equation, t_2 and t_1 are time measured in generations, and

$s_{\ln x}$ is the pooled standard deviation from the natural log Trinidad and Bermuda

measurements (Gingerich, 2001).

We banded captured kiskadees with unique combinations of colour bands on

Bermuda. These bands allowed us to estimate annual survival rates for marked Bermuda

kiskadees and to evaluate whether the measured morphological variables could explain

individual differences in this rate. We captured 84 adult kiskadees and resighted 30 over

the span of four years. We analysed the four years of mark–recapture data within

program MARK (White & Burnham, 1999), which allows the constraint of survivorship

models based on individual covariates, such as morphometrics. We thus found an overall

survival rate (used in above calculations), and determined whether the morphological

characters of each Bermuda individual impacted upon its annual survival probability. We

used time independent analyses to maximize the power of the parameter estimates.

Program MARK relies on an information-theoretic approach to assess the relationship

between covariates and annual survival probability. Thus, we derived 12 biologically

relevant models involving combinations of morphological covariates and principal

components from *a priori* expectations of the intercorrelation of the individual characters

and their relation to bird ecology. Our models were: (1) bill dimensions only (head

length, bill depth, bill width), (2) body size measures only (body mass, wing chord, tarsus

length), (3) all six morphological characters, (4) each individual dimension as a covariate,

(5) PCI and PCII, and (6) no covariates. Bill dimensions are important to foraging

efficiency and determine the size range of food items that can be consumed. Overall

body size is correlated with many life history parameters, including clutch size, neonate

weight, life span, maturation time, and gestation time (Blueweiss *et al.,* 1978). We

included all covariates as a possible model because some combination of overall body

size and bill dimensions (i.e., proportions) may have an important effect on survival. A

model with no covariates was included to measure overall survivorship probability. We

also used each of the six morphological characters as an individual covariate in

independent models (one covariate per model). Principal component scores were

included to determine whether overall body size (PCI) or proportions (PCII) influence

survivorship. We evaluated the models using Akaike's information criterion (AIC:

Akaike, 1974), which assigns each model an AIC value based on the overall fit to the

data with penalties for using more parameters. The model with the lowest AIC score is

considered to be the best model (i.e., best fits the data without overfitting), and we used

ΔAIC (AIC score of the best model subtracted from the AIC score of the model being

considered) scores to determine which model(s) best fits the observational data.   We

considered ΔAIC scores of <2 to indicate models with considerable support (Burnham &

Anderson, 2002). Models with a ΔAIC score of 2 –7 have some support, and models

with scores >7 have essentially no support.

RESULTS

There was a 1.54 to 4.89 % mean difference in body size dimensions and mass between

locations (Table 1). All six morphological characters were larger on Bermuda than on

Trinidad (Table 1), with mass and bill width remaining significant after sequential

Bonferroni correction (Rice, 1989). When we account for the intercorrelation of these

morphological characters using principal components analysis, we still see evidence for

increased overall size within the Bermuda kiskadee population (PCI $P < 0.01$). The

differences between islands, however, relate only to size and not relative proportions

(PCII $P = 0.93$).

The N_e values derived from the Lande (1976) equation ranged between 35 and

396 depending on the level of trait heritability we utilized. Most of these values fell

below the known founding population size of 200 individuals (Table 2). Body mass and

bill width showed little evidence of observed changes being accounted for by drift;

however, under the strong heritability assumption, observed increases in the other

characters may be due to drift.

Divergence rates measured in darwins and haldanes (Table 3) indicate very rapid

divergence following the initial establishment of kiskadees on Bermuda. These rates fall

in the middle of published rates for other examples of contemporary evolution (Stockwell

et al., 2003), and are nearly the same as those observed by Grant & Grant (2002) for

Galapagos finches over a 30-year period.

Analysis of survivorship with Program MARK indicated an overall annual

survival probability for adult great kiskadees on Bermuda of 0.6525 (no covariates

model). The model that best fit the observed data included only bill width as a covariate

(Table 4). This model was the only one with ΔAIC <2, and it had an associated model

weight of 0.48. These results suggest that, of the covariates evaluated, differences in bill

width best describe observed differences in individual annual survivorship of Bermuda kiskadees. Bill width had a negative effect on survivorship.

DISCUSSION

Great kiskadees on Bermuda demonstrate significant morphological differences from their native source population on Trinidad, including an increase of nearly 5% in mass in a span of 50 years. These changes are consistent with expectations stemming from the Island Rule, which suggest that the relatively more insular nature of Bermuda should lead to an increase in size for this, and any similarly or smaller sized, species. Our results add to a growing body of literature indicating rapid divergence in exotic populations (St. Louis & Barlow, 1988; Maron *et al.,* 2004; Amiot *et al.,* 2007), and to the few that show such changes conforming to well-established biogeographical principles (Johnston & Selander, 1971; Gilchrist *et al.*, 2004). That these principles were developed from observations of native species indicates that biogeographers can profitably utilize exotic species as potent probes into the evolutionary mechanisms that produce these large-scale patterns.

Lomolino (2005) suggests three mechanisms to account for the increase in size associated with the Island Rule. These are immigrant selection, ecological release from competitors and predators, and intensified intraspecific competition. Immigrant selection, resulting in a founder effect, is not likely a factor here because of the transportation of the founding members by human agency. There is no reason to believe that those individuals captured in Trinidad were a morphologically non-random sample of all kiskadees on the

island. We captured kiskadees in the same area of Trinidad as did those responsible for the original introduction, thus accounting for any small-scale patterns in the morphological traits across Trinidad. A more plausible explanation for the differences we observed is encapsulated in the other two possible mechanisms.

The first mechanism, increased intraspecific competition on Bermuda, could have resulted in selection for larger body size, larger individuals being better able to win competitions with conspecifics for limited foraging and nesting habitat. We conducted kiskadee counts in Bermuda and Trinidad and found 3.4 times more kiskadees per kilometre on Bermuda than in Trinidad. Perhaps equally plausible is that great kiskadees on Bermuda have undergone ecological release because the numbers of potential competitors and predators are much smaller than in the native Trinidad range (Fig. 1). Kiskadees have a variety of confamilial competitors in their native range that are absent in the exotic range. In particular, the boat-billed flycatcher (*Megarynchus pitangua*), tropical kingbird (*Tyrannus melancholicus*), and streaked flycatcher (*Myiodynastes maculatus*) all have similar foraging habits, body sizes and prey types. In Bermuda, no tyrannid flycatchers occur naturally and none have been introduced aside from the kiskadee. These absences may have allowed the kiskadee to exploit a wider range of resources in Bermuda relative to those available in the native Trinidad range.

The absence of competitors on Bermuda, and the resulting expansion of the great kiskadee's niche, is also consistent with the observed increase in bill width. The Island Rule does not provide clear expectations regarding bird bill dimensions; however, our observation of an increase in bill size is consistent with other studies examining evolution of birds on islands (Grant, 1965; Clegg & Owens, 2002). These authors suggest that more

types of food may be available on islands due to decreased interspecific competition, allowing island populations to consume food items usually unavailable to them in the more highly competitive communities found on mainlands.

Our finding that larger bill width results in decreased survivorship is counterintuitive when considering the observed size increase in this character for the Bermuda population. This effect is well supported by the models, bill width having a negative effect on survivorship whenever present as a covariate in a model. According to Fisher's Theorem of Natural Selection (Fisher, 1930), our observation of the absence of an obvious connection between morphology and survivorship should be expected if the population has reached equilibrium. The effects of body dimensions might have been quite strong during the early stages of adaptation to the novel environment encountered in Bermuda, but such effects may have dissipated if a fitness optimum has been reached in this population.

Our study documents phenotypic divergence over a short time period (~17 generations). We did not establish, however, whether this phenotypic differentiation is the result of natural selection (i.e., evolution) or is instead phenotypic plasticity from disparate environmental influences. We can discount the likelihood that the changes we observed are due to drift alone, especially for body mass and bill width. There are a variety of tools available to evolutionary ecologists to determine whether observed differences between populations are due to genetic evolution or phenotypic plasticity. Unfortunately, most of these options are either unethical (e.g., transplant experiments using a known invasive species) or impractical (e.g., common garden experiments) in this context. However, the traits in question have been studied in other passerine birds and

found to have high heritabilities and to evolve rapidly on islands (Grant, 1965; Clegg & Owens, 2002). More recently, morphological divergence has been shown to be concordant with genetic divergence across multiple populations of an insular species of passerine bird (Phillimore *et al.*, 2008). The same morphological traits that we document as diverging between Bermuda and Trinidad were shown by Grant & Grant (2002) to have evolved amongst Galapagos finches. The methods that these authors employ (e.g., parent–offspring regressions) are practical for great kiskadees on Bermuda, and are an important next step in this research.

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TABLES

Table 1 Morphological data from Bermuda and Trinidad great kiskadees (*Pitangus sulphuratus*). Values are means with one standard deviation in parentheses. These data are based on a sample size of 84 and 62 for Bermuda and Trinidad, respectively. Characters larger on Bermuda (after sequential Bonferroni correction) are in bold. Principal component loadings are presented in the last two columns.

Character	Bermuda	Trinidad	% Larger	*P*-value	PC1	PC2
Mass (g)	62.7 (4.7)	59.8 (5.4)	4.89	**0.0009**	0.476	0.252
Wing chord (mm)	109.8 (3.9)	108.1 (4.1)	1.54	0.0157	0.308	0.794
Head length (mm)	55.49 (1.7)	54.96 (1.5)	0.97	0.0579	0.410	-0.204
Bill depth (mm)	8.68 (0.4)	8.53 (0.3)	1.74	0.0135	0.392	-0.200
Bill width (mm)	9.84 (0.6)	9.50 (0.5)	3.66	**0.0001**	0.386	-0.470
Tarsus length (mm)	24.69 (1.1)	24.26 (1.3)	1.77	0.0417	0.455	-0.046

Table 2 Estimates of maximum founding population size of great kiskadees (*Pitangus sulphuratus*) on Bermuda allowing genetic drift to account for the morphological changes found in this study. As actual heritability values are unknown for great kiskadees, here we provide a range of heritability (h^2) values, from high (i.e., 0.6) to low (i.e., 0.2). Estimates were compared to the known founding population size of 200 individuals such that values >200 indicate drift may be a reasonable explanation for observed divergences between Bermuda and Trinidad great kiskadees.

	N_e*		
	$h^2 = 0.6$	$h^2 = 0.4$	$h^2 = 0.2$
Mass	107	71	36
Wing chord	223	149	74
Head length	396	264	132
Bill depth	278	185	93
Bill width	104	69	35
Tarsus length	270	180	90

Table 3 Evolutionary rates for the six morphological characters measured in Bermuda great kiskadees (*Pitangus sulphuratus*).

Character	darwins	haldanes
Mass	959	0.0320
Wing chord	301	0.0231
Head length	189	0.0180
Bill depth	334	0.0225
Bill width	700	0.0354
Tarsus length	354	0.0200

Table 4 Bermuda great kiskadee (*Pitangus sulphuratus*) survivorship model comparisons with and without biologically-relevant covariate combinations. AICc values are Akaike's information criterion (AIC) values corrected for small sample sizes. ΔAIC values are derived by subtracting the lowest AICc value (i.e., the best model's AICc value) from the AICc value of the model being compared.

Model	AICc	ΔAIC	AICc weight	Model likelihood
Bill width	136.2034	0.0000	0.48181	1.0000
Tarsus length	138.9343	2.7309	0.12299	0.2553
PCI	139.1916	2.9882	0.10814	0.2244
Bill dimensions	140.0754	3.8720	0.06952	0.1443
No covariates	140.2274	4.0240	0.06443	0.1337
PCII	141.8878	5.6844	0.02809	0.0583
Wing chord	141.9157	5.7123	0.02770	0.0575
Mass	142.1996	5.9962	0.02403	0.0499
Head length	142.2295	6.0261	0.02368	0.0491
Bill depth	142.3289	6.1255	0.02253	0.0468
Mass/wing/tarsus	142.8166	6.6132	0.01765	0.0366
All covariates	144.0711	7.8677	0.00943	0.0196

FIGURE LEGEND

Figure 1 Map showing the locations of Bermuda (exotic great kiskadee (*Pitangus sulphuratus*) population) and Trinidad (native great kiskadee source population). Biotic and abiotic characters of the two islands are presented in the table. Data from ffrench (1991) and Dobson (2002).

FIGURE

Figure 1

	Bermuda	Trinidad
Land area	55 km^2	4808 km^2
Distance to nearest mainland	1000 km	11 km
Nearest kiskadee population	2000 km	11 km
Maximum elevation	76 m	940 m
Breeding bird species richness	22	250
Native vascular plant diversity	165	2500
Native tyrannid flycatchers	0	27
Breeding raptors	0	10+
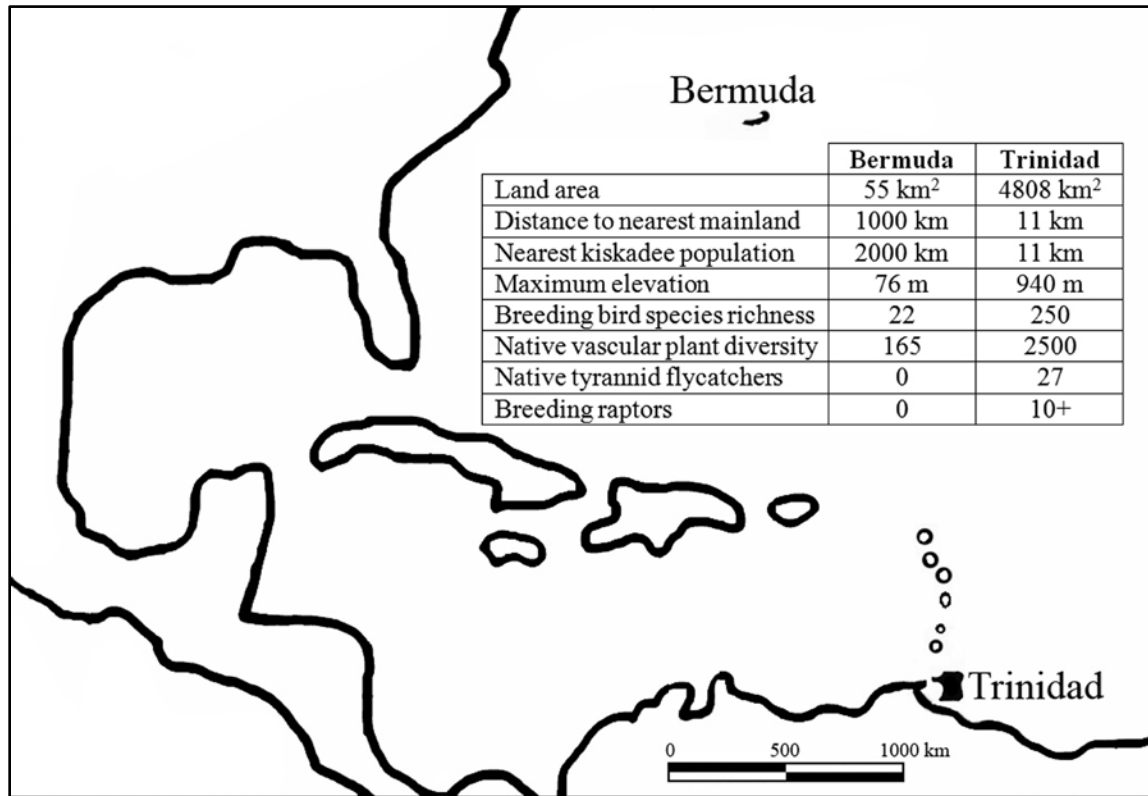
Chapter 2

Article Type: Original Article

Article Title: Contemporary evolution of exotic bird morphology in response to insularization: does the Island Rule hold for exotic passerines?

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ABSTRACT

Aim To determine whether 21 exotic bird species have morphologically diverged from their native source populations. If divergence is detected, evaluate whether this divergence is consistent with the Island Rule, which posits that species with small body sizes will increase in size on islands, and large-bodied species will decrease in size on islands. In birds, species below 70 g are predicted to increase in size according to the Island Rule. All species that we examine are below 70 g in their native range, therefore, we expected that they will increase in body size after being isolated on an island. In addition, we investigated individual morphological characters to determine whether any obvious patterns of size increase or decrease occur in these insular populations.

Location The islands of Bermuda, Puerto Rico, the Hawaiian archipelago, Mauritius, and Jamaica.

Methods We measured five morphological characters on 1,488 live and museum specimens from the exotic ranges of 21 passerine species. We measured 649 specimens from these species native source ranges. We compared morphology between the exotic and native source populations, using principal components analyses to derive a metric of overall body size. We evaluated the overall body size metric and the univariate morphological traits to assess whether these populations show patterns of size increase, size decrease, or no change.

Results Island populations displayed diverse patterns of differentiation relative to their native source populations; however, they did not show any consistent pattern of overall body size change. Wing chord and tail length both showed obvious patterns of size change, with the former decreasing and the latter increasing. The other univariate morphological characters did not show any clear patterns.

Main conclusions We did not find any support for the Island Rule amongst exotic passerines established on islands, which adds to similar recent studies showing no Island Rule effect for native taxa. We did find a clear pattern of longer tails and shorter wings in the exotic island populations, and conjecture that these may be the result of evolution for decreased dispersal ability.

KEYWORDS

Contemporary evolution, exotic species, Island Rule, morphological divergence, Hawaii, Bermuda, Puerto Rico, rapid evolution

INTRODUCTION

Morphological evolution has been shown to occur within the span of 20 or fewer

generations within a variety of species (Stockwell *et al.*, 2003). Many of these examples

come from exotic species, which are those introduced by humans to locales outside their

native ranges (Lockwood *et al.*, 2007). The novel environmental and interspecific

interactions that these species experience in their exotic ranges can lead to rapid

evolutionary change for both the exotic and the native species with which it interacts

(Vellend *et al.*, 2007). Given the ubiquity of such adaptations, the importance of

evolutionary dynamics in the study of invasion ecology has grown tremendously in recent

years (e.g., Lambrinos, 2004). Evolutionary change in exotic species also provides us

with unique opportunities to explore the formation of large-scale biogeographical patterns

over tractable time scales, to the extent that their study has been considered a sort of

'experimental arm' within the field of biogeography (Sax *et al.,* 2005, 2007).

Documenting the evolution of exotic species introduced to islands provides the

opportunity to witness the emergence of island forms in real time. Here, we compare

insular populations of exotic passerine bird species to their known mainland source

populations, testing whether a well-known insularization pattern for vertebrates (the

Island Rule), is demonstrable over the time frame since colonization (<100 years).

        The long history of biological investigations into the evolution of island biotas

provides us with clear expectations concerning the evolutionary changes that might occur

when individuals derived from a mainland source become established on an oceanic

island (i.e., they establish an insular population). One such expectation is encapsulated in

the Island Rule, which states that small-bodied species will become larger on islands

while large-bodied species will become smaller (Van Valen, 1973; Lomolino, 1985, 2005). Foster (1964, 1965) first proposed this rule, considering the body mass differences of insular mammals on islands off British Columbia (North America) to be taxonomically based (e.g., species in the Order Artiodactyla become smaller on islands, while those in the Order Rodentia become larger). Lomolino (1985) generalized the rule, suggesting that mammals respond to insularization in a graded fashion, depending on their mainland body mass. This conception implies a tipping point (synonymous with 'fundamental body size'; Lomolino, 2005) where species with body masses below the point will tend to evolve larger body sizes on islands, while species with body masses above this point will evolve smaller body sizes. Clegg & Owens (2002) and Lomolino (2005) extended the Island Rule to birds, proposing the tipping point of no expected change for birds to be between 70 and 120 g. We should thus expect that exotic bird species with mainland body sizes below these values to increase in body size after establishment on islands; and those above these values to decrease in size.

In this study, we examine 39 exotic island populations (from 21 species) of passerine birds that have continental populations as their sources. Grant (1965) examined insular bird species of North America, most of which (> 80%) were passerines, and found patterns of increased tarsus and bill lengths. He did not find any pattern for tail or wing lengths. In spite of having only limited sample sizes for body mass, Grant (1965) also found that nine out of 11 taxa showed a decrease in body mass on islands, with some of these species being larger in all other measured dimensions. These results indicated that morphological adaptation of insular passerines was idiosyncratic and these data have subsequently been cited as evidence that the Island Rule did not apply to birds (e.g.,

Lomolino, 1985). An analysis by Clegg & Owens (2002), however, found strong

evidence for the Island Rule in birds. Their data set was more taxonomically and

geographically comprehensive than that used by Grant (1965), and thus had considerably

greater power to detect a trend, if present. When Clegg & Owens (2002) restricted their

data set to only passerines in order to mimic Grant (1965), they found that insular

passerines were consistently larger than their mainland source populations, as predicted

by the Island Rule. All of the passerine species we consider fall below the hypothetical 70

to 120 g tipping point of the Island Rule for birds that emanates from Lomolino (2005),

therefore we expect all of them to have increased in body size after their insular

introduction, assuming enough time has passed for them to have evolved.

  Despite such evidence as provided by Lomolino (2005), the universality of the

Island Rule has been questioned in recent years. Recent studies of mammals, the taxon

on which the Island Rule was founded, have cast doubt on the validity of the Island Rule

(Meiri *et al.*, 2004, 2006, 2008). Similarly, no Island Rule pattern was found in a study of

island lizards (Meiri, 2007). Given these conflicting results, we must acknowledge the

possibility that we will not find an Island Rule pattern in the exotic passerine populations

that we examine here. However, even if overall body size does not show any clear

pattern of differentiation, the individual morphological characters that we examine may

reveal divergence patterns occurring independently of body size.

  We focus on passerines with established self-sustaining exotic populations on

Bermuda, Puerto Rico, Hawaii, Jamaica and Mauritius. We performed all of our analyses

at the population level, in order to avoid the negative effects of averaging across multiple

populations required for species-level analyses (Lomolino, 2005). Averaging necessarily

masks variation among populations on different islands, and may therefore obscure population-level trends.

The islands that we examine are all relatively small ($< 12,000$ km^2), therefore we also avoid the pitfall of examining mainland-like islands that may not display trends that are obvious on small islands (Lomolino, 2005). Small islands more clearly possess the features believed to drive the creation of the Island Rule, including low total resource availability and fewer species present. These two factors combine to shift selection pressures away from those related to inter-specific interactions (e.g., competition and predation) toward those related to intra-specific competition. This shift is posited as the reason why small-bodied species become larger on islands (Dayan & Simberloff, 1998).

Most of the insular exotic bird populations we consider were introduced some time after the mid-1800s, the last having become established around 1975 (Appendix). Thus, most species have had no more than 100 years to evolve in response to island conditions. This timeframe is well within the range of previously observed shifts in exotic bird morphology (e.g., Johnston & Selander, 1971; see Blackburn *et al.* (2009) for a review), and within the range of times in which other species (native and exotic) have been shown to genetically evolve in response to local conditions (Stockwell *et al.*, 2003).

There are three distinct advantages to considering exotic birds for explorations of the Island Rule. The first is the relatively good records of where the released individuals were captured in the native range. Criticism of past studies pertains to the inability of researchers to pinpoint the source populations from which the introduced populations were derived (Emerson, 2002). Previous examinations of insular evolution in naturally

colonizing species often relied on approximations of the source population, such as assuming that the original propagule came from the nearest point on the mainland (e.g., Meiri *et al.*, 2008). If the source population is incorrectly identified, the comparison to island forms is clearly flawed and may lead to misleading results (e.g., perceived size increase when in fact no change occurred). In contrast, most of the species we consider here were initially imported and released by acclimatization societies or for biocontrol purposes, and therefore have detailed records associated with them. These data allow us to pin down the provenance of the individuals released to very specific locations, or at least to the appropriate subspecies (Appendix).

A second advantage is that immigrant selection probably did not play a role in determining which individuals founded the insular population. Birds dispersing long distances over water may experience very strong selection pressures resulting in a non-random subset of all immigrants reaching the island. If this subset shows morphological differences relative to the mainland source (e.g., bigger body size or longer wings), a potentially severe bias is incorporated into analyses comparing island and mainland populations. In contrast, Blackburn *et al.* (2009) find evidence to suggest that, among exotic birds, most human-introduced individuals were captured haphazardly from within their native range and then transported for release. This observation thus gives us no reason to suspect that the founding propagules for our islands were anything other than a random draw of individuals from their mainland source populations.

The third advantage is the ubiquitous nature of the introduction process, which tends to result in the same species becoming established in several locations (Gilchrist *et al.*, 2004). This pattern provides the rare opportunity to test the robustness of the

proposed mechanisms of evolutionary change. For example, if the same mainland passerine species spawned two exotic island populations, we would expect each population to have increased in size according to the Island Rule. If instead, location-specific factors played as important a role as did the proposed mechanisms for the Island Rule, we should expect idiosyncratic differences in morphology across the exotic island populations. Naturally colonizing species can certainly provide this opportunity (Clegg *et al.*, 2002), however exotic species are unusual in the number of 'replicates' that are generated.

In addition to inspecting body sizes of insular birds, we also examine whether several previously hypothesized factors account for any size changes that we identify here. Hypotheses concerning mechanisms to account for the Island Rule have focused on differing predation pressures, competition, resource availability, climate and dispersal opportunities between islands and mainlands (Dayan & Simberloff, 1998). We use indices for these factors to explore whether the overall patterns of size increases and decreases (rather than the magnitudes of size change) we observe are connected to any of the abiotic or biotic attributes of the islands under consideration.

MATERIALS AND METHODS

Data Sources

We identified 39 populations of 21 species that were common enough in museum collections and in the field to provide acceptable sample sizes for analysis (i.e., at least 10 individuals from exotic and source populations; Table 1). The number of populations per

island were as follows: four on Bermuda, eight on the Big Island (Hawaii), four on Kauai (Hawaii), three on Maui (Hawaii), 11 on Oahu (Hawaii), seven on Puerto Rico, one on Mauritius and one on Jamaica. Populations were found on more than one island for eight of the species that we considered.

The key comparison we make is between the morphological dimensions of individuals from each native, mainland source population and the exotic island population(s) created from it. Thus, we began by using published information to select the source populations for the 39 exotic insular bird populations we considered. We used information in Long (1981) to identify the geographic and subspecific origin of the majority of exotic populations (32). For seven populations, information concerning the exact source population or subspecies was unavailable. In these instances, we inferred the likely source population using historical records of human transportation channels during the era in which the particular introduction took place (e.g., Moreno, 1997), or we used the location from which other exotic populations of the species were derived (Long, 1981). Source populations for two of the species we consider are on islands and not continents. In these two instances, however, the source islands are very large (with respect to the islands to which the species were introduced), and lie geographically very close to continents. These source islands have ecological characteristics that mimic mainlands (e.g., high species richness, migration connection to the continent), and thus our predictions should still be appropriate in these cases.

We collected five morphological dimensions on all individuals from the island and mainland source populations. These were tail length, wing chord, culmen length (base of bill to tip of bill), bill depth (at anterior margin of the nares) and bill width (at

anterior margin of the nares). We also measured tarsus length and mass on live-caught individuals; accurate tarsus measures were difficult to obtain from museum specimens and mass is not often recorded on museum tags. Culmen length, bill depth, bill width and tarsus length were measured to the hundredth of a millimetre with a Mitutoyo dial calliper (Mitutoyo America Corporation, Aurora, IL, USA). Tail length and wing chord were measured with a 15 cm wing rule, which is accurate to one mm (Avinet, Inc., Dryden, NY, USA). Mass was taken using an Ohaus CS200 compact scale (Ohaus Corporation, Pine Brook, NJ, USA), which is precise to one-tenth of a gram.

We collected data concerning the exotic island populations from live individuals captured in the field and from museum specimens previously collected in these same geographic locations. Individual Hawaiian Islands were treated as representing independent populations. We feel that this is warranted as some introduced populations have diverged among the Hawaiian islands (Mathys & Lockwood, In Review). We visited Bermuda four times from 2005–2008, Puerto Rico twice in 2008 and Hawaii once in 2008. During each visit, we captured live individuals using mist nets placed in areas with significant bird activity, generally in open areas (such as parks and wildlife refuges), but occasionally around bird feeders at private residences. In order to decrease the probability of sex bias in our data, no song playback or other gender-specific lures were used. All field measurements were taken by the same investigator (B.A.M). We measured museum specimens from the exotic island ranges housed at the Bishop Museum (Hawaii, USA), American Museum of Natural History (New York, USA), U.S. National Museum (Washington, D.C., USA), Bermuda Aquarium Museum and Zoo, University of Kansas (USA) and Louisiana State University (USA). We combined information from live-

caught and museum specimens representing a single exotic population into a single pool for analysis, using a correction factor that accounts for museum specimen shrinkage in some traits (see below for details).

Morphological data for individuals from the source populations were obtained from museum collections, with one exception (see below). We used capture location information on the specimen tags to identify individuals from the appropriate source regions. Suitable specimens were found at the American Museum of Natural History (New York, USA), U.S. National Museum (Washington, D.C., USA), Natural History Museum (Tring, UK) and Louisiana State University (Baton Rouge, USA). Data concerning native source population body size were collected in the field for one species, the great kiskadee (*Pitangus sulphuratus*), on Trinidad (two visits in 2005 and 2006). We measured the same suite of morphological features on the museum specimens as we did for live individuals (see above). Body mass was available for only a few specimens, and was recorded if present on the museum tag. Most museum measurements were taken by one investigator (B.A.M.), a few being taken by the other investigator (J.L.L.).   Efforts were made to standardize measurement techniques, such as being sure both investigators were using identical biological landmarks to identify morphological characters.

Statistical methods

Body Size Analysis

Due to most museum specimens not having information on mass, we used principal components analysis (PCA) to derive an overall body size metric for each individual.

PCI is known to be highly correlated with overall body size in birds, with the remaining component axes describing relative proportions (i.e., shape) (Rising & Somers, 1989). Tail length, wing chord, bill depth and bill width measurements were available for 38 out of the 39 populations, therefore these four traits were retained for our PCA. We estimated any missing data values in the raw measurements using a maximum likelihood approach with program NORM (http://www.stat.psu.edu/~jls/misoftwa.html) on log transformed data. No more than 5% of our data for any population was estimated in this manner, with a significantly lower percentage in most cases.

We did separate PCA analyses for all of the individuals from a single native source population and the exotic insular population(s) that arose from that source population. For example, we built separate PCI scores for the two nutmeg mannikin (*Lonchura punctulata*) subspecies; one for subspecies *L. p. punctulata* (native to India and introduced to Puerto Rico), and another for subspecies *L. p. topela* (native to Southeast Asia and introduced to Hawaii). We used unscaled and uncentred PCA on log transformed data, as this resulted in all four characters loading positively onto the first principal components axis for all species (Figure 1). We used this method instead of the more common PCA that utilizes correlation or covariance matrices, as these traditional approaches led to morphological characters loading negatively onto PCI for five species. Careful inspection of the data revealed that, in these cases, the data showed between-axis heterogeneity. In such instances, an uncentred PCA represents the structure of the data more clearly (Pielou, 1984). The use of an unscaled PCA is warranted in this case, as all characters were measured on the same scale (millimetres).

There is good evidence that the preparation and subsequent drying of museum specimens leads to mensural changes in some morphological features (Haftorn, 1982; Bjordal, 1983; Jenni & Winkler, 1989; Winker, 1993). Of the features that we consider here, wing chord and tail length are likely to shrink after an individual has been prepared as a museum specimen (Winker, 1993), and thus we need to account for this difference between live and museum specimens to prevent bias in our results. Accordingly, we corrected field measurements of wing chord and tail length prior to analyses so that they could be combined with, and compared to, data derived from museum specimens. This correction was achieved by multiplying the measurements taken in the field by a species- and character-specific correction factor derived from the literature (Table 2; Winker, 1993). When a correction factor was not available for a taxon, we used an average value based on other published shrinkage estimates for passerine birds, or a general wing correction factor of 0.983 as suggested by Winker (1993).

As Lomolino (2005) points out, the use of characters other than mass as indices of overall body size can be problematic, as these characters may be more plastic than mass in their evolutionary response to climate, diet, and other influences. In order to be sure that PCI was a sound surrogate for overall body size, we regressed it against measured body mass for all individuals with both live mass and PCI available (i.e., live-caught individuals and museum specimens with mass information recorded on the tag). This regression showed a strong positive relationship ($r = 0.88$, n = 1267).

In order to determine whether overall body size differed in any consistent way between the exotic and native populations of each species, we compared the 38 introduced populations to their native source populations using a mixed model. This

model treated species as a random block effect, and used status (exotic versus native) as a fixed effect nested within species. We ran this model in program R (R Development Core Team, 2009) using the nlme add-on package (Pinheiro *et al.*, 2009).

In addition to investigating the overall body size trend using PCA, we also explored differences between source and exotic island populations for each morphological character separately. We gauged the degree of inter-correlation between the morphological measures by creating a Pearson's product moment correlation matrix for each native source population (a total of 23 matrices). We compared tail length, wing chord, culmen length, bill depth and bill width measurements from the exotic island population(s) to their source population using *t*-tests and ANOVAs. The Benjamini-Hochberg α correction (Benjamini & Hochberg, 1995) was used to account for multiple comparisons. We used a sign test (Dixon & Moody, 1946) to determine whether there was a difference between the number of size increases and decreases for each character.

Body Size Correlation with Selective Factors

In order to determine which, if any, aspects of the insular environments are correlated with the body size changes that we found, compared linear regression models to determine whether island characters were predictors of overall body size change. Overall body size change was calculated for each exotic population. This was done by subtracting the native population's mean PCI value from the mean PCI value for the exotic population. Island isolation (km from nearest mainland), change in predator species richness, predator species richness in the exotic (island) range, change in

competitor species richness, competitor species richness in the exotic (island) range,

island area (in km^2) and change in latitude were the independent variables. We defined

predators as being terrestrial mammals in the Order Carnivora and birds in the Order

Falconiformes. Change in predator species richness was determined by subtracting the

number of breeding predators that are sympatric with an exotic species in its native

source range from the number of predators in the species' introduced (insular) range.

Native source range was based on range maps as well as localities of the museum

specimens. Competitors were defined as birds in the same taxonomic family as the

species in question. Change in competitor species richness was calculated in a manner

identical to change in predator species richness. Latitudinal change was calculated by

subtracting the mean latitude of the source population specimens from the latitude of the

island (exotic range). Data concerning predator and competitor ranges were derived from

sources such as field and taxon-level guides (Pratt *et al.*, 1987; Raffaele, 1989; Clement,

1993; Restall, 1996; Grimmett *et al.*, 1999; Zimmerman *et al.*, 1999; Mullarney *et al.*,

2000; Dobson, 2002; Stevenson & Fanshawe, 2002; Sibley, 2003; Borrow & Demey,

2004; Ferguson-Lees & Christie, 2005; Robson, 2005). We derived nine models from

this set of explanatory variables. These included a global model with all variables, an

unconstrained base model, and each variable independently (Table 5).   Models were

ranked according to Akaike's Information Criterion (AIC) corrected for small sample

size (AICc) (Akaike, 1974). Models with ΔAIC < 2 were considered to have strong

support (Burnham & Anderson, 2002).

RESULTS

The five morphological variables we collected showed differing degrees of inter-correlation across populations, with the most consistent correlation being a positive one between wing length and tail length (Figure 2). The average correlation coefficients between variables for all other combinations were relatively low (< 0.3) indicating that they do not typically co-vary.

All morphological measures loaded positively onto PCI (Figure 1). The mixed model used to evaluate whether there was any pattern of body size change in these exotic populations indicated that there was no consistent direction of change in body size ($P = 0.91$).

When we evaluated divergence of each morphological trait individually, we found that some traits regularly decreased in size while others tended to increase (Table 4). Tail length showed clear patterns of size increase in the exotic island populations. Out of 21 total differences between source and exotic island populations after Benjamini-Hochberg correction, tail length increased in 19 instances and decreased in two (sign test: $P < 0.001$). Wing chord also demonstrated 21 total differences after Benjamini-Hochberg correction; however, in this case the exotic island populations tended to have shorter wings. Two exotic island populations had larger wing chords than their source populations, whereas 19 exotic island populations had smaller wing chords than their source (sign test: $P < 0.001$). The other three characters (culmen length, bill depth and bill width) did not show clear patterns of size change, although bill depth was close to

significance (sign test: $P = 0.077$) with four increases in depth and 12 decreases after Benjamini-Hochberg correction.

Many species and genera showed different directional change among characters. Changes in opposite directions within the same insular population were common, being found in 18 out of 39 populations (Table 3). For instance, when we compared house finches (*Carpodacus mexicanus*) on Kauai to individuals from their native source population (California, USA), we found increases of overall body size (PCI) and tail length, but a decrease in culmen length. Similarly, changes of bill dimensions of species within the genus *Lonchura* seemed to be idiosyncratic, with both increases and decreases being found for all three bill characters (Table 3). Across all species, six exotic island populations had increased tail length but decreased wing chord, despite the consistent positive correlation coefficients between these two traits in the native range (i.e., in a single population they should be either both increasing or both decreasing, if there is any change).

There was little differentiation between models of hypothesized causative agents for divergence between exotic island and native source populations (Table 5). Indeed, the base model that was unconstrained by island characters had the lowest AIC score. Models that were within 2 AIC units of the top model included the following variables: number of competitors, number of predators, change in number of competitors, and island isolation.

DISCUSSION

Exotic passerine birds that are native to continental mainland areas have regularly diverged in several morphological traits since their initial Our finding of contemporary change provides further support for the ever-increasing body of literature documenting recent divergence in exotic species (Johnston & Selander, 1971; St. Louis & Barlow, 1988; Gilchrist *et al.*, 2004; Maron *et al.*, 2004; Amiot *et al.*, 2007; Mathys & Lockwood, 2009), and our results highlight the usefulness of using exotic species in the testing of biogeographical theory originally developed from observations of native species. Size patterns consistent with the Island Rule have been found in native (Clegg & Owens, 2002; Clegg *et al.*, 2002) and exotic bird species (Mathys & Lockwood, 2009).

However, we found no support for the Island Rule here. Passerines native to continental mainland regions and recently established as exotics on islands did not consistently increase in size. This result stands at odds with previous characterizations of the Island Rule, such as Van Valen's (1973) observation that the Island Rule "seems to have fewer exceptions than any other ecotypic rule in animals." Our results are more in accord with Meiri *et al.* (2008), who recently asked whether the Island Rule was "made to be broken," as they found that mammals do not show a pattern consistent with the Island Rule if phylogeny is considered, something previous studies did not take into account. These authors instead suggest that the evolutionary adaptation that species undergo on islands has more to do with the unique fit between the species' life history traits and the environmental and biological conditions of each island (Meiri *et al.*, 2008). Our results best match this supposition, in that most individual morphological traits

changed in an idiosyncratic manner (but not all, see below), and populations of the same species or very close congeners evinced idiosyncratic changes in traits.

While we found strong directional patterns for two characters (wing chord and tail length), none of the three bill characters showed evidence of diverging strongly in one direction. This result is contrary to what would we would expect given the results of Grant (1965) and Clegg & Owens (2002), who each found increased bill lengths in their analysis of passerine birds on islands. It seems likely that the bill characteristics are more closely tied to very specific island and taxon characteristics, and are not strongly influenced by insularity in general.

The one strong pattern of morphological change that we did detect was that of decreased wing chord and increased tail length within exotic island populations relative to their mainland sources. This result is unexpected in that no similar pattern was noted by Grant (1965) despite that fact that he considered both of these characters. It is also unexpected given the consistent positive inter-correlation of these two traits across populations, which should force the two traits to change in tandem. Given that wing chord and tail length are tied to flight aerodynamics in birds, such that larger birds will tend to have larger wings and tails, we perhaps should expect that those populations that show an overall trend for larger or smaller body size will concomitantly show a coordinated increase or decrease in tail and wing length. However, even if the 10 populations with differences in overall body size (PCI) are eliminated from consideration, then all wing chord changes (16) were decreases and all tail length changes (13) were increases. This observation indicates that these characters are not simply changing isometrically with overall body size, but are changing independently.

Long wings and short tails are considered to be adaptations for long distance movements. Long wings are more efficient for continuous, unidirectional flight (Rayner, 1988). Longer tails result in increased aerodynamic drag, therefore long tails are not usually found in birds that move long distances (Thomas & Balmford, 1995). Since we consider changes in exotic island populations of species native to mainland continental regions, all of our examples are of populations that have experienced drastically reduced dispersal opportunities. The maximum linear distance across the islands in this study (230 km) is similar to the distance many passerine birds are capable of flying in a single day (200-300 km; Hildén & Saurola, 1982), and each island is quite isolated from large continental areas that could serve as migratory destinations. Loss or reduction of morphological adaptations for dispersing have been found in island beetles (Darlington, 1943), plants (Carlquist, 1974; Cody & Overton, 1996) and birds (Worthy, 1988; Livezey, 1989; Diamond, 1991; McCall *et al.*, 1998). Some of the most spectacular examples of evolutionary adaptations to islands derive from the many flightless birds that can be (or were) found on oceanic islands (e.g., the dodo). Even when island birds do not entirely lose their ability to fly, they evolve shorter wings in apparent response to a change in selection pressures from those that favour aerodynamic efficiency in soaring flight to those that favour agility and close-quarters manoeuvrability (Fitzpatrick, 1998). Our findings of decreased wing chord and increased tail length in the exotic island populations of these mainland-evolved species are thus consistent with an evolutionary response to decreased dispersal and year-round residence in complex flight environments (e.g., within dense forest understory).

While we have documented measureable morphological divergence between exotic island populations and their mainland sources, we cannot be certain that these changes are the result of genetically based evolution. They may be partly or solely phenotypic changes, the result of different environmental influences in the exotic versus the native source population habitats (James, 1983). However, the morphological characters that we examined are known to have direct connections to fitness (e.g., the relationship of bill dimensions to foraging efficiency and niche breadth), and these traits have been well-studied in some of the species we evaluate, showing strong heritabilities. For example, house sparrows show average heritabilities (h^2) of 0.54 for bill width, 0.37 for wing length and 0.29 for bill depth (Jensen *et al.*, 2003), and house finches have an average morphological heritability of 0.42 (Badyaev & Martin, 2000 a, b). It is therefore likely that the changes we have found here are indicative of underlying genetic evolution. Nevertheless, this supposition is well worth testing, and we suggest that such investigations consider island-by-species case studies instead of large-scale biogeographical patterns.

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TABLES

Table 1 Sample sizes for principal components analyses of 38 introduced bird

populations. Abbreviations: **B** = Bermuda, **HI-BI** = Hawaii – Big Island, **HI-K** = Hawaii

– Kauai, **HI-M** = Hawaii – Maui, **HI-O** = Hawaii – Oahu, **PR** = Puerto Rico, **M** =

Mauritius, **J** = Jamaica.

Scientific Name	B	HI-BI	HI-K	HI-M	HI-O	PR	M	J	Native
Cardinalis cardinalis	14	16	13		22				25
Copsychus malabaricus					20				10
Carpodacus mexicanus		26	30		59				23
Estrilda astrild					35				21
Estrilda melpoda						46			54
Euplectes franciscanus						95			37
Lonchura cantans		14							30
Lonchura cucullata						30			14
Lonchura malabarica						11			40
Lonchura malacca						17			32
Lonchura p. punctulata						51			30
Lonchura p. topela		40	21		37				31
Leiothrix lutea		29			17				28
Paroaria coronata					20				30
Passer domesticus	104								24
Passer domesticus		22		176	141				37
Pycnonotus cafer					47				22
Pycnonotus jocosus					16		10		26
Pitangus sulphuratus	84								62
Sicalis flaveola		20						20	17
Sturnus vulgaris	16								15
Vidua macroura						10			21
Zosterops japonicus		43	33	10	73				20

Table 2 Shrinkage correction factors, derived from previous studies of specimen shrinkage (Haftorn, 1982; Bjordal, 1983; Jenni & Winkler, 1989; Winker, 1993).

Character	House Sparrow	Bulbuls	All Other Species
Wing Chord	0.9925	0.995	0.983
Tail Length	1.0095	1.011	0.99408

Table 3 Size increase (I), size decrease (D) and no change (N) for 39 populations of passerine birds introduced to islands. Empty cells indicate insufficient sample size for comparison. **B** = Bermuda, **HI-BI** = Hawaii–Big Island, **HI-K** = Hawaii– Kauai, **HI-M** = Hawaii–Maui, **HI-O** = Hawaii–Oahu, **PR** = Puerto Rico, **M** = Mauritius, **J** = Jamaica.

Species	Island	Tail Length	Wing Chord	Culmen Length	Bill Depth	Bill Width
Cardinalis cardinalis	B	N	N		N	I
	HI-BI	N	D		N	I
	HI-K	I	D		N	I
	HI-O	N	D		N	I
Copsychus malabaricus	HI-O	N	D			N
Carpodacus mexicanus	HI-BI	I	N	N	N	N
	HI-K	I	N	D	N	N
	HI-O	I	N	N	D	N
Estrilda astrild	HI-O	D	D	D	D	D
Estrilda melpoda	PR	I	D	D	D	N
Euplectes franciscanus	PR	N	N	N	N	I
Lonchura cantans	HI-BI	I	N	D	D	D
Lonchura cucullata	PR	N	D	N	I	I
Lonchura malabarica	PR	I	N	N	N	N
Lonchura malacca	PR	I	N	N	I	I
Lonchura p. punctulata	PR	I	N	I	N	N
Lonchura p. topela	HI-BI	N	D	N	N	D
	HI-K	N	D	D	N	D
	HI-O	N	D	D	N	N
Leiothrix lutea	HI-BI	N	D	D	N	N
	HI-M	N	N	N		N
	HI-O	N	D	D	N	N
Paroaria coronata	HI-O	I	N	N	N	N
Passer domesticus	B	I	N	I	D	N
	HI-BI	N	N	I	D	N
	HI-M	N	D	I	D	N
	HI-O	N	N	I	D	I
Pycnonotus cafer	HI-O	N	D	N	N	I
Pycnonotus jocosus	M	N	I	N	I	I
	HI-O	I	N	D	N	N
Pitangus sulphuratus	B	I	I	I	I	I
Sicalis flaveola	HI-BI	I	N	N	D	N
	J	N	N	N	D	N
Sturnus vulgaris	B	I	D		D	N
Vidua macroura	PR	D	D	D	D	N
Zosterops japonicus	HI-BI	I	D	N	N	N
	HI-K	I	D	N	N	N
	HI-M	I	N	N		N
	HI-O	I	D	N	N	N

Table 4 Number of morphological characters

different between native introduced ranges after Benjamini-

Hochberg correction (Benjamini & Hochberg, 1995). Sign tests

were used to derive the *P* values in the last column.

Character		# of Changes	*P* value
Tail Length	Increase	19	<0.001
	Decrease	2	
Wing Chord	Increase	2	<0.001
	Decrease	19	
Culmen Length	Increase	6	0.455
	Decrease	10	
Bill Depth	Increase	4	0.077
	Decrease	12	
Bill Width	Increase	11	0.118
	Decrease	4	

Table 5 Comparison of linear regression models concerning island characters and size change of 38 exotic bird populations. Lower AICc score indicates better model fit. Models within 2 AIC units of the top model are considered to be equally good at explaining the data. Effect sizes are provided for the characters with ΔAIC < 2.

Model	AICc	Δ AICc	Effect Size
No Island Characters	115.69	0	----
Number of Competitors	116.46	0.77	-0.0781
Δ Competitors	116.83	1.14	-0.0117
Island Isolation	117.47	1.78	-0.0001
Number of Predators	117.55	1.86	0.0672
Island Area	117.76	2.07	----
Δ Predators	117.94	2.25	----
Change in Latitude	118.00	2.31	----
Global Model (all characters)	123.94	8.25	----

FIGURE LEGENDS

Figure 1 Factor loadings for the principal components analysis use to construct PCI. Higher loading value indicates greater influence on the PCI value for that character. Mean ± 1 standard deviation is displayed for each character.

Figure 2 Correlation coefficients (mean ± 1 SE) from Pearson product moment correlations among the five morphological characters examined in this study. Higher values indicate that those two characters more strongly correlate with each other.
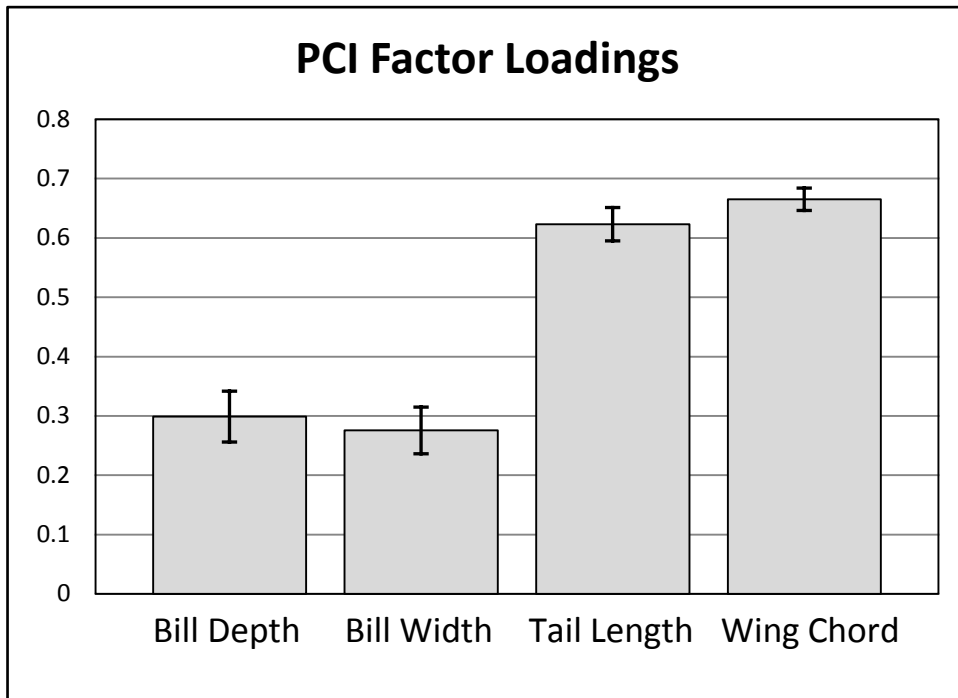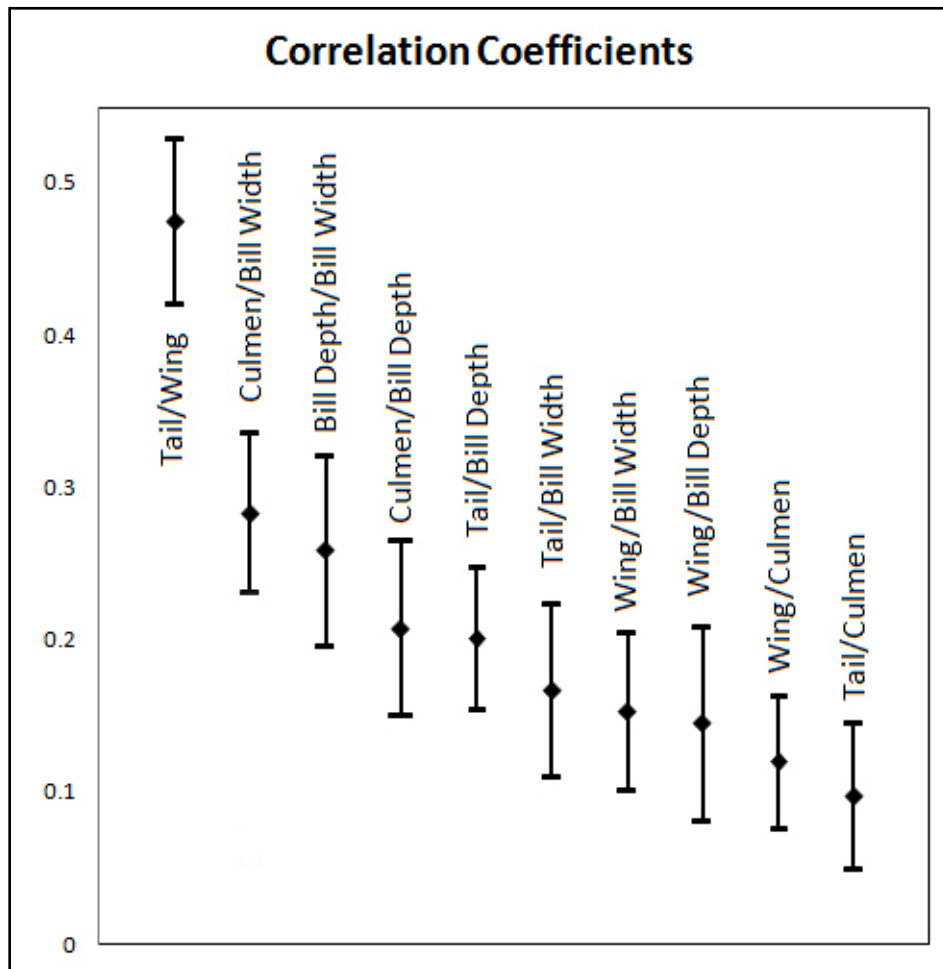
FIGURE 1

PCI Factor Loadings

FIGURE 2

Appendix. Shrinkage-corrected data (mean and standard error (SE)) for all 38 populations used in principal components analyses (PCA). Date of introduction and source population specificity derived from Long (1981), Pratt *et al.* (1987), and Moreno (1997).

Common Name	Scientific Name	Intro Date	Source Specificity	Location	Tail Mean	Tail SE	Wing Mean	Wing SE	Culmen Mean	Culmen SE	Bill Depth Mean	Bill Depth SE	Bill Width Mean	Bill Width SE
Northern Cardinal	*Cardinalis cardinalis*	1600s?	Species (Eastern U.S.A)	Bermuda	90.89	1.171	92.54	0.832			12.42	0.149	9.87	0.165
				Big Island	92.16	1.095	85.28	0.714			12.13	0.118	9.46	0.142
		1929-1931		Kauai	96.74	1.215	86.89	0.863			12.45	0.143	9.44	0.172
				Oahu	94.69	0.934	89.38	0.664			12.30	0.110	9.37	0.132
				U.S.A.	92.25	0.800	93.08	0.568			12.15	0.115	8.59	0.113
White-rumped Shama	*Copsychus malabaricus*	1931-1940	Subspecies	Oahu	118.65	3.361	87.03	0.860					4.29	0.066
				SE Asia	132.08	7.856	92.96	0.999					4.32	0.105
House Finch	*Carpodacus mexicanus*	< 1870	Subspecies (San Francisco area)	Big Island	58.04	0.595	76.93	0.433	11.91	0.183	7.88	0.063	6.73	0.053
				Kauai	59.40	0.532	75.25	0.396	10.89	0.164	7.99	0.056	6.98	0.049
				Oahu	56.88	0.386	75.80	0.287	11.60	0.122	7.81	0.041	6.77	0.035
				U.S.A.	54.43	0.608	76.57	0.460	11.97	0.191	8.07	0.065	6.81	0.057
Common Waxbill	*Estrilda astrild*	Early 1900s	Species	Oahu	40.65	0.438	42.69	0.224	8.30	0.075	5.55	0.033	4.41	0.042
				S. Africa	49.40	0.953	48.74	0.525	9.70	0.085	6.00	0.080	4.65	0.054
Orange-cheeked Waxbill	*Estrilda melpoda*	< 1874	Subspecies	Puerto Rico	42.19	0.385	45.12	0.217	8.82	0.055	5.79	0.032	4.81	0.038
				Africa	40.86	0.484	46.22	0.210	9.23	0.065	6.07	0.049	4.72	0.040
Orange Bishop	*Euplectes franciscanus*	< 1971	Subspecies	Puerto Rico	34.25	0.255	57.81	0.345	12.90	0.057	6.49	0.029	5.74	0.028
				Africa	32.99	0.596	59.04	0.473	13.15	0.144	6.89	0.065	5.36	0.065
Red-billed Leiothrix	*Leiothrix lutea*	1928-1929	Subspecies	Big Island	53.84	0.531	66.53	0.495	14.11	0.116	4.56	0.044	3.84	0.042
				Maui	53.35	0.888	67.36	0.817	14.48	0.192			3.80	0.073
				Oahu	55.10	0.681	66.32	0.639	14.47	0.150	4.58	0.053	3.81	0.054
				SE Asia	54.00	0.531	69.55	0.512	15.05	0.139	4.47	0.043	3.75	0.044
African Silverbill	*Lonchura cantans*	1970s	Species	Big Island	41.12	0.917	52.02	0.294	9.93	0.082	7.55	0.065	6.32	0.037
				Africa	38.55	0.683	52.43	0.274	10.48	0.100	8.13	0.086	6.76	0.052
Nutmeg Mannikin	*Lonchura p. punctulata*	1960s	Subspecies	Big Island	38.75	0.418	51.68	0.280	11.59	0.079	7.59	0.040	6.83	0.045
				Kauai	39.28	0.570	51.59	0.386	11.36	0.109	7.56	0.055	6.75	0.062
				India	37.38	0.542	54.28	0.483	11.79	0.087	7.89	0.074	7.03	0.046
				Puerto Rico	41.81	0.443	54.00	0.184	12.14	0.057	7.94	0.038	7.07	0.038
	Lonchura p. topela	1865	Subspecies	Oahu	37.64	0.442	52.34	0.291	11.41	0.082	7.67	0.043	6.91	0.047
				SE Asia	37.62	0.477	54.06	0.318	11.75	0.090	7.70	0.049	7.02	0.051
Bronze Mannikin	*Lonchura cucullata*	< 1866	Subspecies	Puerto Rico	28.82	0.425	47.08	0.318	9.92	0.057	6.84	0.050	5.50	0.057
				Africa	29.04	0.361	48.71	0.339	9.77	0.084	6.51	0.067	5.30	0.054

Common Name	Scientific Name	Intro Date	Source Specificity	Location	Tail Mean	Tail SE	Wing Mean	Wing SE	Culmen Mean	Culmen SE	Bill Depth Mean	Bill Depth SE	Bill Width Mean	Bill Width SE
Indian Silverbill	*Lonchura malabarica*	1960s	Country	Puerto Rico	45.41	0.844	53.63	0.175	9.96	0.091	7.27	0.084	6.19	0.047
				India	41.16	0.658	52.91	0.298	10.23	0.089	7.41	0.076	6.30	0.047
Chestnut Munia	*Lonchura malacca*	< 1971	Subspecies	Puerto Rico	34.28	0.353	55.74	0.235	12.28	0.124	8.78	0.067	7.57	0.053
				India	32.66	0.357	55.63	0.262	12.20	0.074	8.47	0.046	7.33	0.053
Red-crested Cardinal	*Paroaria coronata*	1928	Species	Oahu	80.48	0.656	99.16	0.843	16.72	0.185	8.65	0.059	6.70	0.086
				S. America	77.07	0.661	98.55	0.612	16.48	0.228	8.61	0.093	6.53	0.106
House Sparrow	*Passer domesticus*	1870s	Subspecies	Bermuda	55.22	0.229	75.01	0.218	14.13	0.081	7.70	0.026	6.87	0.027
		1871	Subspecies	N. America	51.92	0.416	75.32	0.395	13.69	0.144	8.13	0.064	6.86	0.071
				England	53.74	0.347	75.24	0.341	12.80	0.104	7.84	0.040	6.65	0.042
				Oahu	54.27	0.178	75.35	0.175	14.95	0.055	7.69	0.021	6.86	0.022
				Maui	53.02	0.160	73.43	0.156	14.67	0.048	7.49	0.018	6.77	0.019
				Big Island	54.66	0.450	74.07	0.442	13.50	0.135	7.55	0.054	6.55	0.055
Red-vented Bulbul	*Pycnonotus cafer*	1965	Species	Oahu	90.13	0.558	96.54	0.610	20.44	0.138	5.34	0.041	5.05	0.047
				Nepal	90.93	1.120	100.44	0.827	20.90	0.210	5.40	0.066	4.74	0.055
Red-whiskered Bulbul	*Pycnonotus jocosus*	1965	Subspecies	Oahu	78.68	1.098	79.40	0.794	16.95	0.211	4.62	0.052	4.28	0.079
		1892	Subspecies	Mauritius	76.50	1.388	84.00	1.005	18.18	0.266	4.94	0.066	4.69	0.100
				SE Asia	74.45	0.830	80.98	0.580	17.96	0.156	4.50	0.044	4.35	0.058
Great Kiskadee	*Pitangus sulphuratus*	1957	Subspecies	Bermuda	81.31	0.357	107.92	0.417	29.39	0.168	8.68	0.042	9.84	0.061
				Trinidad	79.54	0.415	106.29	0.521	28.66	0.193	8.53	0.042	9.50	0.063
Saffron Finch	*Sicalis flaveola*	1960s	Species	Big Island	52.89	0.472	70.09	0.530	11.31	0.168	6.54	0.059	5.37	0.058
		~1823	Species	Jamaica	48.53	0.472	70.40	0.592	11.76	0.187	6.69	0.072	5.35	0.065
				S. America	49.94	0.512	71.79	0.642	11.09	0.203	7.06	0.079	5.38	0.071
European Starling	*Sturnus vulgaris*	Early 1950s	Species, area	Bermuda	62.66	0.560	121.22	0.834			6.10	0.069	6.59	0.055
				U.S.A.	57.33	0.836	125.67	0.607			6.72	0.087	6.47	0.087
Pin-tailed Whydah	*Vidua macroura*	< 1971	Species	Africa	46.67	0.947	64.00	0.834	10.17	0.088	6.59	0.075	4.73	0.049
				Puerto Rico	41.25	0.654	60.23	0.733	9.43	0.167	6.10	0.061	4.87	0.064
Japanese White-eye	*Zosterops japonicus*	1928-1937	Subspecies	Big Island	41.91	0.356	57.44	0.280	14.56	0.090	2.93	0.026	2.84	0.031
				Kauai	42.27	0.387	56.35	0.271	14.50	0.087	2.88	0.025	2.88	0.030
				Maui	42.00	0.671	59.64	0.560	14.33	0.188			2.91	0.061
				Oahu	41.30	0.262	57.23	0.217	14.77	0.070	2.97	0.020	2.84	0.024
				Japan	38.16	0.511	59.58	0.415	14.57	0.136	2.96	0.039	2.92	0.045

Chapter 3

Article Type: Research Article

Article Title: Contemporary morphological diversification of passerine birds introduced to the Hawaiian archipelago

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ABSTRACT

Species that have been introduced to islands experience novel and strong selection pressures after establishment. There is evidence that exotic species diverge from their native source populations; further, a few studies have demonstrated adaptive divergence across multiple exotic populations of a single species. Exotic birds provide a good study system, as they have been introduced to many locations around the world, and we often know many details concerning the origin of the propagule, time of introduction, and dynamics of establishment and dispersal within the introduced range. These data make them especially conducive to examination of contemporary evolution. Island faunas have received intense scrutiny from biologists, therefore we have expectations concerning the patterns of diversification that we may observe in exotic species. We examine six species of passerine birds that were introduced to the Hawaiian archipelago less than 150 years ago. We find that five out of these six species show morphological divergence among islands in the time since they have become established on the archipelago. We are able to demonstrate that some of this divergence can not be accounted for by genetic drift, and therefore we must invoke adaptive evolution to explain it. We also evaluate evolutionary rates of divergence for these species and find that they are diverging at similar rates to those found in other published studies of contemporary evolution.

1. INTRODUCTION

Naturalists and biologists have long considered islands to be showcases of evolution (Grant 1998; Whittaker & Fernández-Palacios 2007). Many island species have greatly diverged from their mainland ancestors, in some cases making it difficult to determine the mainland species that is most closely related to the island taxon (e.g., Veron & Catzeflis 1993; Caccone *et al.* 1999; Burns *et al.* 2002). This lack of information has limited our ability to explore rates of morphological diversification and the role of genetic drift in the production of trait differences between islands for native taxa, as their history of change cannot be safely inferred from their present day condition (Grant 2001). Using species that have recently colonized islands (either naturally or by human-mediated processes), we have the rare opportunity to directly observe the dynamics of diversification that occur immediately following the arrival of colonizing species onto islands (Sax *et al.* 2005, 2007).

The most striking examples of adaptation on oceanic archipelagos are taxa that have diverged in life history and morphology on multiple islands, resulting in many closely related yet taxonomically distinct forms, known as adaptive radiations (Schluter 2000). Silversword plants (Witter & Carr 1988), *Drosophila* fruit flies (Carson & Kaneshiro 1976), and songbirds (Lovette *et al.* 2002) on Hawaii are well known examples of this process. These groups are each thought to have derived from one (or a few) original species that colonized the Hawaiian archipelago, with individuals eventually becoming isolated on each island and diverging into the various forms found at present.

Exotic species are useful 'unplanned experiments', as they provide us with the opportunity to observe evolutionary processes in real time (Sax *et al.* 2005, 2007). Further, we often know many of the details of the original introductions (e.g., date, geographic and subspecific identity of the source population, exact introduction location) that are completely unavailable in natural colonizations and may be important in understanding the dynamics and mechanisms of divergence. Therefore, a focus on the evolution of exotic species can give us the opportunity to observe the genesis of insular diversification, and provide insights into the inter-specific variability of responses to insularity (Sax *et al.* 2005, 2007). In particular, we can produce relatively unbiased evaluation as to whether evolution was the result of genetic drift, founder effects, or adaptive selection. We can also test hypotheses concerning correlates of diversification that are impossible to know if the founding taxon is unknown or extinct.

We examine six species of passerine birds that have been introduced to the Hawaiian archipelago and we determine whether among-island differentiation of morphological features has occurred in the time since these species were initially released. In previous work, we showed that these same species have diverged in morphological traits relative to individuals from their native source populations (Mathys & Lockwood in review). These results indicated that these species were able to manifest detectable morphological change in the time since they were released to Hawaii. Here we ask whether these six species have diverged from one another across four of the six main islands of the Hawaiian archipelago. Using the abundant information on each species' introduction history, we tease apart the roles of adaptive and non-adaptive evolution in the generation of between island population differences in morphology.

In the context of exotic bird introductions to islands, morphological divergence can occur via three mechanisms: phenotypic plasticity, non-adaptive evolution or adaptive evolution. Phenotypic plasticity is non-genetic morphological shifts due to environmental effects (DeWitt & Schoener 2004). If environments among islands are sufficiently different, and a morphological feature is phenotypically labile, different populations of that species will display differences among islands such that traits are matched to the environmental constraints of each island. The degree to which phenotypic plasticity contributes to observed differences in avian traits (including several of the morphological traits we consider here) across populations has seen modest amounts of study in the past, and these result indicate that, although common, phenotypic plasticity is nearly always coupled with significant genetic evolution (Merilä *et al.* 2001). In addition, while phenotypic plasticity is not genetically mediated, it can serve as a stepping stone allowing an exotic population to persist long enough to genetically adapt to the novel environment (e.g., Collyer *et al.* 2007).

Alternately, populations distributed across islands in an archipelago may diverge in morphology via non-adaptive evolution if either non-random subsets of individuals make up the colonizing propagules on each islands (a founder effect; Mayr 1942), or if genetic drift sends each population along a unique but random evolutionary trajectory (Lande 1976). Either scenario is very likely to have occurred for exotic birds introduced to the Hawaiian Islands, and indeed for exotic species overall (Facon *et al.* 2008). The number of individuals of exotic birds released is usually below 50 (Blackburn *et al.* 2009), making genetic drift nearly inevitable (Connor & Hartl 2004). This scenario is all the more likely here given that, within the Hawaiian archipelago, several exotic birds

spread to all the islands from one initial introduction point on a single island (Lockwood 2001). Although not as common, exotic birds have been released onto each island in the archipelago on independent occasions with introductions stemming from different native source populations. This scenario presents the possibility that any between island differences in morphology are due to founder effects, such that each island population simply reflects traits from a geographically structured native range.

Finally, exotic bird populations can adapt (via natural selection) to the biotic and abiotic conditions present on each island. It is well-documented that introduced species change quickly in their introduced ranges (Huey *et al.* 2000; Lee 2002; Mathys & Lockwood 2009), and it has been demonstrated several times that observed morphological changes in exotic birds are consistent with adaptive responses to local environments (e.g., Johnston & Selander 1971; Baydaev *et al.* 2000). Adaptation can only occur, however, for traits that are heritable and possess genetic variability (Schluter 1996). Each morphological trait that we examine here has been shown to have moderate to high heritability scores within passerines, with some of these measures based on the species we consider (Badyaev & Martin 2000 a, b; Jensen *et al.* 2003). Although there is the expectation that the process of introduction should reduce genetic variation within exotic species, thus far such reductions have not limited the evolutionary potential of a wide variety of exotic species (Lockwood *et al.* 2007) and exotic birds in particular (Blackburn *et al.* 2009). Thus, the amount of morphological divergence we see here could be determined by the magnitude and direction of selection pressure experienced by the populations on each island.

We now highlight the relevant introduction history of the six species we consider in order to gauge the likelihood of these three alternative modes of diversification discussed earlier. The house finch (*Carpodacus mexicanus)*, nutmeg mannikin (*Lonchura punctulata)*, and house sparrow (*Passer domesticus)*, were each introduced to the Hawaiian archipelago only once, to a single island, and each propagule came from one known source region (Long 1981). From those initial island populations, these species spread to the other five main islands under their own power (i.e., there is no indication that the human residents in the islands purposefully moving them between islands; Long 1981). Based on this introduction history, the most parsimonious expectation is that these species continue to exchange individuals today via dispersal and thus will demonstrate little morphological differentiation. If we do observe divergence in morphology between islands, this must have arisen via *in situ* changes (adaptation or genetic drift), as a single introduction eliminates the possibility of observed differences being the result of morphologically distinct propagules arriving from more than one native source population.

The other three species, northern cardinal (*Cardinalis cardinalis)*, red-billed leiothrix (*Leiothrix lutea*) and Japanese white-eye (*Zosterops japonicus*) were introduced to more than one island, with some introduction events stemming from different native source regions (Long 1981). Given this history, the most parsimonious expectation is that these species will show some divergence in morphology due to founder effects alone. If genetic drift and/or adaptation come into play, any existing founder-based divergences in morphology may be deepened. Alternatively, if we find no differences in morphological traits between populations of these species, dispersal between islands must

be great enough to have overcome founder effects and, may potentially be preventing the development of island-specific types.

Finally, we assess the influence of evolutionary potential on the degree of morphological divergence we see among island populations for our six exotic passerine species on Hawaii. Here we are acknowledging that certain lineages seem to be prone to specific or subspecific diversification, whereas others do not appear to have diverged to any extent over long periods of time. A good example of the former are *Zosterops* species, which are situated within an avian family (Zosteropidae) that contains the largest number of island colonizers of any passerine group (Moreau 1964; Clegg *et al.* 2002). We should perhaps expect that once Japanese white-eyes (*Z. japonicus*) established in Hawaii, they would quickly colonize all other islands (which they did; Long 1981) and diverge into island-specific forms (which we test here). We will use two metrics of evolutionary history as possible predictors of contemporary changes, examining whether these predictors relate to the degree of divergence we observe among islands. These two predictors are the species richness of the genera in which these species are found and the number of recognized subspecies in each species.

2. MATERIALS AND METHODS

In order to determine whether insular populations of our six exotic passerine birds have morphologically diverged between islands in the Hawaiian archipelago, it was necessary to obtain measurements of body dimensions from individuals on multiple islands. These measurements were taken on field and museum specimens. Only adults were measured,

as young individuals are still growing and do not provide accurate measures of adult body dimensions. The following characters were measured: mass, tail length, wing length, head length (from tip of bill to back of head), culmen length, bill depth (at anterior margin of nares), bill width (also at anterior margin of nares), and tarsus length. Mass was measured in grams and all other characters were measured in millimetres. Mass of live individuals was measured using an Ohaus CS200 compact scale (Ohaus Corporation, Pine Brook, NJ, USA), which has one-tenth of a gram precision. Culmen length, head length, bill depth, bill width, and tarsus length were measured with a Mitutoyo dial calliper (Mitutoyo America Corporation, Aurora, IL, USA) to one-hundredth of a millimetre precision. Tail length and wing length were measured with a 15 cm wing rule accurate to one millimetre (Avinet, Inc., Dryden, NY, USA).

Three Hawaiian Islands were visited to obtain field measurements. We visited Kauai, Oahu, and the Big Island (Hawaii) once each during the summer of 2008 to capture live individuals of all introduced passerine species encountered. Mist nets were placed in areas that experience regular bird activity. No lures or baits were used in order to prevent bias in the sex ratio of captured individuals. All eight morphological measurements were taken on field-captured individuals. In addition to live individuals, museum specimens were measured at the Bishop Museum (Hawaii, USA), U.S. National Museum (Washington, D.C., USA), Natural History Museum (Tring, England), University of Kansas (USA), and Louisiana State University (USA). Mass was recorded from museum specimens when it was present on the museum tag. Tail length, wing length, culmen length, bill depth, and bill width were measured on museum specimens. The technique for preparing avian museum specimens often involves the removal of the

back of the skull, therefore the head length measurement is not appropriate for museum specimens. Tarsus length is difficult to measure on museum specimens, and is often impossible to obtain without damaging the specimen, therefore it was not taken for most museum specimens. Data from live-captured individuals and museum specimens were combined for each island. Population locations and sample sizes are presented in table 2.

It has been well-documented that bird specimens experience changes in mensural characters after preparation (Haftorn 1982; Bjordal 1983; Jenni & Winkler 1989; Winker 1993), the result of drying of the skin. In order to be able to compare the measurements from live individuals to museum specimens, we multiplied field measurements of tail length, wing chord, and tarsus length by taxon and character specific correction factors. These factors were derived from the literature mentioned above, with averages being used for taxa that have not been specifically studied. These correction factors are presented in table 1. The appropriate correction factors were applied to the field measurements prior to the analyses below. Pearson product moment correlation coefficients were computed for all eight morphological characters. Most correlations were small (across species mean < 0.5), although wing chord/tail length and head length/culmen length were higher (mean $\pm$ 1 SD: 0.62 ± 0.21 and 0.68 ± 0.09, respectively). However, due to the variability in correlation, these characters were retained in the analysis.

We used analysis of variance to determine which species showed morphological differentiation among populations. Tukey's post-hoc test was used to determine which populations differed from each other within each species. In order to correct for employing multiple comparisons per species, we used the Benjamini-Hochberg (1995) α

correction at the species level. This technique reduces the likelihood of making a Type I

error without greatly increasing the frequency of Type II errors. It is similar to but not as

strict as the more common sequential Bonferroni correction (Rice 1989), and is often

employed in situations where extra Type I errors would be more detrimental to data

analysis than increased Type II errors.

Lynch (1990) provides the following equation to determine whether genetic drift

is likely to account for observed differences between two populations (or species):

$\Delta = \frac{var_b}{t \times var_w}$. This equation is based on the variances within (var_w) and between (var_b) the

two populations, as well as the divergence time, expressed as number of $T = \alpha + \frac{s}{1-s}$

generations (t). The neutral expectation is that this metric, Δ, will be between 0.0001 and

0.01 (i.e., if Δ is between these values, the observed differences between populations can

likely be accounted for solely by drift). Details of the calculation of var_b, var_w, and t can

be found in Lynch (1990). Generation times (T) for the species examined were estimated

in the same manner as Saether *et al.* (2005): where T is generation time, α is age at

maturity, and s is annual adult survival rate. We assumed $\alpha = 1$ for all of these species,

as there is no evidence of delayed breeding in these species. Adult survival rate was

gleaned from the literature for three species (*Cardinalis cardinalis*: Karr *et al.* 1990;

Carpodacus mexicanus: DeSante & Kaschube 2006; *Passer domesticus:* Jensen *et al.*

2008). The average of those generation times were used for the other three species, as

adult survival rate data were not available. We determined the value of Δ for each

character in all populations that Tukey's post-hoc test indicated were different. This

value was then compared to 0.01 (the upper bound of neutral expectation), to determine

whether the observed differences between populations could be accounted for solely by

drift, or whether adaptive evolution must be invoked. The percentage of populations

showing divergence (whether adaptive or due to genetic drift) was determined for each

species, for each island, and for each morphological character.

We measured the evolutionary rate of change for these characters, comparing the

island populations to their native source populations (native data from Chapter 2).

Evolutionary rate was measured in haldanes (*H*), which $$H = \frac{(\ln X_2 - \ln X_1)/S_{\ln x}}{t_2 - t_1}$$

are calculated as

where $\ln X_1$ and $\ln X_2$ are the means of natural log measurements from the introduced and

native populations, respectively, t_2 and t_1 are time measured in generations, and $s_{\ln x}$ is the

pooled standard deviation from the natural log measurements for both populations

(Gingerich 2001). Stockwell *et al.* (2003) provide us with an expectation by which to

gauge whether the rates that we observe here are fast or slow as compared with other

studies of contemporary evolution.

We performed linear regressions to determine whether the evolutionary history of

a species is a predictor of the proportion of populations that were found to have diverged

for each species (see previous paragraph). The species richness of the genus and the

number of subspecies recognized for each species were used as the predictor variables in

linear regressions. These data were derived from field guides, Birds of North America

accounts, and the primary literature (*Cardinalis cardinalis*: Halkins & Linville 1999;

Carpodacus mexicanus: Clement 1993; Hill 1996; *Leiothrix lutea*: Male *et al.* 1998;

Lonchura punctulata: Restall 1996; *Passer domesticus*: Lowther & Cink 2006; *Zosterops*

japonicus: Monroe & Sibley 1997; Van Riper 2000). The dependent variable was the

number of populations that diverged divided by the total number of population comparisons for each species. We also regressed proportion of populations diverging against time since each species was first introduced to the archipelago, in order to evaluate the possibility that interspecific differences in divergence were simply a result of some species having more time to evolve once established within the Hawaiian archipelago.

3. RESULTS

Out of 132 between-island population comparisons, 38 showed divergence for the morphological trait in question (Appendix). Of these, eight were found to have $\Delta > 0.01$, indicating that the differences were probably not due to genetic drift. The extent of between-island divergence varied markedly across species, from all eight characters showing at least some divergence among islands (house sparrows, with 15 out of 18 between-island comparisons indicating divergence) to no character showing any divergence among islands (red-billed leiothrix showed no differences for 16 comparisons; table 3). The characters that diverged the most among islands were mass and wing length (table 3). We found mass differences among islands for 10 out of 15 between-island comparisons. However, the Δ values associated with these differences indicated that nine out of these 10 could be accounted for by genetic drift alone. Wing length differences were found in nine out of 21 comparisons, but unlike the situation with mass divergences, Δ values indicated that five of these nine could not be accounted for by drift (table 3, appendix). We found that head length and tarsus length diverged at the lowest frequency.

Individual islands had similar proportions of morphological traits that showed

divergence, with no single island emerging as a leader in the number of times traits

diverged within populations that existed on it.

The average evolutionary rate measurements were found to range from 0.004 to

0.042 haldanes for the five characters with native range data available. These rate

measurements are presented in table 4. In figure 1, we graph these in order to evaluate

how they compare to other estimates of contemporary evolutionary rates.

The linear regression of proportion of between-island comparisons showing

divergence for each species versus generic species richness was not statistically

significant ($R^2 = 0.0.013$, $p = 0.830$). Similarly, a regression of number of subspecies

versus population divergence proportion was not significant, although the trend was in

the direction predicted such that species with many subspecies tended to show more

morphological divergences between populations in the Hawaiian Islands ($R^2 = 0.076$, $p =$

0.597). We found no relationship between time since introduction and proportion of

populations that have diverged ($R^2 = 0.202$, $p = 0.371$).

4. DISCUSSION

Five out of the six species that we considered here show a measurable degree of

morphological divergence in at least one trait across islands in the Hawaiian archipelago

after only 70 to 140 years of putative isolation from each other. In four of these species,

we were able to show that at least some of this divergence was likely a result of

evolutionary adaptation to the local conditions on each island. Three of these species

were released to one island only and then spread to the others under their own colonizing

power, thus showing the behavioural propensity to disperse over the sometimes

expansive stretches of open water between islands (e.g., the distance between Oahu and

Kauai is 115 km). There is no reason to believe individuals are not continuing to disperse

across these islands today, and therefore that gene flow among island populations is

persistent. Adaptive evolution is possible despite such gene flow (e.g., Hendry *et al.*

2000; Kinnison *et al.* 2001), and in fact moderate gene flow has been found to encourage

adaptive evolution in some cases (Gomulkiewicz *et al*. 1999; Garant *et al*. 2007). It is

not clear what local island conditions may be causing these selective differences. The

islands differ in total area, maximum elevation, and human population density (Pratt *et al.*

1987). These differences may lead to varying selection pressures resulting in the among-

island divergences we found here.

The remaining morphological differences we observed between island

populations of exotic passerines in the archipelago were likely due to genetic drift. Drift

is speeded when there are very few individuals in a population (Connor & Hartl 2004).

Population sizes were likely very low (< 50 individuals) for all the species we considered

here right after their initial introduction (Long 1981; Blackburn *et al.* 2009). Since their

initial release, four of the six species we consider here quickly grew in population size

and are now commonly found across all six main islands, likely reducing the effects of

drift. However, red-billed leiothrix is only locally common today and experienced

serious declines after initial large population increases. Similarly, house sparrows

dispersed to all main islands from a single introduction, but never attained the very high

population densities seen in other introduction areas (e.g., mainland North America)

(Long 1981; Pratt *et al.* 1987). That we see relatively pervasive evidence of drift in the observed morphological differences in these species should be of no great surprise. What may be surprising is the degree of these differences. For example, house finches probably became established from a very small number of escaped cage birds but is now quite common on all main islands (Long 1981). The morphological differences between islands that we document here are within the range of those reported by Baydaev & Hill (2000) for differences among exotic populations in North America, and even sometimes exceed those differences (e.g., mass). These authors have shown that, amongst the exotic house finch populations of North America, observed differences are consistent with adaptation to local conditions.

Our estimates of evolutionary rates match those found in other studies, as reviewed in Stockwell *et al.* (2003). Most reports of rates of contemporary evolution find variability around the trend line from figure 1 in Stockwell *et al.* (2003), and the six species in our study are no exception. The scaling of evolutionary rate with time seems to be a general trend across taxa, and our results add further support for this conclusion (Kinnison & Hendry 2009). This trend is probably the result of periods of stasis and evolutionary reversals being averaged across longer time periods; in our study and other similar examinations of evolutionary changes over short time scales, evolution is likely unidirectional and constant, leading to a higher average rate.

The number of islands a species was introduced to in the Hawaiian archipelago did not seem to have any connection to the amount of divergence we observed. We expected that independent introductions of a species to several islands might result in greater structure across islands via founder effects. If that were the case, what we

interpret here as divergence might mirror any spatial morphological structure maintained within the native source population. However, the two species in which we found the most divergence, house sparrows and house finches, were each only introduced to the archipelago once, to a single island. In addition, we did not find any among-island divergence in red-billed leiothrix, which was introduced more than once from very different sources (propagules came from captive populations in California as well as from the native range in Asia; Long 1981). Based on these observations, we suggest that the morphological differentiation that we found is the result of *in situ* change on each island and does not derive from separate morphologically distinct propagules.

The six species varied in the number and pattern of character divergences among island populations. It appears that the house sparrow is especially disposed to change, as all characters that we have data for evinced differences among islands and most of the between-island population comparisons (15 out of 18, in six total characters) were different. Similarly, house finches changed in six out of eight characters and for half (10 out of 20) of the between-island population comparisons. These two species have been the subject of extensive study within other parts of their exotic ranges, and in all cases, significant morphological divergence has been documented (reviewed in Blackburn *et al.* 2009). At the other end of the spectrum, nutmeg mannikins had only one character diverge out of eight measured characters, and red-billed leiothrix did not change at all for any of six characters across three islands. These latter two species have not been studied elsewhere in their exotic range, so we cannot judge the uniqueness of this failure to diverge in Hawaii. We did test whether the previous history of divergence in a genus (i.e., generic species richness and number of subspecies) in the native range was a predictor of

the proportion of populations diverging in our study. We expected that greater generic species richness and more subspecies in the native range would correlate with an increased divergence in the species that we examined. Our results did not support this, although there was some indication that the number of subspecies in the native range was related to the degree of differentiation in Hawaii.

One advantage to examining exotic species as we do here is that we can compare our results to what has already happened amongst native species. Do the exotic passerines of Hawaii mimic patterns in divergence among the native passerines of Hawaii? Divergence in naturally occurring Hawaiian forms is quite variable, with some bird families showing extensive divergence and others not diverging at all. As an example, the Family Mohoidae is endemic to the Hawaiian archipelago and consists of only five total living and extinct species (Fleischer *et al.* 2008). This result can be contrasted with the Hawaiian honeycreepers, another endemic taxon which has 29 or more living and extinct members (Pratt *et al.* 1987). The two taxa have had a similar amount of time to diverge in Hawaii (~ 16 my) (Sibley & Ahlquist 1982; Fleischer *et al.* 2008), yet the latter group contains more than five times as many total species. We cannot, of course, predict if and to what extent exotic passerines will continue to diverge in Hawaii; however, we did find that some species (e.g., house sparrows) have diverged much more than other species (e.g., nutmeg mannikin). It remains to be seen whether adaptive and non-adaptive evolution will continue to build differences in some exotic birds while leaving others largely unchanged, as it did with the native passerines of Hawaii.

Our results add to the growing body of literature that documents contemporary divergence of exotic birds (Johnston & Selander 1971; St. Louis & Barlow 1988; Amiot *et al.* 2007; Mathys & Lockwood 2009). We further highlight the utility of using such species to observe differentiation in real time using human-mediated colonization events with well-documented details. Such data are rarely, if ever, available for native colonizations, and therefore using exotic species provides us with a powerful tool to study the effects of translocation on the phenotypes of colonizing populations. We show that information concerning date of release and number of independent release events allowed us to formulate hypotheses about morphological divergence in these species. We were able to test those hypotheses, determining that some of the changes we found were not attributable to genetic drift, because we had specific information on introduction time. We hope that our work here will encourage more detailed analyses of these exotic species so that further insight, such as evaluation of causal mechanisms for differences in divergence, can be gleaned from these unplanned experiments.

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TABLES

Table 1. Specimen shrinkage correction factors, derived from published values

(Haftorn 1982; Bjordal 1983; Jenni & Winkler 1989; Winker 1993).

Character	House Sparrow	Other Five Species
Wing Chord	0.9925	0.9830
Tail Length	1.0095	0.9941
Tarsus Length	0.9880	0.9866

Table 2. Population locations and sample sizes for the six species examined. Species with an asterisk were introduced to the Hawaiian archipelago more than once. Last two columns provide data concerning the initial human-mediated introduction(s).

Species	Big Island	Kauai	Maui	Oahu	Introduction Date	Introduction Island(s)
*Cardinalis cardinalis**	19	13		22	~1930	Oahu, Kauai, Big Island
Carpodacus mexicanus	26	31		59	< 1870	Maui
*Leiothrix lutea**	30		11	18	1918 - 1928	All 5 main islands
Lonchura punctulata	40	21		37	1865	Big Island
Passer domesticus	22		176	141	1869	Oahu
*Zosterops japonicus**	44	47	11	73	1929	Oahu, Big Island; Maui?

Table 3. Summary of Appendix information, indicating proportion of populations diverging between islands. Column 5 = (column 2 / column 1) x 100%; Column 6 = (column 3 / column 2) x 100%. These data are based on 132 total two-island comparisons. Values in last four rows of column 1 are double what might be expected, because each comparison is counted twice (e.g., a statistically significant result in the wing chord comparison between Oahu and Maui for *Zosterops japonicus* would count twice, once for Oahu and once for Maui).

| Total Comparisons	Number Statistically Different	Number Statistically Different with $\Delta > 0.01$		Percent Showing Divergence	Percent of Divergences with $\Delta > 0.01$
21	5	2	*C. cardinalis*	23.8	40.0
20	10	1	*C. mexicanus*	50.0	10.0
16	0	0	*L. lutea*	0.0	
22	2	0	*L. punctulata*	9.1	0.0
18	15	2	*P. domesticus*	83.3	13.3
35	6	3	*Z. japonicus*	17.1	50.0
15	10	1	Mass	66.7	10.0
21	4	0	Tail Length	19.0	0.0
21	9	5	Wing Chord	42.9	55.6
6	0	0	Head Length	0.0	
21	6	2	Culmen	28.6	33.3
18	3	0	Bill Depth	16.7	0.0
21	5	0	Bill Width	23.8	0.0
9	1	0	Tarsus Length	11.1	0.0
83	21	5	Big Island	25.3	23.8
63	18	2	Kauai	28.6	11.1
84	24	5	Oahu	28.6	20.8
34	13	4	Maui	38.2	30.8

Table 4. Evolutionary rates (in haldanes) for the six species examined in this study, comparing Hawaiian populations to native source populations. Data points are averages across all populations of that species. Native range data were only available for these five morphological characters.

	Tail Length	Wing Chord	Culmen Length	Bill Depth	Bill Width
Cardinalis cardinalis	0.015	0.042		0.009	0.038
Carpodacus mexicanus	0.014	0.005	0.007	0.007	0.005
Leiothrix lutea	0.005	0.023	0.022	0.009	0.007
Lonchura punctulata	0.005	0.015	0.009	0.005	0.009
Passer domesticus	0.005	0.008	0.025	0.014	0.008
Zosterops japonicus	0.034	0.024	0.004	0.005	0.007

FIGURE LEGEND

Figure 1. Evolutionary rates in haldanes, graphed versus generations for the six

species in this study. Each data point represents one morphological character (see

table 4 for actual rate values). Black line is trend line taken from Stockwell *et al.*

(2003), and is based on many other studies of evolutionary rates.

Figure 1
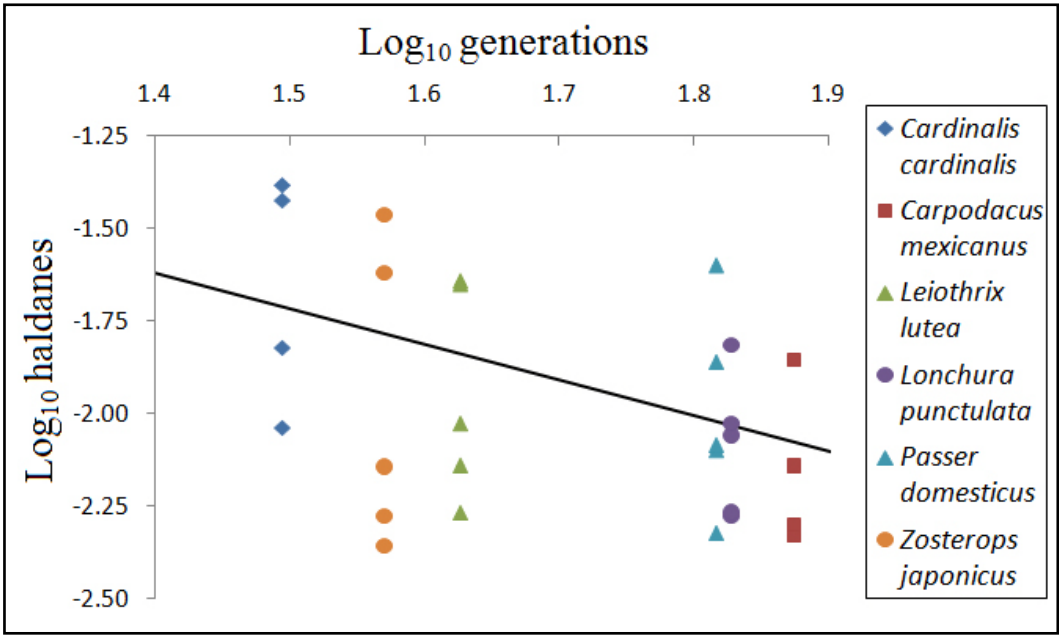
Appendix. Color-coded table displaying divergence patterns in six passerine species introduced to the Hawaiian archipelago. Blank cells indicate that data were not available to test the divergence between those two island populations for that character in that species. Dark grey cells were found not to differ between populations for that character in that species ($P > 0.05$ for ANOVA, or Tukey's post-hoc test indicated no divergence). Salmon cells were found to be different according to Tukey's post-hoc test (performed after $P < 0.05$ found for species level ANOVA for that character), but that difference was found to be in the range attributable to genetic drift ($0.0001 < \Delta < 0.01$). Orange cells same as salmon, except $\Delta > 0.01$, indicating that genetic drift probably is not sufficient to explain the divergence and therefore adaptive evolutionary change is implicated. In these eight instances, Δ ranged from 0.0102 to 0.0200 (mean = 0.0160). These divergences are further summarized in table 3.

		BIG ISLAND							
		M	TL	W	H	C	BD	BW	TS
K	Ccard								
A	Cmex								
U	Llutea								
A	Lpunct								
I	Pdom								
	Zjapon								
	Ccard								
O	Cmex								
A	Llutea								
H	Lpunct								
U	Pdom								
	Zjapon								
	Ccard								
M	Cmex								
A	Llutea								
U	Lpunct								
I	Pdom								
	Zjapon								

M = Mass
TL = Tail Length
W = Wing Chord
H = Head Length

C = Culmen Length
BD = Bill Depth
BW = Bill Width
TS = Tarsus Length

Ccard = *Cardinalis cardinalis*
Cmex = *Carpodacus mexicanus*
Llutea = *Leiothrix lutea*
Lpunct = *Lonchura punctulata*
Pdom = *Passer domesticus*
Zjapon = *Zosterops japonicus*

CONCLUDING REMARKS

In my research, I have examined whether birds that have been introduced to islands in the recent past display measureable phenotypic evolution. I have found that evolution, despite originally being envisioned as a long process, can be documented over contemporary time scales. I have also tried to find patterns in these changes, evaluating whether a biogeographical rule holds for these species. The Island Rule was originally described for native mammals, but has since been generalized to birds and a variety of other taxa. However, it has not been previously been evaluated in exotic bird populations.

The Island Rule does seem to hold for some of the populations that I examined, however overall differentiation does not demonstrate any clear pattern, indicating that the Island Rule is weak if operating at all in these species. In chapter one, I examine the morphological shift found in a single species, the great kiskadee. This shift is distinct and in the direction predicted by the Island Rule. However, in my second chapter, I found that 39 introduced bird populations do not follow this rule when it is examined at an interspecific level. It should be noted, however, that only 10 of the 39 populations showed divergence from the native source population. The other 29 populations may differentiate in the future, at which point a re-evaluation of the these same populations might lead to a different conclusion.

Despite not showing a clear pattern of overall body size evolution, the populations that I examined in chapter two did show an obvious pattern of reduction in wing chord and increase in tail length. These results indicate that these populations are adapting to their exotic ranges. I interpret this as possible adaptation for decreased dispersal ability.

Nearly all of these species originally came from mainland regions. After being introduced to islands, these species experienced a marked decline in dispersal opportunity. They may have shifted away from adaptations for moving long distances (e.g., long, pointed wings), and towards adaptations for agility (e.g., long tails).

The species that I examine here were introduced for a variety of reason, including aesthetics and biocontrol. The individuals and groups responsible for these introductions often kept detailed records concerning the time of introduction, source population, and propagule size of the exotic species; these data are unavailable for most if not all native colonizations. Knowing how long these populations have been isolated allowed me to evaluate the rate of differentiation, in order to determine whether the observed differences are the result of random processes (e.g., genetic drift) or adaptive evolution. While it is not possible to say that all of the changes that I have found are adaptive, I have shown that at least some of them can not be accounted for by genetic drift (e.g., some great kiskadee characters and some of the characters examined in the third chapter). This indicates that these species are adapting to their introduced ranges, and that this adaptation is detectable through close examinations of these populations. The evolutionary differentiation that I found here, both adaptive and non-adaptive, may be the first step in the emergence of genetically isolated island populations that could eventually evolve into endemic species. The rates of evolution that I report in this dissertation are consistent with other studies that have examined contemporary evolution in extant species.

These results highlight the usefulness of using exotic species to investigate the genesis of biogeographical patterns. It is my hope that the results and conclusions that I

present here will encourage examination of these and other exotic species to further

describe patterns of diversification and to elucidate the evolutionary mechanisms

responsible for these patterns.

Curriculum Vitae

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Education

Year Completed	Institution	Degree
2002	Ohio Northern University	B.S. Biology, Field Biology minor
2010	Rutgers University	Ph.D. Ecology and Evolution

Employment

2009 – 2010	Visiting Instructor	The Richard Stockton College of New Jersey
2004 – 2009	Teaching Assistant	Rutgers University
2003 and 2004	Field Technician, Cape Sable Seaside Sparrow Fire Study, FL	University of California, Santa Cruz
2004	Intern, Northern Elephant Seal monitoring, Southeast Farallon Island, CA	PRBO Conservation Science
2003	Hawk Counter at Chelan Ridge Raptor Migration Project, WA	HawkWatch International

Peer-reviewed Publications

2009   Mathys, B.A. & Lockwood, J.L. Rapid evolution of great kiskadees on Bermuda: an assessment of the ability of the Island Rule to predict the direction of contemporary evolution in exotic vertebrates. *Journal of Biogeography*, **36**, 2204-2211.