

LOYOLA UNIVERSITY CHICAGO

INVESTIGATING DISPERSAL ABILITY TO INFER DIVERSIFICATION IN THE BIRDS
OF MADAGASCAR

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ABSTRACT

The objective of this study was to investigate whether dispersal ability, as measured by a proxy of hand-wing index, influenced diversification of the birds of Madagascar at two scales. Madagascar is home to several avian lineages that have diversified greatly while other lineages are only represented by a single species. A key question in evolutionary biology is why some of these lineages diversified while others did not. One way to address this is to examine what features of these lineages promoted their diversification. Recent studies have focused on the relative importance of dispersal ability to diversification at the continental and island scales. To further test this relationship, I investigated whether dispersal ability, as measured by hand-wing index, influenced diversification in the birds of Madagascar at a large regional scale and smaller local scale within Madagascar. To assess whether dispersal ability influenced diversification of the birds of Madagascar I compared hand-wing index of Malagasy and source (closest non-Malagasy relatives) clades of five radiating and three non-radiating lineages. I treated each lineage as an independent case study with the goals of identifying a pattern reflecting a shift in dispersal ability upon colonization of Madagascar in radiating lineages. At a smaller local scale of macrohabitats within Madagascar, I examined whether variation in dispersal ability (HWI) within widespread Malagasy species differed between subspecies restricted to macrohabitats reflecting local adaptation and divergence across macrohabitats. My study found that Malagasy species did not shift in their dispersal ability after colonizing Madagascar and thus, dispersal ability is not critical to the diversification of Malagasy endemics from their source

clade in radiating or non-radiating lineages. However, at a scale of Malagasy macrohabitats, I found variation in dispersal ability was likely due to local adaptations to macrohabitats. This study adds to our knowledge of dispersal ability and diversification patterns in Malagasy avifauna. This is a leading step towards additional studies to investigate the impact of potential geographic barriers to dispersal ability in the birds of Madagascar and provides further insights into diversification patterns.

CHAPTER 1

INTRODUCTION

A key question in evolutionary biology is why some lineages diversify while others do not. One way to address this is to examine what features of these lineages promotes their diversification. Recent studies have focused on the relative importance of dispersal ability in the evolutionary processes of speciation and diversification at the continental and island scales (Claramunt et al., 2012; Weeks and Claramunt, 2014; Kennedy et al., 2016; White 2016). Dispersal can stimulate speciation and diversification by allowing species to overcome barriers and expand geographically or colonize new regions. It can also inhibit speciation by maintaining gene flow between populations (Claramunt et al., 2012). Here, I define dispersal as the movement of an organism across an already existing geographic barrier. Dispersal ability is a quantitative measure of an organism's potential capability to overcome a geographical barrier.

Dispersal ability and its impact on diversification varies greatly across taxa. Birds, compared to other tetrapods, are generally considered to be better at dispersal due to their ability to fly but even some birds can be limited in their dispersal ability (Adler et al., 1995; Moore et al., 2008; Kisel and Barraclough, 2010; Pigot and Tobias, 2015; Kennedy et al., 2016). Several recent avian studies have found negative or no relationships between dispersal ability and diversification rates (Claramunt et al., 2012; Weeks and Claramunt, 2014; Kennedy et al., 2016). Claramunt et al. (2012) found a negative relationship between dispersal and diversification rates in Furnariidae (woodcreepers). Similarly, Weeks and Claramunt (2014)

found dispersal had a negative relationship with diversification in an Australasian archipelago study of avifauna. In these examples of continental and island groups the negative relationship between dispersal ability and diversification means higher dispersal ability leads to lower diversification. Over the past century scientists have devised numerous ways to study dispersal ability.

Quantifying avian dispersal directly is difficult, therefore indirect methods have been developed. Approaches such as tracking organisms using radiotelemetry and satellite or mark-recapture studies can be costly and time-consuming to obtain adequate samples (van Noordwijk 1984; Martin et al., 2008; Dawideit et al., 2009) and hard to implement for a wide array of species. A simple yet reliable way to study and quantify dispersal ability is to use measurements of wing shape taken from closed-wing museum skin specimens to create a hand-wing index (Kipp 1959; Claramunt et al., 2012; Weeks and Claramunt, 2014; Kennedy et al. 2016; White 2016). The hand-wing index is a simple index of aspect ratio, a proxy of long-distance flight performance and wing shape (Kipp 1959; Lockwood et al., 1998; Claramunt and Wright, 2017). The hand-wing index has been used in previous avian studies for investigating population structure and diversification in Borneo, the relationship between dispersal ability and diversification rates in a South American continental radiation of Furnariidae and the avifauna of Australasian archipelagoes, range expansions, habitat preferences, foraging stratum, and migratory behavior (Chua et al., 2017; Claramunt et al., 2012; Weeks and Claramunt, 2014; Vanhooydonck et al., 2009; White 2016; Kennedy et al., 2016). *To further test whether there is a relationship between dispersal ability and diversification, I used the hand-wing index as a proxy for dispersal ability to compare island and continental radiations of birds.*

Dispersal ability and diversification

In order to colonize new habitats, islands, or regions animals frequently must overcome geographical barriers which requires enough dispersal ability. Dispersal differs from migration, which is the reoccurring two-way movement of an organism between its wintering and breeding site. Dispersal can be split into two types - range expansion (also referred to as dispersion or diffusion) and long-distance (jump) dispersal. Range expansion is defined as a particular population expanding at the edges of its' geographic range as previously limiting barriers disappear. In contrast, long-distance dispersal is when a small group of individuals move to a new location that is a considerable distance away from the edge of a species range (Wilkinson 2017). The former usually occurs in the absence or disappearance of a barrier, while the latter requires overcoming an otherwise natural barrier. For example, birds that reached Madagascar from Africa or India overcame oceanic barriers to reach this island (Prum 1993; Yamagishi et al., 2001; Kirchman et al., 2001; Groombridge et al., 2002; Warren et al., 2003, 2005; Beresford et al., 2005; Marks and Willard, 2005; Yoder and Nowak, 2006).

Dispersal ability can have positive and negative effects on diversification. High dispersal ability can have a positive effect on diversification by promoting the opportunity to colonize a new area such as a remote island and thus providing speciation opportunities such as founder event speciation or ecological speciation when exposed to new habitats, foraging niches, and changes in selective pressures; however, high dispersal ability across islands can also result in few effective geographical barriers so gene flow is high between populations, therefore decreasing the chance for speciation due to a lack of reproductive isolation (Claramunt et al., 2012; Weeks and Claramunt, 2014). Low dispersal ability results in difficulty overcoming

geographical barriers such as oceans and channels, therefore decreasing the chance of successfully colonizing a new area such as an island and in turn, the opportunity for geographical speciation; low dispersal ability may also promote diversification by limiting gene flow between geographically separated populations aiding reproductive isolation (Claramunt et al., 2012; Weeks and Claramunt, 2014; Kennedy et al., 2016). The intermediate dispersal model predicts that lineages with intermediate dispersal ability will have an ideal mixture of geographical range expansion and reproductive isolation that results in high speciation rates (Fig. 1; Claramunt et al., 2012; Weeks and Claramunt, 2014; Kennedy et al., 2016).

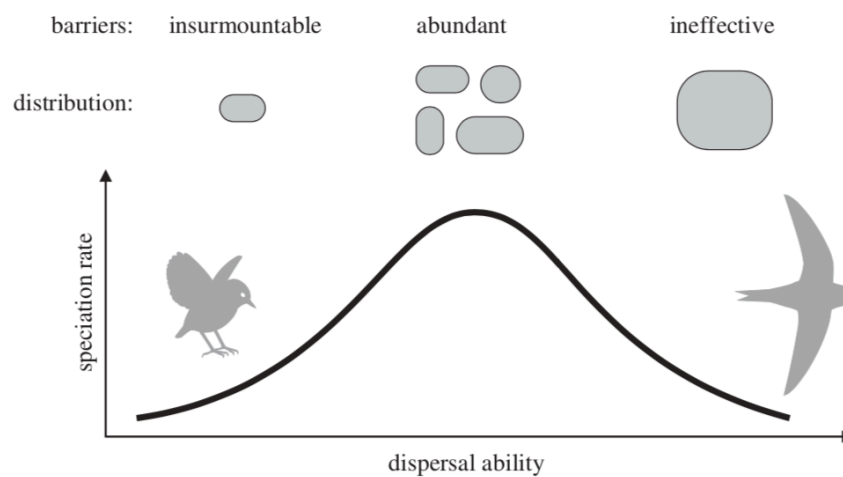


Figure 1. Intermediate dispersal model. According to this model, lineages with low dispersal ability are unable to overcome barriers and remain restricted to small areas so their speciation rates are low. Any lineage possessing intermediate dispersal ability may overcome geographic barriers and have higher rates of speciation in these new isolated areas. Those lineages possessing high dispersal abilities are easily able to overcome geographic barriers, so their gene flow remains high in their large distribution and therefore decreases their speciation rates (reproduced from Claramunt et al., 2012, Figure 1).

Island biogeography and island syndromes

In order to establish a population on an island, a bird must have enough dispersal ability to colonize via over-water dispersal; this is a first step leading to the production of endemic biodiversity via allopatric speciation (Cowie & Holland, 2006). Subsequent dispersal into subregions, or distinct large habitats, can lead to further allopatric speciation and the transitions into these distinct subregions may stimulate local adaptive divergence (Fine et al., 2014; Warren et al., 2014; Schenk and Stepan, 2018). The general belief is that older continental land masses, such as Africa or Asia, are the source of colonizing lineages to younger islands, also known as the island progression rule (Whittaker et al., 2017). Island species-area relationships are noted for having an increasing number of species as island size increases (Whittaker et al., 2017). Larger islands tend to have a higher number of endemic species in part due to their ability to support *in situ* diversification resulting from a combination of evolutionary processes and opportunities (MacArthur and Wilson, 1967; Whittaker et al., 2017). Another general belief is the more isolated an island is the less likely lineages are able to reach it so there is a negative relationship between isolation and species richness (MacArthur and Wilson, 1967). Species fortunate enough to successfully colonize islands with available resources and/or open niches have greater potential to diversify *in situ* (Losos and Ricklefs, 2009).

The removal and/or addition of selection pressures on islands can have evolutionary implications. After successful colonization of an island, organisms are typically exposed to differing abiotic and biotic conditions that may lead to changes in morphology, behavior, and ecology; these changes in colonizing lineages are referred to as island syndromes (Adler and Levins, 1994; Whittaker and Fernandez-Palacios, 2007; Novosolov et al., 2013; Patino et al.,

2017). Several notable syndromes have been documented in birds after they have colonized islands. Island birds exhibit trends of evolving flightlessness or reduced dispersal ability, inability to recognize predators, and changes in body size (Roff, 1994; Brown and Lomolino, 1998; Losos and Ricklefs, 2009; Lomolino et al., 2013; Wright et al., 2016; Kennedy et al., 2016). Reduction in dispersal ability or evolution towards flightlessness has been suggested to be the result of release from selection pressures such as predation and the high energetic costs required to fly (Wright et al., 2016; Kennedy et al., 2016). *Little is known about the changes in the Madagascar endemic birds and their in situ dispersal and radiation.*

Avian colonization of Madagascar

Madagascar provides a unique model for studying island biogeography and *in situ* diversification due to its temporal and geographical isolation. Madagascar is one of the largest islands in the world at 587,000 square kilometers. Madagascar has had no connections to another landmass for over 80 million years (Vences et al. 2009) when it was last connected to India. Madagascar and India are now geographically separated by 3,769 kilometers of ocean (Safford and Hawkins, 2013). Madagascar has been geographically isolated from continental Africa for the past 158 million years by the 300-kilometer-wide barrier called the Mozambique Channel (Vences et al., 2009).

These daunting barriers have made colonizing Madagascar rare for most fauna. For example, only five mammalian lineages - lemurs, rodents, tenrecs, carnivores, bats - have successfully colonized the isolated island. Alternatively, many independent lineages of birds have colonized Madagascar (Yoder et al., 1996; Yoder et al., 2003; Olson and Goodman, 2003; Poux et al., 2005; Russell et al., 2007; see Fig. 4). This is not surprising since birds are volant,

however, not all birds are capable of dispersing across these barriers due to variation in their dispersal ability. This is reflected in the fact that not all African lineages are represented in Madagascar.

Due to Madagascar's long history of geographical and temporal isolation, modern birds have colonized Madagascar via over water dispersal (Prum 1993; Yamagishi et al., 2001; Kirchman et al., 2001; Groombridge et al., 2002; Warren et al., 2003, 2005; Beresford et al., 2005; Marks and Willard, 2005; Yoder and Nowak, 2006). It has been commonly assumed that species colonize islands from the nearest continental source, however, this is not always the case. The stepping-stone island theory has been proposed to explain lineages with closer affinities to Asia than Africa. This theory suggests that birds from Asia dispersed across the Indian Ocean during times of low sea level that caused stepping-stone islands to emerge (Warren et al., 2010). Another theory is that birds dispersed across the Mozambique Channel from Africa. The deep Mozambique Channel supports the consensus that a majority of Madagascar's endemic lineages with African origins were the result of over-water dispersal (Prum 1993; Yamagishi et al., 2001; Kirchman et al., 2001; Groombridge et al., 2002; Warren et al., 2003, 2005; Beresford et al., 2005; Marks and Willard, 2005; Yoder and Nowak, 2006) and not any purported land-bridge.

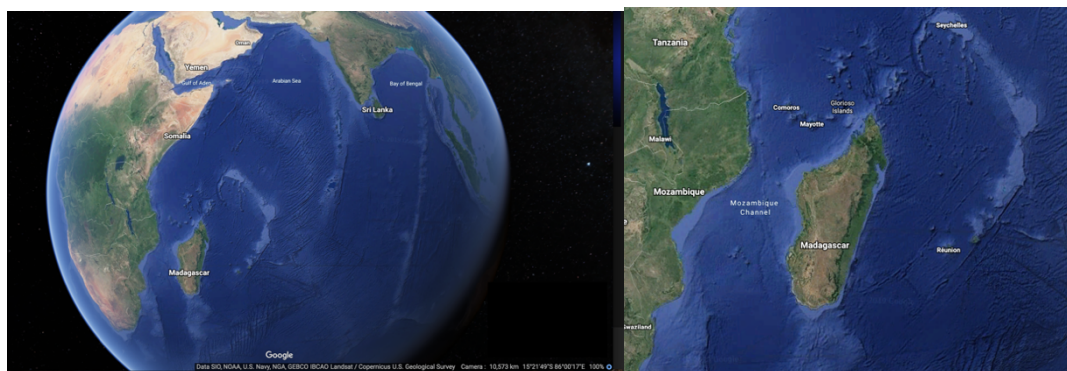


Figure 2. Visual representations of the distance between Asia and Madagascar (A; left) and Africa and Madagascar (B; right). Both figures taken from Google Earth (data provided to them by: SIO, NOAA, U.S. Navy, NGA, GEBCO IBCAO Landsat/ Copernicus U.S. Geological Survey).

Birds and habitats of Madagascar

Madagascar is divided into three major habitats (see Fig. 3A, Harper et al., 2007) or *macrohabitats*. The eastern humid rainforest (47,000 km²), the western dry deciduous forest (32,000 km²), and the southwestern spiny desert (24,000 km²). Given the varied resources in these macrohabitats, they each support different numbers of endemic species with the eastern humid forest having the highest (~44), the western dry forest with nine, and the southwestern spiny desert with 12 endemic avian species (Safford and Hawkins, 2013). The east and west macrohabitats are a closed *habitat class* (defined here as dense foliage that can obstruct flight), which is known for influencing a low dispersal ability wing shape (blunt, rounded wings); the southwest macrohabitat is an open habitat class (defined as a lack of dense foliage so flight is unobstructed) which is known for influencing a more dispersive wing shape (longer, more pointed wings; White 2016). Madagascar has three large massifs that have formed in the north, center, and south (Mt. d'Ambre, Ankaratra, Andringitra) (see Fig. 3B, Vences et al., 2009). Rivers flow from the central highlands down to the lowlands of the eastern humid forest and

western dry forest (Fig. 3B). These macrohabitat differences and geographical barriers are likely to drive local adaptation and diversification of species within Madagascar. The levels of avian endemism among these macrohabitats are likely underrepresented due to an increasing number of recent discoveries of cryptic species (Block et al., 2012; Younger et al., 2018).

Madagascar has many barriers ranging from rivers and massifs that provide several potential mechanisms for species diversification. The strong differences between the west and east macrohabitats may have influenced the formation of new species via adaptation to their respective macrohabitat's ecological conditions and divergence from one another, a mechanism known as the ecogeographic constraint (Yoder and Heckman, 2006; Vences et al., 2009).

Divergent clades have been found in *Xanthomixis zosterops* that are posited to have become isolated by elevation in the humid forests (Block et al., 2015); this may possibly be an example of ecologically mediated speciation within Madagascar's habitats. *Newtonia amphichroa* represents an example of the montane refugia hypothesis; *Newtonia amphichroa* inhabits montane humid forest habitats and during the early Pleistocene interglacials some populations became isolated resulting in vicariant speciation (Younger et al., 2018). We do not know for certain how effective rivers can be as barriers to Madagascar birds, although they may act as dispersal barriers in other areas of the world (Pastorini et al., 2003; Goodman and Ganzhorn, 2004; Moore et al., 2008).

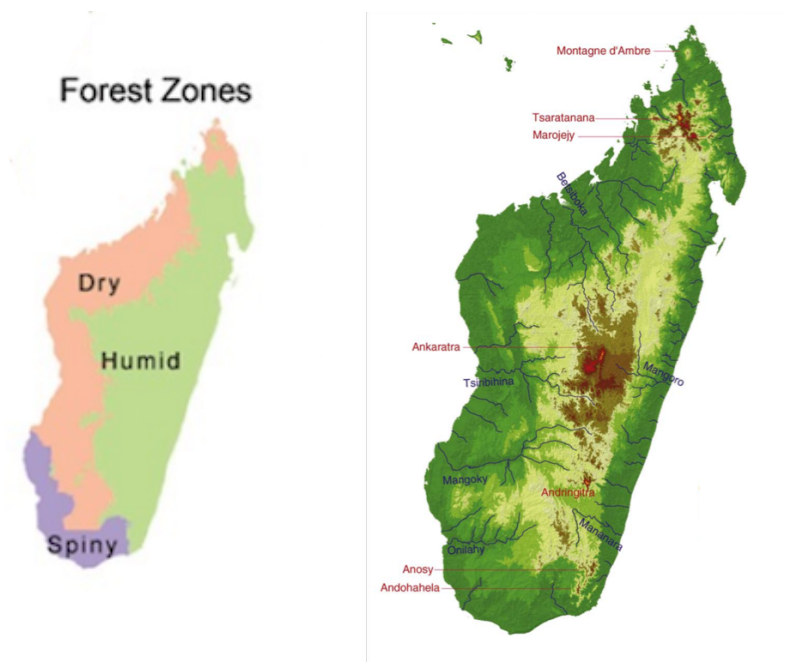


Figure 3. Macrohabitats and potential geographical barriers in Madagascar. (A; left) visually summarizes the three major habitats (macrohabitats) of Madagascar; (B; right) highlights the massifs in red coloration and blue lines represent rivers (Figures 3A and 3B borrowed from Harper et al., 2007, Figure 1 and Vences et al., 2009, Figure 1A respectively).

Investigating avian dispersal ability on Madagascar

Madagascar provides a model system to investigate dispersal ability and how it relates with morphology, ecology, and geography. My study investigates how dispersal ability has influenced diversification in the birds of Madagascar by comparing lineages that have radiated to non-radiating lineages. I studied eight endemic lineages (Fig. 4) of birds in Madagascar that were chosen based on sample availability and published phylogenetic trees (Table 1). Five of these lineages are considered radiating (Vangidae, Bernieridae, Locustellidae, Ploceidae, Cuculidae), meaning they diversified *in situ* at least once; the three others are considered non-radiating (Nectariniidae, Pycnonotidae, Monarchidae) as they did not diversify *in situ* within Madagascar but had ample time to do so. I treated each lineage as a case study with the goal of identifying an overall pattern of features in radiating versus non-radiating lineages that may explain why certain

lineages diversified in Madagascar and others (non-radiating) failed to do so. None of the species in my study are migratory, therefore the comparisons of hand-wing index as a metric of dispersal ability should be related to diversification potential.

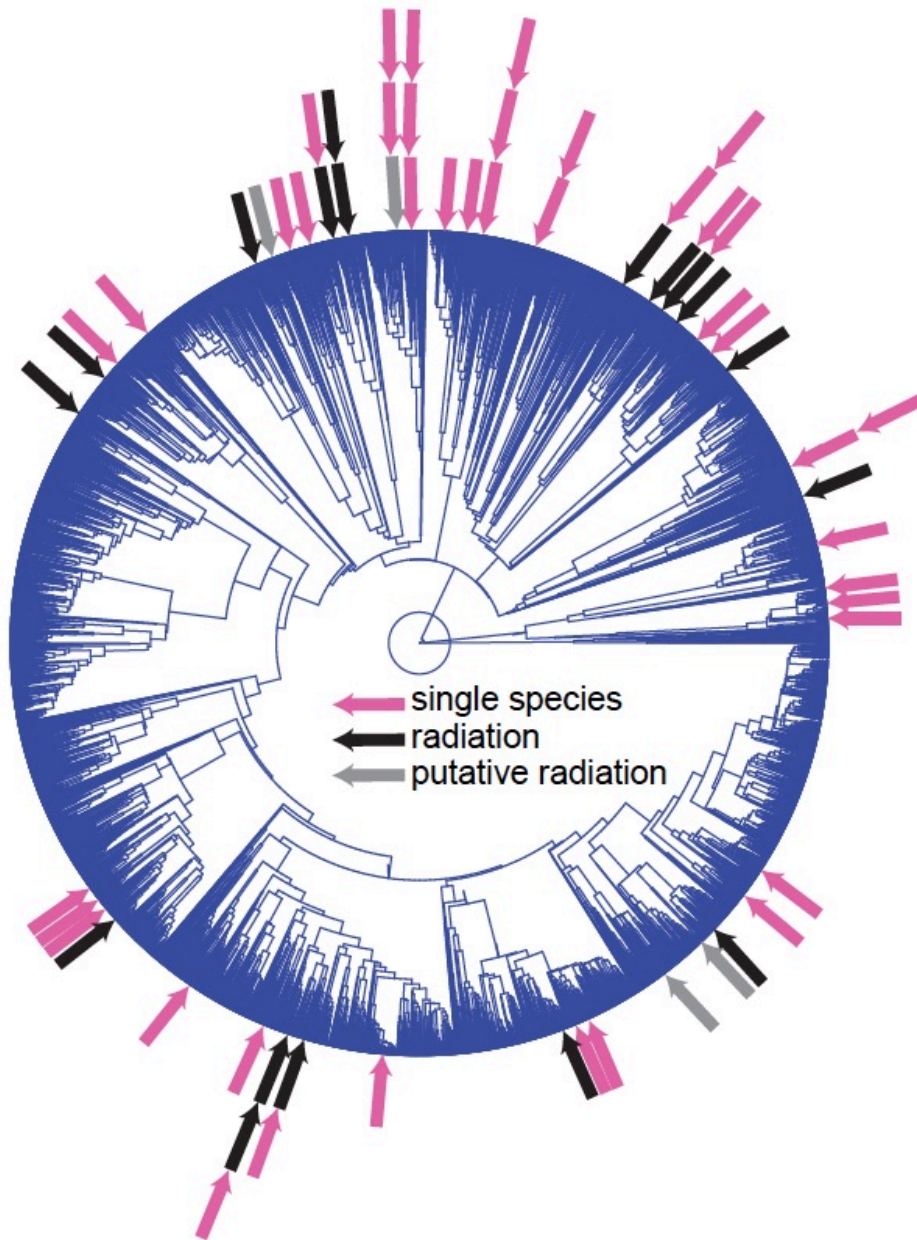


Figure 4. Phylogenetic tree of the extant birds of the world highlighting colonizing and radiating Malagasy lineages. A majority of these independently colonizing lineages are represented by a single species (source: Reddy, in prep.; modified from Jetz et al., 2012).

Table 1. Summary of the endemic avian lineages in Madagascar. Listed is their respective number of endemic species, estimated colonization of Madagascar, number of colonization events, whether said lineage is a radiation, and published phylogenetic trees referenced. *One extinct species was not included in the study of *Coua* lineage.

Malagasy Lineage	Family	# of Endemic Species	Estimated Colonization (Mya)	Hypothesized # of Colonization events	Radiating	Publication
Vanginae	Vangidae	21	20	1	Yes	Reddy et al. 2012
<i>Bernieridae</i>	Bernieridae	11	9-25.2	1	Yes	Cibois et al., 2001; Beresford et al., 2005; Alstrom et al., 2018
<i>Bradypterus/Amphilais</i>	Locustellidae	2	<5.7	1	Yes	Alstrom et al. 2018
<i>Nelicurvius Foudia</i>	Ploceidae	2 2	5.13-7.05 <1.2	2	Yes	Warren et al., 2012; De Silva et al., 2017
<i>Coua</i>	Cuculidae	10	N/A	N/A	Yes	Johnson et al., 2000; Payne and Sorenson, 2005
<i>Cinnyris notata</i> <i>Cinnyris sovimanga</i>	Nectariniidae	2	<4 <4	2	No	Warren et al. 2003
<i>Hypsipetes madagascariensis</i>	Pycnonotidae	1	0.6-2.6	1	No	Warren et al., 2005; Oliveros and Moyle 2010
<i>Terpsiphone mutata</i>	Monarchidae	1	~<2	1	No	Fabre et al., 2012; Bristol et al., 2013

Vanginae (Vangidae) is the largest passerine family in Madagascar with 21 species present. It is unclear exactly what mainland source this lineage colonized from, but Africa and Asia are both considered possible dispersal routes to Madagascar (Reddy et al., 2012). Shortly after colonization of Madagascar this lineage speciated rapidly and it is believed to have been driven by adaptation to available ecological niches (Reddy et al., 2012). This lineage is a unique adaptive radiation that displays a wide range of diversity in terms of their morphology (particularly bill shape), foraging behaviors, and ecology.

Bernieridae is the second largest adaptive radiation of Malagasy passerines. It is currently composed of eight genera and 11 species but ongoing investigations into cryptic speciation within this family may reveal additional new species. Beresford et al. (2005) estimated the divergence of this Malagasy clade from its continental source occurred approximately 25.2 -19.2 Ma, but other studies put the estimate as more recent at about 9-17 Ma (Cibois et al. 2001; Younger et al. Submitted). The hypothesized origin of the Malagasy lineage is uncertain but optimal trees (with weak bootstrap support) suggest an African origin (Cibois et al., 2001). A majority of the species within this lineage can be found gleaning prey at low to mid elevations in the eastern humid forest although some species deviate from this pattern (Safford and Hawkins, 2013).

There is one lineage of Locustellidae that radiated on Madagascar. This lineage, commonly known as the emu-tails, is composed of *Bradypterus brunneus* and *Amphilais seebohmi*. Both species exhibit gleaning behaviors but differ in habitat preferences. *Bradypterus brunneus* occurs in the eastern humid forest understory, whereas *Amphilais seebohmi* prefers marshy habitats in the eastern humid forest at mid to high elevations.

Ploceidae is a family with two endemic Malagasy species in each genus of *Foudia* and *Nelicurvius*. These genera are believed to have independently colonized Madagascar from Africa (De Silva et al., 2017). These species are known for their non-breeding flocking behaviors which may have aided them in establishing populations upon colonization of Madagascar; this flocking behavior is also documented in their mainland relatives such as *Quelea quelea* (Safford and Hawkins, 2013). Within the genus *Foudia*, the two species prefer different habitat classes but are altitudinal generalists (Safford and Hawkins, 2013). *Foudia madagascariensis* is widespread across Madagascar preferring the open habitat class whereas *Foudia omissa* is restricted to the closed eastern humid forest. Within the genus *Nelicurvius*, the two endemic species differ in habitat class as well. *Nelicurvius sakalava* prefers to forage from the ground in dry open habitats compared to *Nelicurvius nelicourvi* which prefers to glean and probe in the middle story of the closed eastern humid forest trees (Safford and Hawkins, 2013).

The genus *Coua* (Cuculidae) has not been well studied in terms of phylogenetics and their estimated colonization time remains unclear. *Coua* consists of three arboreal (*C. cristata*, *C. verreauxi*, *C. caerulea*) and six primarily terrestrial species (*C. gigas*, *C. coquereli*, *C. cursor*, *C. reynaudii*, *C. serriana*, *C. ruficeps*) that are found in the various macrohabitats of interest throughout Madagascar. Several populations can be found such as in *Coua cristata* which has been split into three populations or subspecies found in the open southwestern spiny desert (*Coua c. pyropyga*), closed western dry deciduous forest (*Coua c. dumonti*), and closed eastern humid forest (*Coua c. cristata*). This is also true for two subspecies of *Coua ruficeps* found in the west (*Coua r. ruficeps*) and southwest (*Coua r. olivaceiceps*) habitats.

Nectariniidae consists of two species that independently colonized Madagascar and their close relatives can be found throughout the nearby islands in the Malagasy region. The Long-billed Green Sunbird (*Cinnyris notata*) and Souimanga Sunbird (*Cinnyris sovimanga*) clades both colonized Madagascar within the last 3.9 million years with a hypothesized continental origin of Africa (Warren et al., 2003). It is believed that the *sovimanga* clade initially colonized the Comoros archipelagoes followed by an expansion from Anjouan that led to their colonization of Madagascar (Warren et al., 2003). Both species of *Cinnyris* are widespread in Madagascar and present at all elevations. These species are nectar specialists but also exhibit glean foraging strategies.

Pycnonotidae is a family that has not radiated within Madagascar but is species-rich elsewhere. The Malagasy clade has only a single species (*Hypsipetes madagascariensis*) present. This genus is peculiar because it has relatives throughout Asia and in some of the nearby Indian Oceanic islands but is absent in continental Africa (Warren et al., 2005). Warren et al. (2005) finds evidence of a single colonization event from Asia with support for a route pattern consistent with an initial arrival in Madagascar followed by immigrating to the smaller nearby islands. The Madagascar Black Bulbul (*Hypsipetes madagascariensis*) is widespread throughout all of Madagascar's elevations and habitats (except for open grasslands) and employs a wide variety of foraging behaviors making it a generalist (Safford and Hawkins, 2013).

Monarchidae is a highly dispersive family of birds with species and subspecies occurring on nearby islands around Madagascar; there is one species (two subspp) on Madagascar. Bristol et al. (2013) and Fabre et al. (2012) agree that the *Terpsiphone* species occurring on the Indian ocean islands and the African continent have an Asian origin; however, it remains unresolved as

to whether the Indian Ocean islands were colonized directly from Asia or via Asia to Africa to the islands. The Madagascar Paradise Flycatcher (*Terpsiphone mutata*) is a widespread low to mid altitude species that displays the foraging behaviors of sally-gleaning and aerial hawking primarily. One subspecies resides in the closed western dry deciduous forest (*Terpsiphone m. singetra*) and the other inhabits the closed eastern humid rainforest (*Terpsiphone m. mutata*).

Objectives and hypotheses

This study will investigate how dispersal ability has influenced diversification in the birds of Madagascar at two scales. In chapter 3, I will investigate at a broad scale whether the endemics Malagasy lineages shifted in their dispersal ability from their closest continental relatives after colonizing Madagascar. In chapter 4, I will investigate, at a smaller scale, whether variation in dispersal ability is influenced by local adaptation to the macrohabitats within Madagascar.

The first goal of this study (chapter 3) is to examine if Malagasy species shift in their dispersal ability after colonizing Madagascar. I compared the dispersal ability, as quantified by the hand-wing index (Claramunt et al., 2012; Weeks and Claramunt, 2014; Kennedy et al., 2016; White 2016) of present-day Malagasy species to their closest non-Malagasy relatives (here-by referred to as the ‘Malagasy clade’ and ‘source clade’, respectively) for each radiating and non-radiating lineage. I referred to published phylogenetic trees of Malagasy and their source clades to choose the sampled species for this study. I measured adult male and female museum specimens for various linear body measurements including hand-wing index. I conducted multivariate analyses (principal component analysis; MANOVA) and univariate analyses (dot-

box-plot and ANOVA) to compare morphological variation between Malagasy and source clades.

For each clade, I examined the difference in the morphospace occupancy between two groups, Malagasy and source clades. For radiating lineages, I predict the Malagasy clades will be separated in morphospace from the source clades reflecting a morphological shift to Madagascar (Fig. 5C&D). For non-radiating lineages, I predict the Malagasy clade will be in the same morphospace as its source clade (Fig. 5A or 5B). I will interpret the possible outcomes as follows:

- 1) There is no significant difference between Malagasy and source morphospace (Fig. 5A)—both groups occupy an equal volume (disparity) and are in the same region of morphospace (centroids are similar). I will interpret this to mean the Malagasy endemics did not diverge morphologically from their close relatives (source) and does not reflect an adaptive shift to an island.
- 2) There is a significant difference in the volume of morphospace occupied but the two groups are in the same region (centroids are similar) of morphospace (Fig. 5B)—one group occupies a smaller volume of morphospace than the other, larger, morphospace occupying group. I will interpret this as the two clades do not differ substantially in morphology.
- 3) There is significant difference in the Malagasy and source clade occupancy of morphospace (Fig. 5C&D)—if the groups occupy different regions of morphospace, this indicates that both groups differ substantially in morphology. Furthermore, if one group occupies a greater volume of morphospace, I will interpret this as evidence of morphological changes in response to establishment on Madagascar, as in the following:

- a. If the volume of morphospace occupied is greater in Malagasy clade than source (Fig. 5C), then I will interpret this to reflect a shift to Madagascar with considerable subsequent morphological diversification after establishment.
- b. If the volume of morphospace occupied is greater in source clade than Malagasy (Fig. 5D), then I interpret this to reflect a shift to Madagascar with little subsequent morphological diversification after establishment in Madagascar.

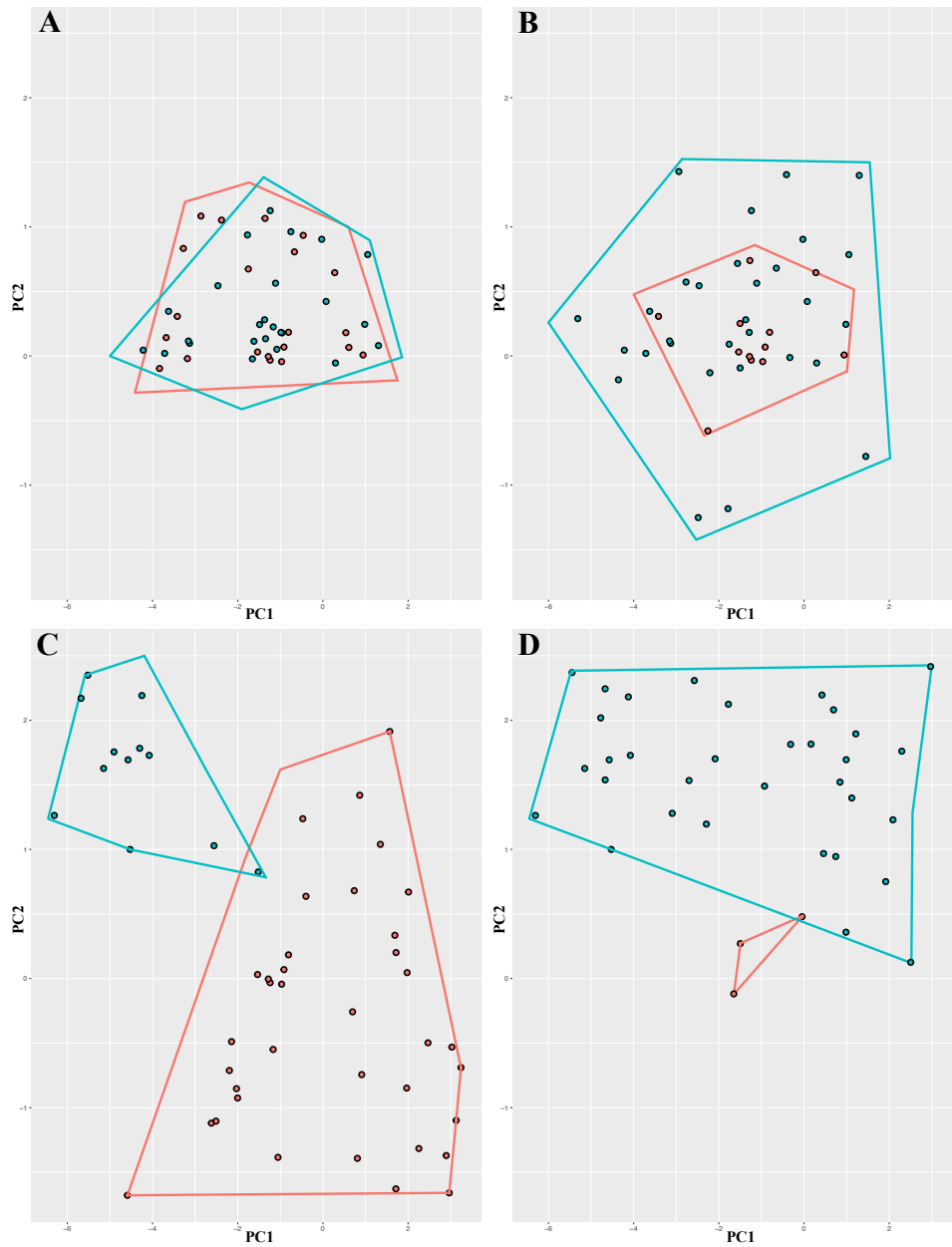


Figure 5. Cartoon examples of potential results of multivariate principal component analysis for objective 1. Orange depicts Malagasy clade and blue is source clade. (A) depicts outcome 1 of no significant differences between the centroids (center of occupancy) or disparity (volume) of Malagasy and source clade in morphospace; (B) depicts outcome 2 of no differences in centroids, but one group has greater disparity than the other; (C) depicts outcome 3A of significant differences in the centroids of the groups but disparity is greater in Malagasy than source; (D) depicts outcome 3B of centroids of each group being significantly different but disparity is greater in source clade than Malagasy.

I also conducted comparisons between the two clades for all morphological variables, focusing primarily on hand-wing index (HWI2), to understand how and in which traits a lineage may have diverged morphologically. For radiating lineages, I expect a reduction in dispersal ability (HWI2) in the Malagasy clade compared to source clade reflective of a shift to Madagascar (Fig. 6B). For non-radiating lineages, I expect the Malagasy clade to have maintained high dispersal ability (no significant difference between clades; Fig. 6A). I will interpret the possible outcomes as follows:

- 1) The hand-wing index of the Malagasy clade does not differ from source (Fig. 6A)—I will interpret this to mean dispersal ability did not play a key role in diversification of this group.
- 2) The hand-wing index of the Malagasy clade is smaller than source (Fig. 6B)—I will interpret this to mean the Malagasy endemics have reduced dispersal ability after colonizing Madagascar.
- 3) The hand-wing index of the Malagasy clade is larger than source (Fig. 6C)—I will interpret this to mean the Malagasy endemics have greater dispersal ability after colonizing Madagascar.
- 4) Other morphological trait(s) is/are significantly different between Malagasy and source clade—I will interpret this to mean another trait (ex: tarsus length) is important for diversification of the Malagasy endemics from the source group.

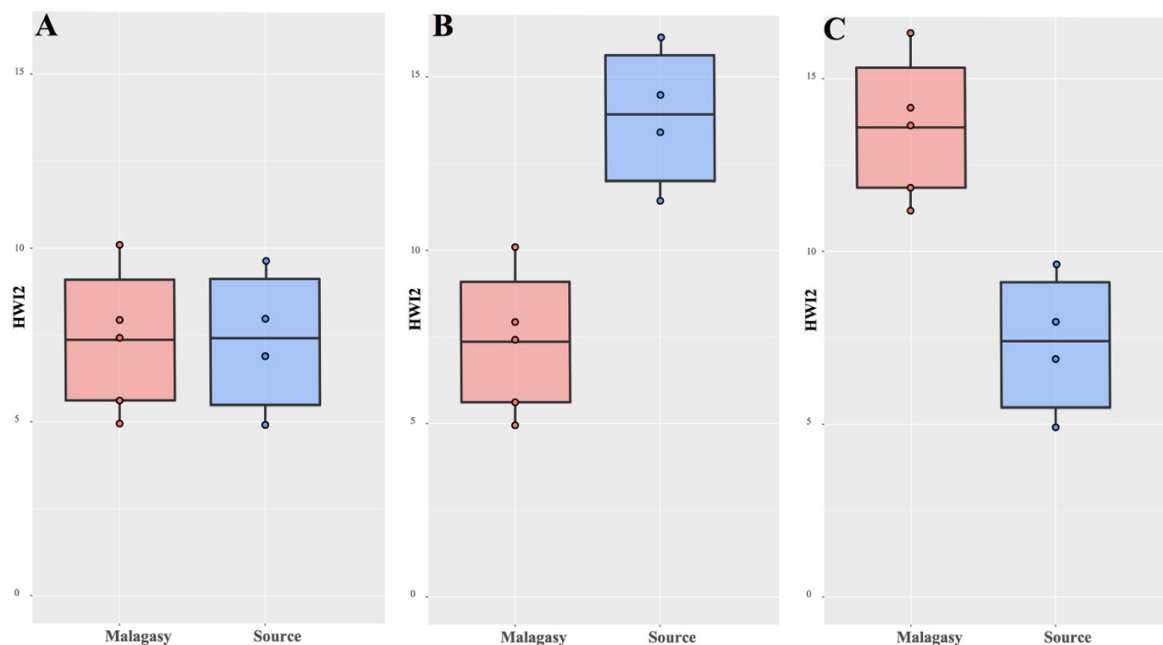


Figure 6. Cartoon example results of univariate comparisons of trait values between Malagasy (orange) and source (blue) clade. (A) depicts outcome 1 of no significant difference in hand-wing index between the two clades. (B) depicts outcome 2 of significant differences in hand-wing index with Malagasy clade being lower. (C) depicts outcome 3 of a significant difference in hand-wing index between the two groups but Malagasy being greater than source.

*The second goal of this study (chapter 4) was to investigate variation in dispersal ability within widespread endemic species residing in multiple macrohabitats within Madagascar to test whether they adapted and diverged across macrohabitats rather than or in addition to colonizing Madagascar. Wing shape is known to vary among populations in association with the habitat type and precipitation levels (Vanhooydonck et al. 2009). I examined morphological variation across widespread species by examining populations across the island to investigate if there were differences in trait values across different macrohabitats and/or habitat classes. Within each endemic Malagasy lineage, I compared the dispersal ability of widespread species populations to their macrohabitats (example: in Cuculidae, *Coua cristata* has three subspecies- one in each macrohabitat). For each widespread species, I examined the difference in the morphospace*

occupancy between three macrohabitats: the open southwestern spiny desert, the closed western dry forest, and the closed eastern humid rainforest. I predict each macrohabitat will occupy a distinct region in morphospace from each other reflective of diversification via local adaptation to the environmental and ecological conditions of each macrohabitat. I will interpret the possible outcomes as follows:

- 1) There is no significant difference in the morphospace occupancy between the three macrohabitats (Fig. 7A)—if all three macrohabitats occupy the same region of morphospace, I will interpret this to mean they did not diversify across macrohabitats and habitat classes.
- 2) There is a significant difference in the southwest versus east and west morphospace occupancy (Fig. 7B)—if the southwest occupies a different region of morphospace and east/west occupy the same region of morphospace, I will interpret this as a shift to habitat classes. Due to the similarity of the closed forests of the east and west they diversified by open versus closed habitat classes.
- 3) There is a significant difference in the morphospace occupancy between all three macrohabitats (Fig. 7C)—if each macrohabitat occupies a different region in the morphospace, I will interpret this as they diversified by local adaptation to the environmental and ecological conditions of each macrohabitat.
- 4) There is a significant difference in the morphospace occupancy between the west and east macrohabitats but southwest is the same as either east or west (Fig. 7D)—if the southwest occupies a similar region of morphospace as the west or east, I will interpret this as they diversified due to shared similarities such as environmental factors.

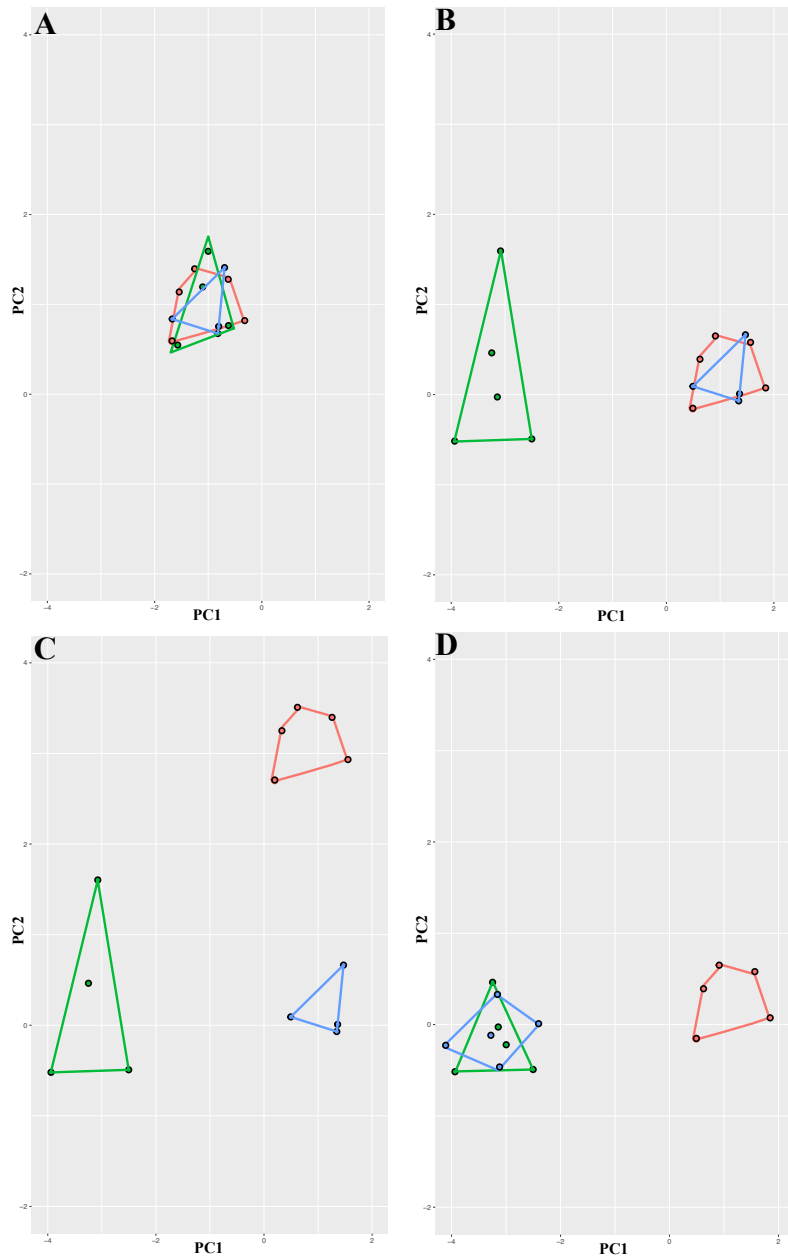


Figure 7. Examples of potential results of multivariate principal component analysis for objective 2 outcomes. (A) depicts outcome 1 of all three macrohabitats occupying the same morphospace; (B) depicts outcome 2 of southwest separated in morphospace, but overlap between the east and west macrohabitats; (C) depicts outcome 3 of all three macrohabitats occupying different morphospace; (D) depicts outcome 4 of southwest occupying the same morphospace as west, but east and west occupy different morphospace. Colors are as follows: green = southwest, orange= east, blue= west.

For each widespread species, I conducted comparisons between the three macrohabitats for each morphological variable, focusing primarily on hand-wing index (HWI2), to understand how and in which traits a species may have diverged across macrohabitats and/or habitat classes. I predict the populations in the open southwestern spiny desert macrohabitat will have the greatest hand-wing index followed by those in the closed western dry forest and closed eastern humid forest. I will interpret the possible outcomes as follows:

- 1) The hand-wing index does not differ between macrohabitats (Fig. 8A)—I will interpret this to mean dispersal ability was not important for diversification across macrohabitats.
- 2) The hand-wing index of the southwest is significantly greater than east and west, but east and west are not significantly different (Fig. 8B)—I will interpret this to mean these populations evolved differently in open and closed habitat classes.
- 3) The hand-wing index significantly differs between all macrohabitats (Fig. 8C)—I will interpret this to mean dispersal into distinct macrohabitats stimulated local adaptation to the environmental and ecological conditions of each macrohabitat.
- 4) Other morphological trait(s) is/are significantly different between macrohabitats—I will interpret this to mean another trait (ex: bill width) is important for driving diversification across macrohabitats.

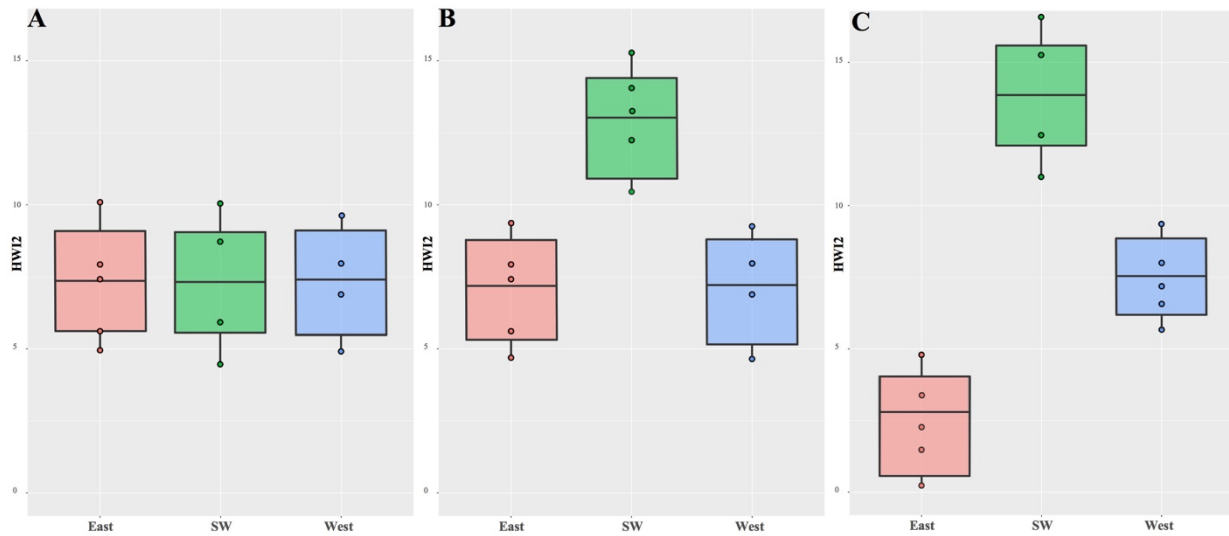


Figure 8. Cartoon example results of univariate comparisons of trait values between macrohabitats for objective 2 outcomes. (A) depicts outcome 1 of no significant difference in hand-wing index 2 between all macrohabitats. (B) depicts outcome 2 of southwest having significantly greater hand-wing index 2 and no significant difference between the east and west macrohabitats hand-wing index 2. (C) depicts outcome 3 of significant differences in hand-wing index 2 between all three macrohabitats.

CHAPTER 2

USING MORPHOMETRIC DATA TO EXAMINE PATTERNS OF DIVERSIFICATION

I used the same methodology in this study for objective 1 (chapter three) and objective 2 (chapter four) with only minor differences. In objective 1, I compared morphological traits between the Malagasy and source clades of families; in objective 2, I compared traits of widespread Malagasy species by comparing populations in different macrohabitats.

Morphometrics & measurements

In this study I took seven standardized morphometric measurements (bill depth, bill width, bill length, wing chord length, secondary feather length, tarsus length, and tail length) of 508 museum skin specimens from the collections of the Field Museum of Natural History (FMNH) and the American Museum of Natural History (AMNH). See Table 3 for a complete list of specimens measured. I made sure to select only specimens that were adults and had intact bills, wings, tails, and legs. Using digital calipers (Mitutoyo), I took the standardized morphometric measurements as follows: bill depth and bill width measured at the anterior edge of the nostrils (Baldwin et al., 1931; J. Tobias, personal communication, October 23, 2017); bill length (sometimes referred to as total culmen) measured from the anterior edge of the skull to the tip of the bill (Baldwin et al., 1931); wing chord length measured from the carpal joint to the tip of the longest primary feather (Baldwin et al., 1931); secondary length (S1) was measured from the carpal joint to the tip of the first secondary feather (Claramunt et al., 2012); tarsus length was measured from the inner notch of the knee to the third scute of the ankle (Baldwin et al., 1931),

and tail length was measured from the base of the rectrices (where they attach to bone) to the tip of the longest rectrix (Baldwin et al., 1931). In one family, Monarchidae, male specimens in breeding plumage had long central tail feathers (presumably under sexual selection). For these, I measured the second longest tail feather to keep all specimens comparable within that clade. While the primary focus of this study is concerned with dispersal ability, data for additional morphometric variables were collected to explore any potential associations with lineages diversification and account for body size. For each museum skin specimen (adults only) all measurements were taken using Mituyoto digital calipers; all measurements were repeated three times to ensure precision and accuracy.

In order to effectively and reasonably study dispersal ability, I converted wing measurements (wing chord length and S1) into hand-wing index 2 (HWI2; see Fig. 9). This hand-wing index is used as a metric of dispersal ability because it is a measure of wing shape and due to its relationship with determining long-distance flight efficiency (Claramunt et al., 2012; Weeks and Claramunt, 2014; Bitton and Graham, 2015; White 2016; Kennedy et al., 2016). Hand-wing index 2 is calculated as follows: $HWI2 = 100 \times (\text{wing chord length} - S1 / \text{wing chord length})$ (Claramunt et al., 2012; Weeks and Claramunt, 2014). A small HWI2 value is associated with a more rounded wing shape whereas a large HWI2 value indicates more pointed wings that are associated with being stronger fliers or more efficient at long-distance flight (Bitton and Graham, 2014).

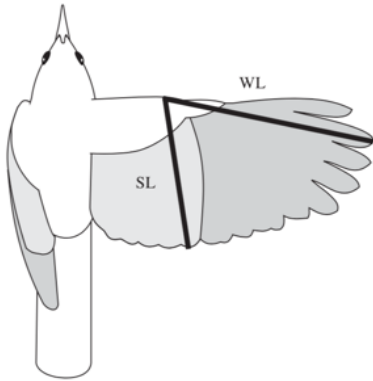


Figure 9. Linear measurements of hand-wing index 2 (reproduced from Claramunt et al., 2012, Figure 2). This diagram depicts the linear measurements of wing chord length (WL) and secondary length (SL or referred to as S1 in this study).

Museum skin specimens

Using museum skin specimens to study dispersal ability provides a unique framework for investigating the effects of dispersal on ecological and evolutionary processes (Claramunt and Wright, 2017). Museum specimens are reliable for quantifying wing shape because the bone and keratin that make up wings and feathers do not degrade over time as preserved by well-maintained collections (Bitton and Graham, 2014). I noted additional data from specimen toe tags including locality, body mass, latitude and longitude coordinates, elevation, and sex that may be relevant to interpreting their measurements across populations and species.

Checking the data

All repeated measures I took for a morphological variable of a specimen were within 0.15mm of each other except for tail length (within 1mm). Prior to running analyses, each specimen was checked for outliers and errors by confirming that all repeated measurements were within one standard deviation. Any suspicious data points were removed or measured again prior to further analysis. For subsequent analyses, I used the average of the repeated measurements.

This study was part of a larger collaborative lab project, so I combined data collected by another investigator (T. Olivia Helms) for a related purpose. In order to make sure there was no significant systematic differences between our measurements, I conducted ANOVA comparisons between the two investigators' data for five morphological variables (bill depth, bill width, bill length, tarsus length, tail length). I did not compare measurements of wing chord length or secondary length between investigators because I only used data collected by myself (RL) for wing measurements of all specimens in this study. For the ANOVA comparisons I needed specimens measured by both investigators so I (RL) measured 94 specimens that Olivia Helms (OH) measured. Of the five linear measurements, bill width (ANOVA $p < 0.05$) and tarsus length (ANOVA $p < 0.001$) were statistically different in how they were measured between investigators (see Table 2). To correct for the differences in how investigators measured bill width and tarsus length I performed a simple linear regression for each (Fig. 10). A simple linear regression (R package: Stats) was performed to create an equation to adjust bill width and tarsus length data from OH, so it is consistent with the RL measurements. The regression equation for bill width is: $RL_Bill_width = -0.52609 + 0.93714 * OH_Bill_Width$ and for tarsus length it is: $RL_Tarsus_Length = 0.41268 + 0.87643 * OH_Tarsus_Length$. For each specimen with borrowed OH data ($n=66$), for bill width and tarsus length I inserted OH's data values into the appropriate equation to generate a corrected value compatible with RL measurements. These corrected values replaced the borrowed OH data for bill width and tarsus length and allowed me to perform analyses on combined datasets with no significant systematic differences in measurements between investigators.

Table 2. Summary of ANOVA comparison results between RL (taken by Robert Lauer) and OH (taken by T. Olivia Helms) for five linear measurements of commonly measured museum skin specimens. Red font and asterisks indicate those linear measurements with significant differences between investigators.

Linear Measurement	F	p
Bill Depth	0.093	0.761
Bill Width	5.822	0.016*
Bill Height	0.005	0.943
Tarsus Length	11.220	<0.001***
Tail Length	0.229	0.633

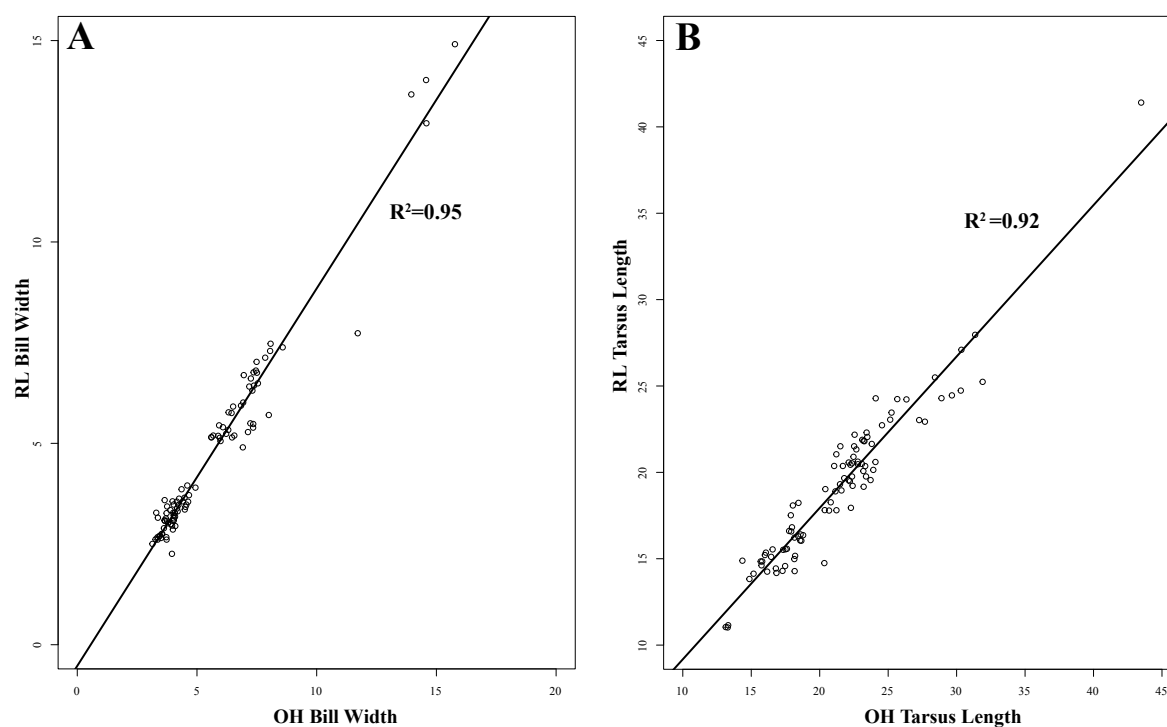


Figure 10. Simple linear regression plots comparing measurements of (A) bill width and (B) tarsus length taken by RL and OH for 94 specimens. I reported the R-squared value in each plot along the linear regression lines.

Sampling objective 1 (chapter 3)

The first goal of this study was to understand if Malagasy species shift in their dispersal ability after colonizing Madagascar. I measured all Malagasy species and as many species from the source clade as were available at FMNH and AMNH. Source clade species were selected

using published phylogenetic trees. I sampled at least five specimens per species (typically three males and two females) to encompass the variation for each species of the endemic Malagasy clade. I sampled two specimens (one male, one female) for each species in the source clade. Region classifications were organized by using the museum specimen collection tag localities to assign them to source areas (Africa, Asia, West Indian Ocean Islands) and Malagasy (Madagascar).

Objective 1 data analysis

I checked for sexual dimorphism in morphological traits within each family by performing ANOVA and boxplot comparisons between males and females for each trait using their raw repeated measures. If there were significant differences between males and females in a morphological trait(s), I analyzed males and females separately for that family. I took the five individual specimens I measured for each Malagasy species and averaged their repeated measures collectively for each trait to get a “species average”. I obtained a species average for source species the same way but with the two individual specimens I measured per species. I used these species averages for subsequent analyses in objective one. Due to the morphological variables having very different variances I standardized the variables before conducting a principal component analysis. To standardize the data for principal component analysis, I performed a scale function on the species averaged data so that the variances of each morphological variable were comparable (Coghlan 2017). I generated a scree plot of the proportion of variance each principal component explained to determine how many principal components with minimally 5% variation to retain. Principal components were plotted with minimum convex polygons grouping species in source and Malagasy clades using ggplot2 in R.

In the multivariate analyses, I examined the difference in the morphospace occupancy between Malagasy and source clade for each family using principal component analysis. I conducted two tests: I performed a multivariate analysis of variance (MANOVA) to test if the centroids, the multivariate mean of each clade, are statistically different between clades. This test assesses if these clades are located in different regions of morphospace. Next, I examined disparity, the volume occupied in multivariate space, of each group to test if the extent of morphospace is different across these two clades. I generated a disparity plot using the sum of the variances of principal components incorporating greater than five percent variance and performed a non-parametric Wilcoxon test to determine if there was a significant difference in the volume of morphospace occupied between the two clades (R package: *DispRity*; Guillerme 2018). Additionally, for results that were significantly different using MANOVA or disparity, I examined PC loadings to determine if HWI2 or wing measurements contributed substantially to variation explained by these PCs.

For univariate analyses I used raw (not standardized) species averaged data. For each family, I conducted ANOVA comparisons between the two clades for all morphological variables, focusing primarily on the HWI2, to understand how and which traits were important to the diversification of Malagasy lineages. A dot-box-plot was generated to visualize the trait value differences between clades (R package: *ggplot2*; Wickham 2016).

Sampling objective 2 (chapter 4)

The second objective of this study is to investigate whether variation in dispersal ability within widespread Malagasy species differed between populations restricted to one of three macrohabitats (eastern humid rainforest, western dry forest, southwestern spiny desert) or two

habitat classes (east/west= closed, southwest = open). The second aim of this study focused on four widespread species (*Schetba rufa*, *Cooua cristata*, *Cooua ruficeps*, *Terpsiphone mutata*, Table 3) from three families (Vangidae, Cuculidae, and Monarchidae). For each widespread species with multiple subspecies, I measured five specimens per subspecies (where specimens were available in collections). I classified each individual's macrohabitat by using the locality information from the specimen tag. The classifications were decided based on what macrohabitat the locality was recorded to be within (see Chapter 1 Fig. 3)

Objective 2 data analysis

Similar to objective one, I standardized morphological variables for principal component analysis, generated a scree plot, generated plots of principal components, performed a MANOVA, and conducted ANOVA comparisons of traits between groups that are visualized in dot-box-plots. The only exceptions are that I used specimen-averaged data (see below), compared traits by macrohabitat groups, conducted pairwise t-tests (for groups of more than two), and did not perform a test of disparity.

I took the repeated measures for each individual specimen and averaged them for each trait to get a "specimen average". I used these specimen averages for subsequent analyses in objective two. I generated morphospace in a principal component analysis (PCA) for each widespread species with minimum convex polygons grouping specimens into each macrohabitat. I performed a multivariate analysis of variance (MANOVA) to see if the centroids of the three macrohabitats statistically differed.

For univariate analyses I used raw (not standardized) specimen-averaged data. For each widespread species, I conducted ANOVA comparisons between the three macrohabitats for each

morphological variable, focusing on HWI2, to understand how and in which traits a species may have diverged across macrohabitats. These differences, or lack thereof, are visualized in dot-box-plots (R package: ggplot2). If there were significant differences (ANOVA) overall for a morphological trait between macrohabitats, then I conducted pairwise t-tests to see which macrohabitats specifically significantly differed from each other.

Table 3. List of all specimens and their measurements (averaged from 3 repetitions). Abbreviations are as follows: sex (M=male, F=female), museum (FMNH= Field Museum of Natural History, AMNH = American Museum of Natural History), measurements (BD= bill depth, BW= bill width, BL= bill length, WL= wing chord length, S1= secondary length, Tar-L= tarsus length, Tail= tail length, HWI2= hand-wing index 2).

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	S1	Tar-L	Tail	HWI2
<i>Calicalicus madagascariensis</i>	304769	Malagasy	M	FMNH	4.91	3.60	13.56	66.46	59.78	16.78	53.43	10.05
<i>Calicalicus madagascariensis</i>	436429	Malagasy	F	FMNH	4.64	3.48	12.90	62.78	55.97	15.58	55.37	10.86
<i>Calicalicus madagascariensis</i>	185771	Malagasy	M	FMNH	4.73	3.48	12.58	65.92	61.08	15.54	55.47	7.34
<i>Calicalicus madagascariensis</i>	413044	Malagasy	M	AMNH	4.80	3.90	13.89	64.74	56.53	16.04	55.86	12.69
<i>Calicalicus madagascariensis</i>	360049	Malagasy	F	FMNH	4.31	3.37	13.22	64.98	60.84	16.56	57.99	6.38
<i>Calicalicus madagascariensis</i>	185769	Malagasy	M	FMNH	5.32	3.95	13.83	66.12	57.13	15.52	46.73	13.59
<i>Artamella viridis annae</i>	185763	Malagasy	F	FMNH	8.33	5.19	25.58	115.15	96.38	20.60	78.62	16.30
<i>Artamella viridis annae</i>	664443	Malagasy	M	AMNH	8.60	5.60	26.18	115.60	91.53	21.10	74.77	20.82
<i>Artamella viridis annae</i>	664434	Malagasy	M	AMNH	8.26	5.71	26.41	119.80	97.50	21.24	80.03	18.61
<i>Artamella viridis annae</i>	412903	Malagasy	M	AMNH	7.54	4.85	26.12	116.47	95.82	20.97	87.43	17.73
<i>Artamella viridis annae</i>	664436	Malagasy	F	AMNH	7.94	5.54	26.13	120.54	99.75	21.04	85.82	17.24
<i>Artamella viridis viridis</i>	412899	Malagasy	M	AMNH	8.74	5.33	23.66	117.97	97.80	20.63	79.39	17.10
<i>Artamella viridis viridis</i>	412893	Malagasy	M	AMNH	8.18	5.42	26.13	114.87	93.93	20.79	76.00	18.23

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Artamella viridis</i>	412883	Malagasy	M	AMNH	8.39	5.39	23.74	114.43	94.59	20.08	76.67	17.34
<i>Artamella viridis</i>	412898	Malagasy	F	AMNH	8.37	4.85	22.86	108.88	87.97	20.29	76.44	19.21
<i>Artamella viridis</i>	412880	Malagasy	F	AMNH	8.27	5.50	24.63	110.63	90.48	20.14	76.14	18.21
<i>Cyanolanius madagascariensis</i>	185766	Malagasy	F	FMNH	6.09	5.19	17.91	86.39	70.69	16.31	69.06	18.17
<i>Cyanolanius madagascariensis</i>	185767	Malagasy	M	FMNH	6.17	5.19	18.02	91.98	73.55	16.22	72.48	20.04
<i>Cyanolanius madagascariensis</i>	412813	Malagasy	M	AMNH	5.84	5.06	17.55	88.59	74.52	16.41	76.43	15.88
<i>Cyanolanius madagascariensis</i>	412792	Malagasy	F	AMNH	5.82	5.15	17.66	87.89	73.44	16.36	73.80	16.44
<i>Cyanolanius madagascariensis</i>	412795	Malagasy	F	AMNH	5.85	5.14	17.23	85.58	68.93	14.58	73.54	19.45
<i>Newtonia amphichroa</i>	393387	Malagasy	F	FMNH	3.22	2.83	14.74	54.37	51.89	19.24	49.24	4.57
<i>Newtonia amphichroa</i>	363856	Malagasy	M	FMNH	3.11	2.97	15.90	52.02	48.08	18.81	46.70	7.57
<i>Newtonia amphichroa</i>	438751	Malagasy	F	FMNH	3.54	3.43	13.75	52.55	50.34	19.31	47.62	4.22
<i>Newtonia amphichroa</i>	438750	Malagasy	M	FMNH	3.43	3.55	14.50	55.63	52.56	20.90	47.71	5.51
<i>Newtonia archboldi</i>	436447	Malagasy	F	FMNH	3.21	3.15	12.98	48.21	34.75	15.57	46.33	27.91
<i>Newtonia archboldi</i>	436446	Malagasy	M	FMNH	3.24	3.63	13.53	48.14	46.03	17.52	45.97	4.39
<i>Newtonia archboldi</i>	411915	Malagasy	M	AMNH	3.07	3.70	13.19	47.90	45.42	17.56	51.51	5.18
<i>Newtonia archboldi</i>	352945	Malagasy	M	FMNH	2.92	3.55	13.41	50.35	47.66	18.35	50.60	5.34
<i>Newtonia archboldi</i>	411912	Malagasy	F	AMNH	3.32	3.53	13.02	47.31	44.55	16.10	46.47	5.83
<i>Newtonia fanovanae</i>	345890	Malagasy	M	FMNH	3.21	2.75	14.62	58.53	52.55	15.21	47.09	10.21
<i>Newtonia fanovanae</i>	413023	Malagasy	F	AMNH	4.12	4.54	15.47	55.55	50.38	16.41	52.50	9.31

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	S1	Tar-L	Tail	HWI2
<i>Newtonia brunneicauda brunneicauda</i>	436438	Malagasy	M	FMNH	2.94	3.59	13.44	47.43	43.47	16.58	48.06	8.34
<i>Newtonia brunneicauda brunneicauda</i>	436439	Malagasy	F	FMNH	2.96	3.28	13.36	49.97	46.44	16.61	49.23	7.05
<i>Newtonia brunneicauda brunneicauda</i>	411882	Malagasy	M	AMNH	3.33	3.70	13.93	53.55	50.36	17.86	47.51	5.94
<i>Newtonia brunneicauda brunneicauda</i>	345873	Malagasy	M	FMNH	3.56	3.06	14.22	53.58	49.95	16.97	44.81	6.78
<i>Newtonia brunneicauda brunneicauda</i>	393377	Malagasy	F	FMNH	3.30	3.46	15.45	55.74	50.80	20.22	44.96	8.87
<i>Newtonia brunneicauda monticola</i>	411901	Malagasy	M	AMNH	3.17	3.25	13.20	58.08	55.54	18.58	55.30	4.37
<i>Newtonia brunneicauda monticola</i>	411902	Malagasy	M	AMNH	3.28	3.57	13.78	57.00	53.87	18.29	53.56	5.50
<i>Newtonia brunneicauda monticola</i>	411903	Malagasy	M	AMNH	3.10	2.87	13.11	54.28	50.81	18.01	52.59	6.39
<i>Newtonia brunneicauda monticola</i>	411905	Malagasy	F	AMNH	3.59	3.49	13.58	56.40	51.98	18.73	51.45	7.84
<i>Newtonia brunneicauda monticola</i>	411906	Malagasy	F	AMNH	3.29	3.46	12.02	58.28	54.96	16.43	53.71	5.70

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Hypositta corallirostris</i>	423651	Malagasy	M	AMNH	3.76	3.27	13.75	76.56	63.71	14.62	61.90	16.78
<i>Hypositta corallirostris</i>	413105	Malagasy	M	AMNH	4.09	3.34	13.92	80.99	65.33	14.84	62.42	19.34
<i>Hypositta corallirostris</i>	393117	Malagasy	F	FMNH	3.75	3.08	13.53	74.29	62.10	14.44	63.94	16.41
<i>Hypositta corallirostris</i>	30978	Malagasy	M	FMNH	3.84	3.28	12.99	76.43	59.08	14.75	59.34	22.71
<i>Hypositta corallirostris</i>	438712	Malagasy	F	FMNH	4.04	3.11	13.07	76.67	62.32	15.96	61.25	18.72
<i>Leptopterus chabert chabert</i>	412861	Malagasy	M	AMNH	6.90	5.86	18.02	97.95	67.06	16.25	59.27	31.54
<i>Leptopterus chabert chabert</i>	412866	Malagasy	M	AMNH	6.19	5.77	17.90	93.66	67.54	15.55	57.18	27.88
<i>Leptopterus chabert chabert</i>	412857	Malagasy	M	AMNH	7.11	5.15	17.65	93.10	62.82	14.84	57.13	32.53
<i>Leptopterus chabert chabert</i>	412836	Malagasy	F	AMNH	6.26	5.60	20.06	95.27	68.90	14.85	56.75	27.68
<i>Leptopterus chabert chabert</i>	412823	Malagasy	M	AMNH	6.75	5.36	20.02	99.04	67.71	15.14	57.44	31.63
<i>Leptopterus chabert chabert</i>	185764	Malagasy	F	FMNH	6.07	5.24	19.28	94.21	67.97	15.17	54.90	27.85
<i>Leptopterus chabert schistocercus</i>	412840	Malagasy	M	AMNH	6.54	5.40	16.23	91.32	66.72	14.25	56.68	26.94
<i>Leptopterus chabert schistocercus</i>	412862	Malagasy	M	AMNH	6.38	5.94	17.53	98.29	69.70	14.13	58.19	29.09
<i>Leptopterus chabert schistocercus</i>	412877	Malagasy	F	AMNH	6.49	5.45	19.79	98.33	73.77	14.28	58.71	24.98
<i>Leptopterus chabert schistocercus</i>	412855	Malagasy	M	AMNH	6.35	5.15	16.88	90.63	63.71	14.30	54.10	29.71

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Leptopterus chabert schistocercus</i>	352883	Malagasy	M	FMNH	6.21	5.33	17.90	91.61	65.41	14.98	54.98	28.60
<i>Leptopterus chabert schistocercus</i>	352884	Malagasy	F	FMNH	6.44	5.35	17.71	89.92	62.97	15.49	53.98	29.98
<i>Euryceros prevostii</i>	431227	Malagasy	-	FMNH	22.84	13.66	44.02	134.93	106.90	22.93	109.70	20.77
<i>Euryceros prevostii</i>	304770	Malagasy	-	FMNH	24.16	12.95	42.73	144.69	111.36	23.03	119.26	23.04
<i>Euryceros prevostii</i>	413082	Malagasy	M	AMNH	25.53	14.13	43.31	138.69	114.36	24.14	118.64	17.54
<i>Euryceros prevostii</i>	413081	Malagasy	M	AMNH	25.62	14.91	47.54	144.84	111.87	24.73	118.36	22.76
<i>Euryceros prevostii</i>	413091	Malagasy	F	AMNH	23.04	14.02	43.67	140.47	109.23	24.29	116.74	22.24
<i>Tylas eduardi albigularis</i>	393165	Malagasy	M	FMNH	5.81	5.72	23.64	114.53	97.24	21.92	93.94	15.09
<i>Tylas eduardi eduardi</i>	185925	Malagasy	F	FMNH	5.98	5.55	23.77	113.96	93.87	20.61	92.20	17.63
<i>Tylas eduardi eduardi</i>	393311	Malagasy	M	FMNH	6.07	5.44	23.47	116.40	95.42	19.45	83.61	18.02
<i>Tylas eduardi eduardi</i>	427336	Malagasy	M	FMNH	5.46	5.44	23.52	112.81	94.87	19.69	82.14	15.91
<i>Tylas eduardi eduardi</i>	412698	Malagasy	F	AMNH	6.77	6.31	23.36	117.05	100.12	19.17	91.10	14.47
<i>Tylas eduardi eduardi</i>	412685	Malagasy	F	AMNH	6.69	6.25	22.99	116.53	97.23	19.97	88.85	16.56
<i>Xenopirostris polleni</i>	306352	Malagasy	M	AMNH	10.86	5.70	29.49	117.16	102.23	23.05	85.80	12.75
<i>Xenopirostris polleni</i>	664428	Malagasy	M	AMNH	11.67	7.49	27.53	124.25	110.28	23.50	86.08	11.24
<i>Xenopirostris polleni</i>	*664429	Malagasy	F	AMNH	11.38	7.80	29.89	127.28	111.12	23.00	89.24	12.70
<i>Xenopirostris polleni</i>	*664430	Malagasy	M	AMNH	12.55	6.91	28.36	116.14	104.51	20.19	86.02	10.02
<i>Xenopirostris polleni</i>	664431	Malagasy	-	AMNH	11.32	6.93	30.86	124.29	103.88	22.09	89.00	16.43
<i>Xenopirostris xenopirostris</i>	412767	Malagasy	M	AMNH	12.82	5.65	27.22	114.70	98.65	23.54	96.50	14.00

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Xenopirostris xenopirostris</i>	412768	Malagasy	M	AMNH	11.77	5.08	25.72	117.94	95.09	22.84	94.29	19.38
<i>Xenopirostris xenopirostris</i>	664426	Malagasy	M	AMNH	12.69	5.97	27.62	115.12	102.75	22.39	93.50	10.75
<i>Xenopirostris xenopirostris</i>	664427	Malagasy	F	AMNH	11.41	5.75	26.74	114.08	103.02	24.29	98.21	9.70
<i>Xenopirostris damii</i>	664432	Malagasy	M	AMNH	12.32	6.61	29.29	111.32	96.48	20.59	87.50	13.33
<i>Xenopirostris damii</i>	206738	Malagasy	F	AMNH	11.96	5.43	28.33	114.67	99.90	23.17	88.90	12.89
<i>Xenopirostris damii</i>	206737	Malagasy	M	AMNH	13.16	5.94	27.21	122.41	107.25	24.44	95.06	12.38
<i>Schetba rufa</i>	412982	Malagasy	F	AMNH	7.84	6.76	23.26	102.86	82.41	22.18	79.23	19.88
<i>Schetba rufa</i>	412983	Malagasy	F	AMNH	7.44	6.26	23.01	96.56	80.60	19.88	77.27	16.53
<i>Schetba rufa</i>	412984	Malagasy	F	AMNH	7.75	6.43	23.38	102.26	82.67	21.82	80.38	19.15
<i>Schetba rufa</i>	412988	Malagasy	F	AMNH	8.96	7.36	25.69	95.12	80.32	21.02	76.13	15.55
<i>Schetba rufa</i>	412979	Malagasy	M	AMNH	7.57	6.69	23.98	98.76	80.29	21.51	72.98	18.70
<i>Schetba rufa</i>	412980	Malagasy	M	AMNH	8.58	7.38	25.04	100.96	82.73	21.88	75.83	18.06
<i>Schetba rufa</i>	412986	Malagasy	M	AMNH	8.14	7.02	24.55	103.44	87.09	21.05	82.74	15.81
<i>Schetba rufa</i>	412987	Malagasy	M	AMNH	9.23	6.80	23.06	100.44	81.98	21.48	78.62	18.38
<i>Schetba rufa</i>	413011	Malagasy	M	AMNH	7.90	6.61	25.75	105.66	83.36	22.30	88.34	21.11
<i>Schetba rufa</i>	413000	Malagasy	M	AMNH	8.74	6.75	26.06	103.00	87.67	22.05	91.56	14.89
<i>Schetba rufa occidentalis</i>	436520	Malagasy	M	FMNH	8.77	6.89	25.73	103.53	81.76	20.61	85.66	21.03
<i>Schetba rufa occidentalis</i>	427382	Malagasy	F	FMNH	7.82	6.34	24.15	108.05	90.26	21.14	94.21	16.46
<i>Schetba rufa occidentalis</i>	393168	Malagasy	F	FMNH	7.90	6.37	23.56	107.03	82.32	21.86	93.12	23.08
<i>Oriolia bernieri</i>	202943	Malagasy	F	AMNH	8.87	5.27	30.18	123.21	98.84	19.54	90.00	19.78
<i>Oriolia bernieri</i>	412916A	Malagasy	M	AMNH	8.28	5.60	26.43	120.74	102.44	20.12	93.00	15.15
<i>Oriolia bernieri</i>	412915	Malagasy	F	AMNH	8.71	5.12	27.75	117.28	98.84	20.06	91.50	15.72

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Oriolia bernieri</i>	664481	Malagasy	F	AMNH	8.83	5.60	29.54	119.39	99.15	20.41	95.00	16.96
<i>Oriolia bernieri</i>	202942	Malagasy	M	AMNH	7.92	5.91	26.88	121.52	97.15	18.27	87.94	20.05
<i>Mystacornis crossleyi</i>	196682	Malagasy	M	AMNH	4.43	3.50	23.19	67.07	62.24	23.34	52.24	7.21
<i>Mystacornis crossleyi</i>	202917	Malagasy	F	AMNH	4.45	3.97	23.03	68.81	62.51	22.95	51.55	9.16
<i>Mystacornis crossleyi</i>	202918	Malagasy	F	AMNH	3.86	3.41	22.20	66.67	59.30	22.05	46.54	11.06
<i>Mystacornis crossleyi</i>	202915	Malagasy	M	AMNH	4.39	4.21	24.82	68.16	61.20	22.32	51.87	10.21
<i>Mystacornis crossleyi</i>	202916	Malagasy	M	AMNH	4.10	3.63	22.27	68.98	62.95	21.93	52.74	8.74
<i>Mystacornis crossleyi</i>	412260	Malagasy	M	AMNH	4.43	3.59	24.08	68.65	63.70	22.63	54.37	7.21
<i>Mystacornis crossleyi</i>	412261	Malagasy	M	AMNH	4.22	3.36	22.06	66.88	59.78	22.73	51.91	10.62
<i>Mystacornis crossleyi</i>	412270	Malagasy	F	AMNH	4.26	3.64	21.93	67.30	61.97	21.35	49.87	7.91
<i>Mystacornis crossleyi</i>	412272	Malagasy	F	AMNH	4.25	3.67	22.35	63.99	58.47	22.05	50.68	8.62
<i>Mystacornis crossleyi</i>	412273	Malagasy	F	AMNH	4.74	3.65	23.16	68.49	62.04	21.80	51.40	9.41
<i>Mystacornis crossleyi</i>	412250	Malagasy	M	AMNH	4.56	4.08	23.19	69.32	65.60	22.29	52.64	5.37
<i>Mystacornis crossleyi</i>	412251	Malagasy	M	AMNH	4.30	3.33	23.14	64.61	57.38	22.53	52.41	11.19
<i>Mystacornis crossleyi</i>	412252	Malagasy	M	AMNH	4.43	3.55	23.10	69.45	61.92	23.02	57.16	10.85
<i>Mystacornis crossleyi</i>	412253	Malagasy	F	AMNH	4.23	3.21	21.10	65.08	59.39	21.33	51.18	8.74
<i>Mystacornis crossleyi</i>	412254	Malagasy	M	AMNH	4.64	3.51	24.07	65.24	60.89	23.19	51.31	6.68
<i>Vanga curvirostris</i>	412933	Malagasy	M	AMNH	10.55	6.93	33.22	111.31	95.35	26.43	108.76	14.34
<i>Vanga curvirostris</i>	412923	Malagasy	M	AMNH	10.75	7.15	33.67	108.96	91.12	26.56	112.21	16.38
<i>Vanga curvirostris</i>	412926	Malagasy	M	AMNH	10.87	7.47	34.21	106.48	95.82	24.46	105.37	10.01
<i>Vanga curvirostris</i>	412927	Malagasy	F	AMNH	10.82	7.29	34.19	102.95	88.44	25.49	101.24	14.10
<i>Vanga curvirostris</i>	412947	Malagasy	F	AMNH	10.17	7.26	32.93	110.74	95.50	26.18	106.17	13.76
<i>Vanga curvirostris</i>	412968	Malagasy	M	AMNH	10.11	7.27	34.09	112.50	96.05	28.11	110.73	14.62
<i>Vanga curvirostris</i>	412955	Malagasy	M	AMNH	11.69	7.50	34.36	108.60	92.00	27.59	104.77	15.29
<i>Vanga curvirostris</i>	412956	Malagasy	M	AMNH	11.15	7.53	34.70	109.36	91.84	27.83	107.08	16.02
<i>Vanga curvirostris</i>	412972	Malagasy	F	AMNH	9.67	6.28	34.44	104.90	91.45	25.56	103.77	12.82

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Vanga curvirostris</i>	412975	Malagasy	F	AMNH	9.99	6.58	35.04	109.70	92.53	25.06	109.34	15.65
<i>Falcula palliata</i>	413663	Malagasy	F	AMNH	8.96	5.34	60.42	152.72	123.39	26.84	101.77	19.21
<i>Falcula palliata</i>	413673	Malagasy	F	AMNH	8.45	5.48	62.88	154.62	128.62	25.24	106.42	16.82
<i>Falcula palliata</i>	413676	Malagasy	M	AMNH	7.74	4.62	56.78	147.84	124.63	26.10	103.30	15.70
<i>Falcula palliata</i>	413680	Malagasy	F	AMNH	8.76	5.35	62.91	152.44	129.22	26.16	106.62	15.23
<i>Falcula palliata</i>	413665	Malagasy	M	AMNH	8.62	5.28	67.48	154.70	126.55	27.96	104.45	18.20
<i>Falcula palliata</i>	*413666	Malagasy	F	AMNH	8.50	4.90	68.54	158.00	135.16	27.10	113.86	14.45
<i>Falcula palliata</i>	413679	Malagasy	M	AMNH	8.24	5.03	67.58	136.05	113.66	26.54	103.87	16.45
<i>Falcula palliata</i>	413682	Malagasy	M	AMNH	9.31	6.92	72.19	154.67	129.04	27.21	109.37	16.57
<i>Pseudobias wardii</i>	411924	Malagasy	M	AMNH	3.62	6.01	15.75	76.53	61.06	11.15	69.97	20.21
<i>Pseudobias wardii</i>	649717	Malagasy	M	AMNH	4.27	6.49	15.93	76.16	59.46	11.04	68.16	21.93
<i>Pseudobias wardii</i>	196697	Malagasy	F	AMNH	4.25	6.41	15.86	74.74	57.72	11.02	66.67	22.78
<i>Pseudobias wardii</i>	411919	Malagasy	-	AMNH	3.96	6.19	16.60	75.14	58.60	11.36	67.97	22.02
<i>Pseudobias wardii</i>	196696	Malagasy	M	AMNH	4.68	5.75	17.14	73.61	59.67	11.73	66.00	18.95
<i>Philentoma pyrrhopterum</i>	212068	Source	M	FMNH	4.69	6.57	19.65	77.08	70.53	15.14	72.70	8.50
<i>Philentoma pyrrhopterum</i>	212069	Source	F	FMNH	5.00	6.48	19.16	79.34	72.97	15.41	71.96	8.03
<i>Hemipus picatus capitalis</i>	215065	Source	M	FMNH	4.25	5.04	16.21	67.33	57.55	11.35	67.25	14.53
<i>Hemipus picatus capitalis</i>	235707	Source	F	FMNH	3.68	4.82	16.69	64.35	55.25	11.20	64.94	14.15
<i>Tephrodornis gularis mekongensis</i>	91572	Source	F	FMNH	7.85	7.71	27.28	117.59	91.69	17.43	84.50	22.03
<i>Tephrodornis gularis mekongensis</i>	91573	Source	M	FMNH	7.23	7.24	25.26	111.01	89.74	15.36	83.43	19.16

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Megabyas flammulatus aequatorialis</i>	298783	Source	M	FMNH	6.09	6.81	24.87	94.82	78.35	14.18	71.67	17.37
<i>Megabyas flammulatus aequatorialis</i>	298785	Source	F	FMNH	6.56	7.13	23.22	91.18	76.08	13.83	71.19	16.56
<i>Batis diops</i>	355977	Source	M	FMNH	3.86	4.31	14.90	60.89	52.93	16.95	43.05	13.07
<i>Batis diops</i>	358103	Source	F	FMNH	3.91	4.92	15.21	61.24	54.73	16.91	43.15	10.64
<i>Bias musicus</i>	271981	Source	F	FMNH	5.67	7.63	22.67	84.46	73.31	11.91	49.23	13.20
<i>Bias musicus</i>	122274	Source	M	FMNH	5.97	8.50	21.18	87.16	71.92	11.35	53.64	17.49
<i>Megabyas flammulatus flammulatus</i>	95831	Source	F	FMNH	5.28	6.69	23.18	85.77	72.02	12.59	60.88	16.03
<i>Megabyas flammulatus flammulatus</i>	271975	Source	M	FMNH	6.16	7.58	23.75	87.72	75.97	13.12	66.76	13.39
<i>Prionops plumata</i>	*285944	Source	M	FMNH	6.92	6.67	22.21	117.24	99.17	17.71	102.94	15.42
<i>Prionops plumata</i>	285945	Source	F	FMNH	7.48	6.92	21.45	115.75	100.09	21.63	101.23	13.53
<i>Bernieria madagascariensis</i>	345730	Malagasy	M	FMNH	5.22	3.27	30.35	87.15	73.59	21.65	80.66	15.56
<i>Bernieria madagascariensis</i>	438690	Malagasy	M	FMNH	4.93	3.31	29.16	86.51	75.32	21.94	81.22	12.93
<i>Bernieria madagascariensis</i>	345732	Malagasy	M	FMNH	4.93	3.48	26.67	83.59	74.47	20.62	66.80	10.91
<i>Bernieria madagascariensis</i>	438685	Malagasy	F	FMNH	4.40	3.46	21.74	71.39	65.24	18.81	66.96	8.61
<i>Bernieria madagascariensis</i>	345729	Malagasy	F	FMNH	4.59	3.71	22.50	69.47	62.32	21.51	65.42	10.29
<i>Bernieria madagascariensis</i>	412189	Malagasy	M	AMNH	5.67	3.73	28.18	86.22	75.23	21.32	84.43	12.74

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Bernieria madagascariensis</i>	412169	Malagasy	M	AMNH	5.64	3.56	27.74	85.33	75.35	21.02	82.16	11.69
<i>Bernieria madagascariensis</i>	412159	Malagasy	F	AMNH	4.48	3.73	22.51	69.90	62.47	18.71	73.37	10.63
<i>Bernieria madagascariensis</i>	412177	Malagasy	F	AMNH	4.33	3.55	22.76	73.59	66.56	18.23	73.37	9.55
<i>Bernieria madagascariensis</i>	412162	Malagasy	M	AMNH	5.16	3.44	27.98	82.96	74.75	21.00	82.24	9.89
<i>Xanthomixis z. zosterops</i>	438700	Malagasy	M	FMNH	3.63	3.01	17.72	73.37	61.58	20.47	67.70	16.07
<i>Xanthomixis z. zosterops</i>	438702	Malagasy	F	FMNH	3.37	2.89	16.23	61.36	55.06	18.95	60.07	10.27
<i>Xanthomixis z. zosterops</i>	412202	Malagasy	M	AMNH	3.97	3.72	16.98	80.24	70.04	19.24	77.03	12.71
<i>Xanthomixis z. zosterops</i>	412231	Malagasy	M	AMNH	3.78	3.56	17.90	75.36	65.02	19.22	76.21	13.72
<i>Xanthomixis z. zosterops</i>	412237	Malagasy	F	AMNH	3.76	3.56	16.15	66.35	59.06	18.90	67.29	10.99
<i>Xanthomixis z. fulvescens</i>	412240	Malagasy	M	AMNH	4.16	3.57	19.36	80.51	67.14	20.84	73.65	16.61
<i>Xanthomixis z. fulvescens</i>	412245	Malagasy	F	AMNH	3.83	3.80	17.59	71.76	63.55	19.07	70.63	11.44
<i>Xanthomixis z. fulvescens</i>	412243	Malagasy	F	AMNH	3.72	3.72	16.97	72.67	62.24	19.00	70.67	14.35
<i>Xanthomixis z. fulvescens</i>	412240	Malagasy	F	AMNH	3.80	3.43	17.08	72.08	61.03	18.95	72.79	15.33
<i>Xanthomixis z. fulvescens</i>	412244	Malagasy	F	AMNH	3.94	3.66	17.18	71.42	59.65	19.07	68.28	16.49
<i>Xanthomixis z. ankafanae</i>	393277	Malagasy	M	FMNH	3.45	2.86	16.88	72.70	64.07	20.37	75.38	11.87

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Xanthomixis z. ankafanae</i>	363820	Malagasy	M	FMNH	3.46	3.00	18.28	76.35	64.61	20.37	72.95	15.37
<i>Xanthomixis z. ankafanae</i>	393275	Malagasy	F	FMNH	3.63	3.14	17.30	65.58	57.26	19.03	63.65	12.68
<i>Xanthomixis apperti</i>	393161	Malagasy	M	FMNH	3.17	2.50	16.01	65.47	56.73	17.81	66.07	13.34
<i>Xanthomixis apperti</i>	393160	Malagasy	M	FMNH	3.31	2.65	15.77	67.76	60.36	17.79	65.21	10.93
<i>Xanthomixis apperti</i>	393159	Malagasy	M	FMNH	3.30	2.61	15.96	70.14	60.67	17.81	68.10	13.50
<i>Xanthomixis apperti</i>	427366	Malagasy	M	FMNH	3.32	2.62	16.93	73.35	64.80	17.95	68.70	11.66
<i>Xanthomixis apperti</i>	360048	Malagasy	F	FMNH	2.87	2.67	14.90	62.67	54.73	16.06	63.99	12.68
<i>Xanthomixis cinereiceps</i>	393293	Malagasy	M	FMNH	3.25	2.93	16.78	72.57	61.60	20.40	64.21	15.12
<i>Xanthomixis cinereiceps</i>	438706	Malagasy	M	FMNH	3.52	3.03	16.87	71.79	61.79	19.74	61.57	13.93
<i>Xanthomixis cinereiceps</i>	363827	Malagasy	M	FMNH	3.17	3.08	16.25	76.25	64.65	19.76	70.45	15.21
<i>Xanthomixis cinereiceps</i>	393286	Malagasy	F	FMNH	3.45	3.09	16.04	71.09	63.59	19.54	64.00	10.55
<i>Xanthomixis cinereiceps</i>	393295	Malagasy	F	FMNH	3.31	3.09	15.02	65.81	58.47	19.55	62.03	11.15
<i>Xanthomixis z. andapae</i>	393272	Malagasy	M	FMNH	4.06	3.86	19.91	81.81	70.47	19.76	82.53	13.86
<i>Xanthomixis z. andapae</i>	393270	Malagasy	M	FMNH	3.94	3.14	18.82	77.23	67.67	20.57	70.50	12.37
<i>Xanthomixis z. andapae</i>	431218	Malagasy	M	FMNH	3.87	3.47	19.65	79.32	68.06	20.36	79.96	14.20
<i>Xanthomixis z. andapae</i>	393269	Malagasy	F	FMNH	3.55	3.18	16.83	67.94	60.42	19.49	64.39	11.07
<i>Xanthomixis z. andapae</i>	393266	Malagasy	F	FMNH	3.88	3.38	17.58	71.41	60.59	19.66	69.94	15.16
<i>Xanthomixis tenebrosa</i>	393278	Malagasy	F	FMNH	3.62	3.08	16.18	58.39	55.32	20.09	42.32	5.25

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Xanthomixis tenebrosa</i>	589232	Malagasy	F	AMNH	3.97	3.87	16.51	66.18	59.51	20.50	54.28	10.08
<i>Xanthomixis tenebrosa</i>	589231	Malagasy	F	AMNH	4.29	3.62	16.38	69.47	61.72	21.81	57.42	11.16
<i>Xanthomixis tenebrosa</i>	295029	Malagasy	F	AMNH	3.70	3.43	17.27	67.69	59.43	22.28	57.03	12.19
<i>Xanthomixis tenebrosa</i>	589235	Malagasy	-	AMNH	3.97	3.17	15.25	60.39	56.34	20.22	49.05	6.70
<i>Crossleyia xanthophrys</i>	393280	Malagasy	M	FMNH	3.37	2.71	14.79	67.19	63.32	24.24	74.20	5.76
<i>Crossleyia xanthophrys</i>	363847	Malagasy	M	FMNH	3.26	2.81	15.98	63.65	59.60	23.75	75.97	6.37
<i>Crossleyia xanthophrys</i>	393279	Malagasy	M	FMNH	3.42	2.70	15.56	65.58	61.08	23.46	70.87	6.85
<i>Crossleyia xanthophrys</i>	393282	Malagasy	F	FMNH	3.06	2.75	13.91	67.10	58.98	20.52	64.84	12.10
<i>Crossleyia xanthophrys</i>	393281	Malagasy	M	FMNH	3.46	2.61	15.51	65.16	60.67	24.22	60.45	6.89
<i>Oxylabes madagascariensis</i>	393355	Malagasy	M	FMNH	4.47	2.90	17.95	65.82	64.55	20.55	72.56	1.92
<i>Oxylabes madagascariensis</i>	438716	Malagasy	M	FMNH	4.71	3.34	18.68	63.57	57.09	20.47	67.70	10.19
<i>Oxylabes madagascariensis</i>	393356	Malagasy	M	FMNH	4.01	3.25	16.90	62.83	57.23	20.74	68.87	8.90
<i>Oxylabes madagascariensis</i>	393348	Malagasy	F	FMNH	4.44	3.31	18.03	61.18	58.56	20.49	63.51	4.28
<i>Oxylabes madagascariensis</i>	393358	Malagasy	F	FMNH	4.02	3.07	16.70	61.17	55.56	20.44	68.90	9.17
<i>Thamnornis chloropetoides</i>	436448	Malagasy	M	FMNH	3.44	2.43	18.81	60.40	52.78	17.17	57.07	12.62
<i>Thamnornis chloropetoides</i>	436449	Malagasy	F	FMNH	3.35	2.73	18.13	57.96	50.23	17.05	69.63	13.33
<i>Thamnornis chloropetoides</i>	412725	Malagasy	M	AMNH	3.37	2.67	18.25	60.68	55.77	18.13	70.32	8.09

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Thamnornis chloropetoides</i>	412720	Malagasy	F	AMNH	3.88	2.26	19.44	57.88	51.47	18.08	62.82	11.08
<i>Thamnornis chloropetoides</i>	412729	Malagasy	M	AMNH	3.88	2.95	16.37	62.03	56.97	16.82	69.75	8.15
<i>Hartetula flavoviridis</i>	438721	Malagasy	F	FMNH	3.15	2.79	13.86	52.85	47.82	13.87	52.77	9.52
<i>Hartetula flavoviridis</i>	427385	Malagasy	F	FMNH	3.14	2.74	13.74	47.72	45.90	13.90	47.46	3.82
<i>Hartetula flavoviridis</i>	345848	Malagasy	F	FMNH	3.12	2.85	14.00	53.38	46.93	13.99	51.15	12.08
<i>Hartetula flavoviridis</i>	412617	Malagasy	M	AMNH	3.47	2.96	14.43	54.42	49.96	15.11	63.12	8.20
<i>Hartetula flavoviridis</i>	412618	Malagasy	M	AMNH	3.77	3.42	14.16	54.85	48.74	15.35	63.13	11.15
<i>Cryptosilvicola randrianasoloi</i>	360059	Malagasy	M	FMNH	2.70	2.30	13.53	50.34	41.79	15.93	46.86	17.00
<i>Randia pseudozosterops</i>	412765	Malagasy	M	AMNH	3.22	2.67	15.43	58.40	49.60	14.89	49.00	15.08
<i>Randia pseudozosterops</i>	412766	Malagasy	M	AMNH	3.27	2.81	14.59	58.27	50.60	12.34	50.00	13.16
<i>Locustella fluviatilis</i>	239956	Source	-	FMNH	3.28	2.86	15.12	75.83	51.34	19.89	56.70	32.30
<i>Locustella fluviatilis</i>	56413	Source	F	FMNH	3.46	3.25	15.19	73.77	50.45	19.34	56.96	31.62
<i>Locustella o. ochotensis</i>	98854	Source	M	FMNH	3.33	2.91	15.53	64.42	46.72	20.83	56.05	27.48
<i>Locustella o. ochotensis</i>	350694	Source	M	FMNH	3.59	2.95	15.95	74.80	51.86	20.99	58.95	30.66
<i>Schoenicola platyura brevirostris</i>	283079	Source	F	FMNH	3.68	2.86	12.42	60.96	50.49	16.65	82.06	17.17
<i>Schoenicola platyura brevirostris</i>	283080	Source	M	FMNH	3.87	2.88	11.77	59.01	53.13	16.71	80.77	9.95
<i>Bradypterus sylvaticus</i>	787312	Source	-	AMNH	3.18	2.44	15.59	61.85	56.14	17.83	62.77	9.23
<i>Bradypterus carpalis</i>	160864	Source	F	AMNH	3.36	2.86	18.19	66.14	62.19	23.98	69.00	5.97
<i>Bradypterus carpalis</i>	160862	Source	M	AMNH	3.73	3.18	19.14	66.11	62.13	24.20	70.12	6.02
<i>Bradypterus graueri</i>	764591	Source	M	AMNH	3.42	2.51	15.96	57.82	52.98	21.87	68.49	8.36

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Bradypterus graueri</i>	263561	Source	F	AMNH	3.29	2.39	15.92	56.11	52.07	21.09	71.40	7.21
<i>Bradypterus cinnamomeus</i>	263562	Source	M	AMNH	3.24	3.00	15.21	64.79	59.74	22.94	74.43	7.79
<i>Bradypterus cinnamomeus</i>	263564	Source	F	AMNH	3.20	2.72	13.27	59.11	55.88	21.28	64.46	5.45
<i>Bradypterus lopezi</i>	781777	Source	F	AMNH	3.27	2.96	13.90	55.34	50.56	21.59	55.29	8.63
<i>Bradypterus lopezi</i>	592283	Source	M	AMNH	3.25	3.21	14.45	58.54	54.60	21.57	61.66	6.74
<i>Bradypterus barratti</i>	802457	Source	F	AMNH	3.28	3.05	14.91	60.79	53.17	20.08	70.57	12.54
<i>Bradypterus baboecala tongensis</i>	468159	Source	M	FMNH	3.16	2.53	15.75	54.74	49.20	18.77	62.88	10.13
<i>Bradypterus baboecala tongensis</i>	468167	Source	F	FMNH	3.05	2.36	14.49	56.51	51.71	18.68	66.40	8.49
<i>Bradypterus baboecala centralis</i>	434547	Source	M	FMNH	3.08	2.29	14.38	54.13	46.74	18.80	65.09	13.66
<i>Bradypterus baboecala centralis</i>	434550	Source	F	FMNH	3.05	2.49	14.49	52.27	46.23	18.26	64.97	11.56
<i>Bradypterus lopezi granti</i>	447571	Source	M	FMNH	3.20	2.99	16.22	61.92	58.04	21.04	70.12	6.26
<i>Bradypterus lopezi granti</i>	444322	Source	F	FMNH	3.61	3.19	15.75	62.68	57.52	21.82	67.49	8.23
<i>Schoenicola platyura alexinae</i>	114838	Source	M	FMNH	3.49	2.80	12.63	59.80	53.03	16.43	73.79	11.33
<i>Schoenicola platyura alexinae</i>	114389	Source	F	FMNH	3.81	2.69	12.69	58.07	50.08	16.90	80.56	13.75
<i>Megalurulus mariae</i>	268461	Source	M	FMNH	4.08	3.07	15.99	65.43	57.68	20.52	87.45	11.85
<i>Megalurulus mariae</i>	268462	Source	F	FMNH	3.79	3.18	16.34	60.30	53.86	20.26	81.12	10.67
<i>Megalurus timoriensis macrurus</i>	280271	Source	M	FMNH	4.32	3.28	15.44	63.12	57.53	24.15	99.61	8.86
<i>Megalurus timoriensis macrurus</i>	280270	Source	F	FMNH	4.12	3.15	14.67	63.59	58.21	21.85	96.07	8.47

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Bradypterus carpalis</i>	438848	Source	M	FMNH	4.28	3.12	18.68	68.71	63.77	24.75	73.94	7.20
<i>Bradypterus carpalis</i>	385081	Source	F	FMNH	4.06	2.89	17.83	67.62	61.77	24.32	71.97	8.66
<i>Bradypterus graueri</i>	438838	Source	M	FMNH	3.30	2.43	16.84	59.28	54.29	19.70	77.47	8.42
<i>Bradypterus graueri</i>	438840	Source	F	FMNH	3.28	2.46	15.97	58.32	51.45	19.66	75.04	11.78
<i>Locustella certhiola</i>	305992	Source	F	FMNH	3.15	3.01	15.30	61.67	46.61	19.49	37.29	24.42
<i>Locustella certhiola</i>	79845	Source	M	FMNH	3.49	2.77	15.70	66.87	50.35	20.31	56.61	24.70
<i>Locustella fasciolata</i>	284067	Source	F	FMNH	4.34	3.73	18.99	74.91	55.02	23.08	66.86	26.56
<i>Locustella fasciolata</i>	284066	Source	M	FMNH	4.65	3.71	20.11	82.09	61.11	24.12	81.22	25.56
<i>Locustella lanceolata</i>	305993	Source	F	FMNH	3.02	2.71	12.89	52.19	40.52	15.85	47.64	22.36
<i>Locustella lanceolata</i>	79844	Source	M	FMNH	2.94	2.20	11.34	52.49	40.70	16.74	49.07	22.45
<i>Locustella luscinioides fusca</i>	239954	Source	F	FMNH	2.98	2.54	16.30	71.34	50.19	18.77	66.41	29.64
<i>Locustella luscinioides fusca</i>	239949	Source	M	FMNH	3.09	2.57	16.85	67.77	48.70	18.49	60.24	28.13
<i>Locustella naevia</i>	239957	Source	F	FMNH	3.00	2.68	13.59	63.92	49.17	17.76	52.99	23.08
<i>Locustella naevia</i>	297113	Source	M	FMNH	2.73	2.40	13.13	57.31	44.72	16.54	57.34	21.97
<i>Locustella pleskei</i>	226100	Source	F	FMNH	3.84	3.46	18.52	72.04	52.80	23.13	65.11	26.71
<i>Donacobius a. atricapillus</i>	251390	Source	M	FMNH	5.23	4.86	28.57	85.95	72.99	31.07	106.66	15.08
<i>Donacobius a. atricapillus</i>	261700	Source	F	FMNH	5.31	4.36	25.61	79.59	69.75	27.35	84.57	12.37
<i>Donacobius a. brachypterus</i>	191026	Source	M	FMNH	5.90	4.98	26.59	79.60	72.69	26.15	107.25	8.69
<i>Donacobius a. brachypterus</i>	35128	Source	F	FMNH	4.75	4.77	23.60	73.78	68.17	24.39	90.92	7.60
<i>Megalurus palustris forbesi</i>	98852	Source	M	FMNH	5.42	4.12	21.07	98.87	81.33	35.11	135.87	17.74

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Megalurus palustris forbesi</i>	20022	Source	F	FMNH	4.84	4.09	20.66	87.22	72.88	30.94	116.78	16.45
<i>Megalurulus whitneyi</i>	264247	Source	M	FMNH	4.34	4.15	18.87	71.11	62.78	24.52	67.91	11.71
<i>Megalurulus whitneyi</i>	264248	Source	F	FMNH	4.35	4.64	18.25	71.62	65.27	24.64	70.63	8.87
<i>Megalurus mathewsi</i>	76847	Source	M	FMNH	4.35	4.11	16.59	94.23	72.42	24.83	87.60	23.15
<i>Megalurus mathewsi</i>	76849	Source	F	FMNH	3.95	3.56	16.57	93.12	72.84	24.92	87.07	21.77
<i>Megalurus gramineus</i>	280284	Source	M	FMNH	3.07	2.80	13.25	56.68	47.47	17.44	71.42	16.24
<i>Megalurus gramineus</i>	280285	Source	F	FMNH	2.77	2.63	13.20	53.75	44.33	17.21	59.29	17.54
<i>Locustella pleskei</i>	226096	Source	M	FMNH	3.67	3.69	18.70	69.92	53.38	21.60	63.53	23.66
<i>Chaetornis striatus</i>	277610	Source	M	FMNH	5.17	4.13	16.61	83.26	69.32	27.19	89.38	16.75
<i>Napothera crispifrons</i>	75754	Source	F	FMNH	5.11	4.02	21.67	75.01	72.00	27.00	75.40	4.01
<i>Napothera crispifrons</i>	75756	Source	M	FMNH	5.07	4.00	22.48	76.01	71.19	26.72	72.05	6.35
<i>Napothera epilepidota</i>	75747	Source	F	FMNH	3.69	3.26	17.49	55.06	53.41	20.08	31.21	3.00
<i>Bradypterus brunneus</i>	412742	Malagasy	M	AMNH	3.26	3.00	13.42	49.83	46.65	17.80	96.70	6.38
<i>Bradypterus brunneus</i>	412741	Malagasy	M	AMNH	3.23	2.90	12.57	47.82	46.84	17.49	90.76	2.05
<i>Bradypterus brunneus</i>	412740	Malagasy	M	AMNH	2.92	2.80	12.78	50.83	47.36	17.82	93.60	6.84
<i>Bradypterus brunneus</i>	412744	Malagasy	F	AMNH	2.89	2.60	12.15	45.87	44.02	15.79	72.39	4.04
<i>Bradypterus brunneus</i>	598256	Malagasy	F	AMNH	2.93	2.75	13.28	49.25	46.08	17.79	70.89	6.44
<i>Amphilais seebohmi</i>	412748	Malagasy	M	AMNH	3.35	2.37	12.91	51.33	47.62	15.29	84.57	7.24
<i>Amphilais seebohmi</i>	412746	Malagasy	M	AMNH	3.15	2.44	12.84	50.70	47.34	15.01	80.50	6.63
<i>Amphilais seebohmi</i>	412749	Malagasy	M	AMNH	3.33	2.34	12.93	52.65	45.96	15.63	91.23	12.72
<i>Amphilais seebohmi</i>	412762	Malagasy	F	AMNH	3.85	2.39	12.66	51.51	47.23	15.87	95.52	8.31
<i>Amphilais seebohmi</i>	412753	Malagasy	F	AMNH	2.75	2.29	11.96	47.19	43.85	14.21	73.12	7.09
<i>Nelicurvius nelicourvi</i>	393460	Malagasy	F	FMNH	7.51	5.76	16.98	71.52	62.08	17.01	53.63	13.20
<i>Nelicurvius nelicourvi</i>	393461	Malagasy	M	FMNH	7.51	5.84	17.66	75.90	64.42	16.98	53.43	15.12
<i>Nelicurvius nelicourvi</i>	393458	Malagasy	F	FMNH	7.71	5.67	16.91	75.08	61.51	17.42	48.82	18.07

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Nelicurvius nelicourvi</i>	393462	Malagasy	M	FMNH	7.80	5.76	18.37	76.25	65.81	16.61	52.44	13.70
<i>Nelicurvius nelicourvi</i>	438769	Malagasy	M	FMNH	7.88	5.84	18.31	77.04	62.54	17.66	52.88	18.81
<i>Nelicurvius sakalava minor</i>	436485	Malagasy	M	FMNH	8.29	5.77	16.51	76.47	62.75	17.61	50.34	17.95
<i>Nelicurvius sakalava minor</i>	436482	Malagasy	M	FMNH	8.25	5.83	16.14	75.11	62.33	17.67	49.71	17.01
<i>Nelicurvius sakalava minor</i>	436481	Malagasy	M	FMNH	8.26	5.82	16.12	71.98	59.30	16.94	47.32	17.62
<i>Nelicurvius sakalava minor</i>	436489	Malagasy	F	FMNH	7.90	5.85	15.50	69.66	57.76	16.05	46.04	17.08
<i>Nelicurvius sakalava minor</i>	436484	Malagasy	F	FMNH	7.89	5.64	15.60	68.83	57.78	15.57	48.39	16.05
<i>Nelicurvius sakalava sakalava</i>	725629	Malagasy	M	AMNH	10.59	7.16	19.11	82.06	67.32	18.67	57.63	17.97
<i>Nelicurvius sakalava sakalava</i>	725628	Malagasy	M	AMNH	9.92	7.06	19.61	82.17	66.46	18.89	55.89	19.13
<i>Nelicurvius sakalava sakalava</i>	413517	Malagasy	M	AMNH	10.44	7.23	19.33	79.99	65.45	18.53	55.11	18.18
<i>Nelicurvius sakalava sakalava</i>	413518	Malagasy	F	AMNH	10.48	7.12	19.12	79.74	65.46	18.07	51.23	17.91
<i>Nelicurvius sakalava sakalava</i>	413521	Malagasy	F	AMNH	9.46	6.71	18.29	75.62	64.16	17.80	51.56	15.15
<i>Malimbus nitens</i>	274307	Source	M	FMNH	8.13	6.82	22.87	89.18	77.71	17.68	56.14	12.87
<i>Malimbus nitens</i>	274300	Source	F	FMNH	8.46	7.23	22.94	82.62	71.85	16.84	51.24	13.03
<i>Malimbus malimbicus</i>	203148	Source	M	FMNH	7.38	6.46	19.68	86.48	74.95	18.42	62.64	13.33
<i>Malimbus malimbicus</i>	429685	Source	F	FMNH	7.50	6.64	20.02	77.59	65.92	16.28	55.90	15.04
<i>Malimbus racheliae</i>	274345	Source	M	FMNH	7.23	6.25	19.31	82.47	62.12	16.63	54.55	24.67
<i>Malimbus racheliae</i>	274346	Source	F	FMNH	7.30	5.50	19.43	79.34	61.38	15.28	49.42	22.64
<i>Malimbus cassini</i>	274326	Source	M	FMNH	7.28	6.04	18.33	90.46	67.27	18.85	52.25	25.64

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Malimbus cassini</i>	274335	Source	F	FMNH	7.11	5.92	18.25	89.16	67.50	18.18	58.59	24.30
<i>Malimbus rubriceps</i>	725461	Source	F	AMNH	6.23	5.62	17.17	75.78	60.51	13.05	58.90	20.14
<i>Malimbus rubriceps</i>	225752	Source	M	FMNH	6.58	5.68	16.96	80.77	66.45	16.94	51.74	17.73
<i>Euplectes albonotatus</i>	468562	Source	M	FMNH	7.85	6.35	15.33	76.10	63.68	18.54	60.07	16.32
<i>Euplectes albonotatus</i>	468558	Source	F	FMNH	7.70	6.04	14.56	64.36	53.68	16.66	46.01	16.59
<i>Euplectes nigroventris</i>	190367	Source	M	FMNH	6.75	5.42	13.18	57.43	48.40	15.31	38.56	15.73
<i>Euplectes nigroventris</i>	203495	Source	F	FMNH	6.98	5.52	13.40	56.74	46.64	15.32	36.28	17.80
<i>Euplectes hartlaubi</i>	441177	Source	M	FMNH	9.18	6.67	17.16	85.04	69.86	22.76	65.93	17.85
<i>Euplectes hartlaubi</i>	468534	Source	F	FMNH	8.45	6.63	15.99	78.45	66.72	20.05	62.38	14.95
<i>Euplectes ardens</i>	455699	Source	M	FMNH	7.34	5.82	14.45	67.78	54.87	16.08	49.87	19.06
<i>Euplectes ardens</i>	468551	Source	F	FMNH	7.13	5.63	13.83	65.29	52.48	15.91	44.00	19.62
<i>Foudia madagascariensis</i>	346015	Malagasy	M	FMNH	7.91	5.61	15.09	67.59	56.26	17.60	50.85	16.75
<i>Foudia madagascariensis</i>	429327	Malagasy	M	FMNH	8.03	5.93	14.81	61.67	53.14	16.57	48.70	13.83
<i>Foudia madagascariensis</i>	393465	Malagasy	M	FMNH	8.30	6.07	14.29	66.04	55.47	16.32	51.56	16.00
<i>Foudia madagascariensis</i>	393510	Malagasy	F	FMNH	7.11	5.23	12.87	59.91	50.31	15.49	49.08	16.01
<i>Foudia madagascariensis</i>	353024	Malagasy	F	FMNH	7.39	5.28	13.64	60.85	51.49	15.45	50.46	15.38
<i>Foudia omissa</i>	346020	Malagasy	M	FMNH	8.61	6.05	15.63	68.02	56.28	18.32	50.88	17.25
<i>Foudia omissa</i>	393480	Malagasy	M	FMNH	8.59	5.98	15.83	71.68	58.47	18.36	54.24	18.43
<i>Foudia omissa</i>	438790	Malagasy	M	FMNH	8.81	6.60	16.25	72.71	59.03	18.45	53.20	18.82
<i>Foudia omissa</i>	393489	Malagasy	F	FMNH	7.96	5.85	15.53	63.16	51.12	16.32	49.82	19.06
<i>Foudia omissa</i>	393477	Malagasy	F	FMNH	8.58	6.02	16.98	70.15	59.36	16.92	53.30	15.38
<i>Foudia aldabrana</i>	725614	Source	M	AMNH	10.40	6.81	19.72	79.72	64.64	19.65	58.60	18.92

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Foudia aldabrana</i>	725612	Source	F	AMNH	9.97	6.84	18.02	81.58	69.35	19.20	57.87	14.98
<i>Foudia eminentissima</i>	725583	Source	M	AMNH	8.74	6.62	18.40	77.06	65.39	18.59	55.07	15.14
<i>Foudia eminentissima</i>	725586	Source	F	AMNH	8.45	6.33	18.26	70.31	59.41	18.06	52.43	15.51
<i>Foudia rubra</i>	725618	Source	M	AMNH	6.58	4.99	17.89	68.89	58.40	17.21	47.67	15.24
<i>Foudia rubra</i>	725617	Source	F	AMNH	6.56	5.40	17.83	66.62	56.42	17.73	45.92	15.30
<i>Foudia sechellarum</i>	725623	Source	M	AMNH	7.05	5.23	15.85	67.31	60.11	17.70	48.26	10.70
<i>Foudia sechellarum</i>	725626	Source	F	AMNH	7.11	5.39	16.96	69.96	61.13	17.28	50.09	12.63
<i>Quelea erythrops</i>	274364	Source	M	FMNH	8.65	6.83	14.64	63.16	48.91	15.92	34.91	22.56
<i>Quelea erythrops</i>	274386	Source	F	FMNH	8.49	6.18	14.83	58.26	46.18	15.02	34.77	20.74
<i>Quelea cardinalis</i>	117958	Source	M	FMNH	8.27	5.55	11.66	57.78	48.10	14.91	36.67	16.76
<i>Quelea cardinalis</i>	117963	Source	F	FMNH	7.64	5.59	12.21	55.83	45.60	14.78	34.06	18.32
<i>Quelea quelea</i>	122552	Source	M	FMNH	7.95	6.47	14.03	63.96	50.65	14.70	38.12	20.81
<i>Quelea quelea</i>	96008	Source	F	FMNH	8.00	6.18	13.38	63.23	49.40	14.77	38.10	21.88
<i>Ploceus megarhynchus</i>	268974	Source	M	FMNH	11.60	7.75	23.06	78.90	67.07	22.23	64.97	14.99
<i>Ploceus benghalensis</i>	244580	Source	M	FMNH	9.24	6.74	16.67	70.84	58.43	14.38	44.37	17.52
<i>Ploceus benghalensis</i>	244577	Source	F	FMNH	8.97	6.34	16.23	69.58	55.66	14.46	46.70	20.00
<i>Ploceus philippinus</i>	244522	Source	M	FMNH	9.76	7.08	19.05	73.29	59.76	18.26	49.76	18.45
<i>Ploceus philippinus</i>	244549	Source	F	FMNH	8.94	6.70	17.47	68.45	55.29	17.33	44.83	19.23
<i>Ploceus manyar</i>	213974	Source	M	FMNH	9.43	6.98	17.85	68.13	58.25	17.18	50.65	14.50
<i>Ploceus manyar</i>	213969	Source	F	FMNH	9.30	6.92	17.11	65.17	48.73	17.00	46.09	25.24
<i>Coua cristata cristata</i>	411601	Malagasy	M	AMNH	10.08	9.36	24.57	133.45	125.27	29.64	211.00	6.13
<i>Coua cristata cristata</i>	411607	Malagasy	F	AMNH	10.17	8.88	24.87	131.79	122.09	28.90	199.50	7.36
<i>Coua cristata cristata</i>	628947	Malagasy	F	AMNH	9.91	8.22	23.76	134.08	125.10	30.94	201.00	6.70
<i>Coua cristata cristata</i>	411593	Malagasy	M	AMNH	9.59	9.52	25.33	128.45	122.05	31.75	206.00	4.99
<i>Coua cristata cristata</i>	411606	Malagasy	M	AMNH	8.78	6.37	25.78	134.67	128.77	37.80	198.67	4.38

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Coua cristata dumonti</i>	196658	Malagasy	F	AMNH	9.49	8.16	24.32	136.96	126.35	31.46	206.50	7.74
<i>Coua cristata dumonti</i>	411611	Malagasy	M	AMNH	9.61	7.55	22.33	131.25	121.89	28.60	201.00	7.13
<i>Coua cristata dumonti</i>	411612	Malagasy	M	AMNH	9.23	7.63	21.49	129.15	121.09	30.44	200.00	6.24
<i>Coua cristata dumonti</i>	411614	Malagasy	F	AMNH	9.00	8.73	21.34	130.94	122.84	29.40	204.67	6.19
<i>Coua cristata pyropyga</i>	628942	Malagasy	M	AMNH	9.37	7.55	23.86	166.33	141.24	31.17	204.67	15.09
<i>Coua cristata pyropyga</i>	411620	Malagasy	M	AMNH	9.83	9.29	22.55	159.67	137.69	34.26	238.00	13.76
<i>Coua cristata pyropyga</i>	411625	Malagasy	F	AMNH	9.93	8.18	23.34	164.33	148.71	32.80	213.00	9.51
<i>Coua cristata pyropyga</i>	411618	Malagasy	M	AMNH	9.38	6.53	23.12	154.67	137.70	37.36	208.00	10.97
<i>Coua verreauxi</i>	411632	Malagasy	F	AMNH	9.24	7.95	20.00	122.80	113.72	27.60	208.00	7.39
<i>Coua verreauxi</i>	411631	Malagasy	M	AMNH	8.19	6.89	18.99	129.51	112.32	28.20	208.00	13.27
<i>Coua verreauxi</i>	411633	Malagasy	F	AMNH	8.96	7.31	18.52	124.43	105.16	30.19	206.00	15.49
<i>Coua verreauxi</i>	628958	Malagasy	M	AMNH	8.89	6.78	20.76	128.21	114.63	27.33	180.00	10.59
<i>Coua verreauxi</i>	628959	Malagasy	M	AMNH	9.19	5.54	18.55	128.12	111.52	33.52	179.67	12.96
<i>Coua verreauxi</i>	411628	Malagasy	M	AMNH	8.63	5.80	19.13	125.89	114.82	32.93	192.67	8.79
<i>Coua verreauxi</i>	411629	Malagasy	M	AMNH	8.50	6.11	20.96	122.29	111.42	33.63	190.00	8.89
<i>Coua verreauxi</i>	411630	Malagasy	F	AMNH	8.32	5.79	19.61	125.78	117.91	33.00	185.00	6.26
<i>Coua coquereli</i>	411680	Malagasy	F	AMNH	8.96	6.85	24.97	137.46	134.89	39.94	255.00	1.87
<i>Coua coquereli</i>	411684	Malagasy	F	AMNH	8.58	7.37	24.34	137.80	124.32	35.50	232.00	9.78
<i>Coua coquereli</i>	411672	Malagasy	M	AMNH	8.76	6.87	24.58	132.59	128.60	38.55	222.00	3.00
<i>Coua coquereli</i>	411678	Malagasy	M	AMNH	9.32	8.17	26.76	146.05	132.22	40.52	245.00	9.47
<i>Coua coquereli</i>	411676	Malagasy	M	AMNH	8.80	5.71	24.97	145.36	135.44	43.50	223.33	6.83
<i>Coua caerulea</i>	411394	Malagasy	M	AMNH	10.05	10.12	30.26	185.00	166.00	43.06	245.00	10.27
<i>Coua caerulea</i>	411528	Malagasy	F	AMNH	10.43	9.44	29.96	191.33	180.33	40.23	268.00	5.75

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Coua caerulea</i>	411523	Malagasy	M	AMNH	11.71	10.78	28.59	192.00	179.67	42.61	239.67	6.42
<i>Coua caerulea</i>	411520	Malagasy	F	AMNH	10.22	7.73	29.57	189.33	164.67	41.41	234.00	13.03
<i>Coua cursor</i>	411667	Malagasy	F	AMNH	8.87	6.91	23.15	126.44	121.21	32.38	210.00	4.14
<i>Coua cursor</i>	411662	Malagasy	M	AMNH	9.55	6.54	24.99	129.32	119.63	33.35	208.00	7.49
<i>Coua cursor</i>	411665	Malagasy	M	AMNH	8.26	4.92	24.37	120.96	117.41	33.39	185.00	2.93
<i>Coua cursor</i>	411666	Malagasy	M	AMNH	6.66	4.46	22.93	120.77	116.36	35.82	174.33	3.65
<i>Coua gigas</i>	411685	Malagasy	M	AMNH	14.26	9.05	36.86	205.00	198.00	53.25	295.00	3.41
<i>Coua gigas</i>	411689	Malagasy	M	AMNH	13.00	9.24	39.68	212.67	190.00	58.29	310.00	10.66
<i>Coua gigas</i>	411687	Malagasy	F	AMNH	14.48	10.99	36.63	197.67	190.00	54.37	310.00	3.88
<i>Coua reynaudii</i>	411540	Malagasy	M	AMNH	10.36	8.19	26.35	134.14	131.37	36.88	225.00	2.06
<i>Coua reynaudii</i>	411564	Malagasy	M	AMNH	10.18	7.49	26.20	135.48	129.72	32.78	242.00	4.25
<i>Coua reynaudii</i>	411576	Malagasy	F	AMNH	9.41	7.86	25.84	135.04	127.92	37.32	226.00	5.27
<i>Coua reynaudii</i>	411552	Malagasy	F	AMNH	11.94	9.11	25.83	135.26	130.54	36.97	235.00	3.49
<i>Coua reynaudii</i>	411578	Malagasy	M	AMNH	9.35	6.52	25.31	137.01	134.47	39.15	214.67	1.86
<i>Coua serriana</i>	411591	Malagasy	F	AMNH	13.21	9.52	29.77	164.00	163.00	46.22	269.00	0.61
<i>Coua serriana</i>	411580	Malagasy	M	AMNH	13.66	8.53	29.83	164.33	163.33	45.91	249.00	0.61
<i>Coua ruficeps ruficeps</i>	411638	Malagasy	M	AMNH	10.24	9.44	28.00	168.33	155.06	45.82	173.00	7.88
<i>Coua ruficeps ruficeps</i>	411639	Malagasy	F	AMNH	10.77	9.66	29.98	159.33	155.25	45.34	164.00	2.56
<i>Coua ruficeps ruficeps</i>	411634	Malagasy	M	AMNH	9.92	8.53	28.36	154.90	151.18	45.75	159.00	2.40
<i>Coua ruficeps ruficeps</i>	411636	Malagasy	F	AMNH	10.77	8.49	28.51	160.67	153.13	45.15	173.00	4.69
<i>Coua ruficeps olivaceiceps</i>	411658	Malagasy	M	AMNH	10.02	8.26	27.72	162.33	152.17	40.16	234.67	6.26
<i>Coua ruficeps olivaceiceps</i>	411654	Malagasy	F	AMNH	10.23	9.27	28.58	168.67	154.67	44.83	262.00	8.30
<i>Coua ruficeps olivaceiceps</i>	411657	Malagasy	F	AMNH	9.49	8.63	28.04	168.67	144.33	40.88	169.00	14.43

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Coua ruficeps olivaceiceps</i>	628937	Malagasy	F	AMNH	9.75	7.83	29.26	158.33	140.33	45.91	210.33	11.37
<i>Coua ruficeps olivaceiceps</i>	411647	Malagasy	M	AMNH	9.21	6.62	25.23	160.33	149.33	49.44	228.67	6.86
<i>Nectarinia notata notata</i>	98050	Malagasy	M	FMNH	3.60	4.39	30.76	69.40	55.13	15.11	52.23	20.57
<i>Nectarinia notata notata</i>	345967	Malagasy	M	FMNH	3.87	4.52	33.56	68.52	53.49	15.71	52.02	21.94
<i>Nectarinia notata notata</i>	393444	Malagasy	M	FMNH	4.10	4.33	31.16	69.06	56.00	14.93	52.46	18.91
<i>Nectarinia notata notata</i>	345968	Malagasy	F	FMNH	4.25	4.28	30.30	64.50	53.76	14.65	48.77	16.65
<i>Nectarinia notata notata</i>	345979	Malagasy	F	FMNH	3.74	4.16	30.07	64.39	52.98	14.61	45.37	17.71
<i>Nectarinia notata moebii</i>	688383	Source	M	AMNH	3.84	4.48	32.83	72.39	59.02	16.80	58.10	18.48
<i>Nectarinia notata moebii</i>	688391	Source	F	AMNH	3.59	4.42	33.42	63.80	53.21	16.80	45.44	16.60
<i>Nectarinia adelberti</i>	186914	Source	M	FMNH	3.07	3.73	19.62	61.10	48.72	13.36	42.11	20.27
<i>Nectarinia adelberti</i>	278959	Source	F	FMNH	2.98	3.54	18.94	58.48	47.59	12.97	38.49	18.61
<i>Nectarinia senegalensis senegalensis</i>	396721	Source	M	FMNH	3.73	3.79	23.25	67.50	54.57	14.82	53.46	19.15
<i>Nectarinia senegalensis senegalensis</i>	396722	Source	F	FMNH	3.64	3.35	22.81	58.46	47.28	13.37	45.48	19.12
<i>Nectarinia erythrocerca erythrocerca</i>	190327	Source	M	FMNH	3.20	3.66	20.28	62.42	52.61	14.39	56.71	15.71

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Nectarinia erythrocerca erythrocerca</i>	117068	Source	F	FMNH	3.07	3.51	18.77	54.68	46.83	14.18	48.33	14.36
<i>Nectarinia sovimanga sovimanga</i>	393425	Malagasy	M	FMNH	3.10	3.38	20.90	51.93	43.88	13.06	40.57	15.50
<i>Nectarinia sovimanga sovimanga</i>	345931	Malagasy	M	FMNH	3.49	3.23	21.26	53.17	44.17	13.90	45.09	16.93
<i>Nectarinia sovimanga sovimanga</i>	438763	Malagasy	M	FMNH	3.25	3.29	22.04	54.33	45.98	13.53	40.20	15.38
<i>Nectarinia sovimanga sovimanga</i>	345955	Malagasy	F	FMNH	3.10	3.41	20.37	49.31	43.04	13.12	36.07	12.70
<i>Nectarinia sovimanga sovimanga</i>	393427	Malagasy	F	FMNH	3.33	3.33	19.92	48.91	41.23	13.15	35.77	15.71
<i>Nectarinia sovimanga sovimanga</i>	352961	Malagasy	M	FMNH	2.95	3.32	20.65	54.61	46.38	14.60	44.91	15.07
<i>Nectarinia sovimanga sovimanga</i>	345933	Malagasy	M	FMNH	3.19	3.38	21.30	54.69	46.21	13.46	44.07	15.50
<i>Nectarinia sovimanga sovimanga</i>	345930	Malagasy	M	FMNH	3.59	3.35	21.68	54.04	46.75	13.45	43.49	13.48
<i>Nectarinia sovimanga sovimanga</i>	436478	Malagasy	F	FMNH	3.08	3.43	20.77	48.30	41.44	13.42	37.50	14.20
<i>Nectarinia sovimanga sovimanga</i>	185783	Malagasy	F	FMNH	3.00	2.88	20.05	49.40	41.95	13.22	38.65	15.08
<i>Nectarinia sovimanga buchenorum</i>	801499	Source	M	AMNH	3.04	3.18	18.65	54.87	48.13	15.06	47.17	12.28
<i>Nectarinia sovimanga buchenorum</i>	801496	Source	F	AMNH	3.20	3.13	17.68	50.62	43.76	14.53	39.09	13.56
<i>Nectarinia sovimanga aldabrensis</i>	701707	Source	M	AMNH	3.03	3.45	18.97	55.45	45.11	13.02	48.27	18.64
<i>Nectarinia sovimanga aldabrensis</i>	701720	Source	F	AMNH	2.65	3.26	17.69	48.29	41.22	12.74	36.48	14.65

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Nectarinia sovimanga comorensis</i>	688740	Source	M	AMNH	3.06	3.73	20.95	54.72	45.27	14.58	41.05	17.28
<i>Nectarinia sovimanga comorensis</i>	688741	Source	M	AMNH	2.98	3.73	20.95	54.73	44.55	14.61	41.31	18.60
<i>Nectarinia coquereli</i>	701663	Source	M	AMNH	3.08	3.52	19.97	51.48	42.28	13.43	33.64	17.88
<i>Nectarinia coquereli</i>	701675	Source	F	AMNH	2.53	3.18	18.33	46.69	39.29	13.38	30.76	15.86
<i>Nectarinia dussumieri</i>	690151	Source	M	AMNH	3.17	3.71	24.80	62.73	52.75	15.65	46.72	15.92
<i>Nectarinia dussumieri</i>	690157	Source	F	AMNH	3.16	4.07	22.68	58.13	48.92	15.43	44.31	15.83
<i>Nectarinia humbloti humbloti</i>	690166	Source	M	AMNH	2.76	3.35	20.55	49.77	43.02	13.52	37.22	13.56
<i>Nectarinia humbloti humbloti</i>	690175	Source	F	AMNH	2.79	3.33	18.20	48.42	38.01	13.01	32.85	21.50
<i>Nectarinia bowvieri bowvieri</i>	122411	Source	M	FMNH	2.91	3.52	20.21	58.45	48.73	14.63	43.85	16.63
<i>Nectarinia bowvieri bowvieri</i>	161466	Source	F	AMNH	3.02	3.74	20.30	51.04	43.17	13.93	36.95	15.41
<i>Nectarinia talatala talatala</i>	8860	Source	M	FMNH	3.54	3.85	23.87	57.92	50.16	13.39	47.15	13.39
<i>Nectarinia talatala talatala</i>	263868	Source	F	FMNH	2.81	3.44	20.39	53.95	46.06	14.15	43.03	14.62
<i>Nectarinia venusta falkensteini</i>	474955	Source	M	FMNH	3.34	3.31	21.50	50.95	42.71	13.78	39.54	16.18
<i>Nectarinia venusta falkensteini</i>	474952	Source	F	FMNH	2.85	3.07	20.00	48.16	40.87	13.43	36.84	15.12
<i>Hypsipetes madagascariensis</i>	431229	Malagasy	M	FMNH	6.23	4.99	26.38	114.76	86.74	16.37	103.00	24.41
<i>Hypsipetes madagascariensis</i>	431228	Malagasy	F	FMNH	5.57	5.13	22.74	102.25	78.14	16.42	89.33	23.57
<i>Hypsipetes madagascariensis</i>	438711	Malagasy	M	FMNH	6.39	5.24	25.15	98.60	75.03	17.13	99.56	23.90
<i>Hypsipetes madagascariensis</i>	345762	Malagasy	M	FMNH	5.83	5.02	24.46	107.72	85.49	16.95	97.59	20.63

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Hypsipetes madagascariensis</i>	393305	Malagasy	F	FMNH	5.69	4.68	24.92	100.45	79.80	17.02	90.16	20.55
<i>Hypsipetes amaurotis</i>	211672	Source	M	FMNH	6.53	5.06	27.35	128.67	99.31	19.11	118.67	22.82
<i>Hypsipetes amaurotis</i>	94408	Source	F	FMNH	7.17	6.10	30.52	117.36	93.71	19.70	117.67	20.15
<i>Hypsipetes rufigularis</i>	73998	Source	F	FMNH	6.68	6.17	27.23	106.55	88.80	16.94	93.67	16.66
<i>Hypsipetes rufigularis</i>	227274	Source	M	FMNH	7.22	4.94	27.83	116.15	95.90	17.46	104.67	17.43
<i>Hypsipetes everetti</i>	275108	Source	M	FMNH	7.88	6.78	27.79	111.66	90.94	17.24	102.95	18.56
<i>Hypsipetes everetti</i>	277971	Source	F	FMNH	7.30	5.97	29.07	103.98	83.30	17.18	96.64	19.89
<i>Hypsipetes mindorensis</i>	20201	Source	M	FMNH	5.81	5.23	25.19	100.70	82.12	16.56	100.67	18.44
<i>Hypsipetes mindorensis</i>	73997	Source	F	FMNH	6.37	5.77	26.60	98.05	79.24	17.55	92.00	19.19
<i>Hypsipetes siquijorensis</i>	219209	Source	M	FMNH	7.53	6.29	30.63	130.86	102.83	19.26	119.67	21.42
<i>Hypsipetes siquijorensis</i>	219218	Source	F	FMNH	7.88	5.73	28.16	121.20	97.50	18.60	116.65	19.55
<i>Hypsipetes philippinus</i>	265980	Source	M	FMNH	6.54	5.45	25.02	97.50	81.23	16.53	91.49	16.69
<i>Hypsipetes philippinus</i>	265998	Source	F	FMNH	6.78	5.38	24.13	90.38	76.65	16.54	94.87	15.18
<i>Hypsipetes everetti catarmanensis</i>	286308	Source	M	FMNH	8.29	6.13	28.33	111.13	92.43	19.45	105.17	16.83
<i>Hypsipetes everetti catarmanensis</i>	284456	Source	F	FMNH	8.41	6.31	29.38	115.93	95.09	18.72	104.31	17.97
<i>Hypsipetes malaccensis</i>	211957	Source	M	FMNH	6.78	5.37	26.21	105.45	86.30	15.84	90.80	18.16
<i>Hypsipetes malaccensis</i>	304613	Source	-	FMNH	6.79	5.29	25.44	103.81	85.01	13.35	90.62	18.11

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Hypsipetes maclellandii</i>	219064	Source	M	FMNH	5.60	5.31	27.05	109.26	88.73	15.04	106.03	18.79
<i>Hypsipetes maclellandii</i>	219066	Source	F	FMNH	5.47	5.01	26.00	103.50	83.29	15.16	102.30	19.53
<i>Hypsipetes leucocephalus</i>	79373	Source	M	FMNH	5.98	5.01	27.55	121.91	91.03	15.30	111.00	25.33
<i>Hypsipetes leucocephalus</i>	79375	Source	F	FMNH	5.90	5.00	24.69	111.99	83.09	15.16	97.06	25.81
<i>Terpsiphone m. mutata</i>	438759	Malagasy	M	FMNH	4.25	5.73	16.90	79.68	65.26	13.99	83.12	18.09
<i>Terpsiphone m. mutata</i>	438756	Malagasy	M	FMNH	4.19	5.08	16.55	77.88	64.78	13.98	89.66	16.82
<i>Terpsiphone m. mutata</i>	345892	Malagasy	M	FMNH	4.41	5.58	16.83	75.23	61.42	14.09	83.31	18.35
<i>Terpsiphone m. mutata</i>	393421	Malagasy	F	FMNH	4.45	5.47	16.21	72.28	60.99	13.41	74.46	15.62
<i>Terpsiphone m. mutata</i>	393422	Malagasy	F	FMNH	3.74	4.82	15.09	74.33	63.12	13.31	74.47	15.08
<i>Terpsiphone m. singetra</i>	431279	Malagasy	M	FMNH	4.43	5.49	15.83	74.85	61.59	12.46	85.98	17.71
<i>Terpsiphone m. singetra</i>	431283	Malagasy	M	FMNH	4.27	5.46	16.83	76.21	61.87	12.48	90.06	18.82
<i>Terpsiphone m. mutata</i>	393423	Malagasy	M	FMNH	4.13	5.35	15.00	72.73	61.30	13.23	79.75	15.71
<i>Terpsiphone m. singetra</i>	431280	Malagasy	F	FMNH	4.03	5.40	15.33	71.28	59.03	12.84	81.77	17.19
<i>Terpsiphone m. singetra</i>	431278	Malagasy	F	FMNH	3.98	5.32	15.44	71.56	57.98	12.64	85.53	18.98

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Terpsiphone m. singetra</i>	431277	Malagasy	M	FMNH	4.17	5.39	15.85	75.80	62.65	13.33	92.54	17.35
<i>Terpsiphone m. pretiosa</i>	652407	Source	M	AMNH	4.67	6.28	17.52	79.12	64.35	13.34	87.04	18.67
<i>Terpsiphone m. pretiosa</i>	652390	Source	M	AMNH	4.55	6.23	17.12	76.30	62.54	13.81	85.65	18.03
<i>Terpsiphone comorensis</i>	652413	Source	-	AMNH	4.08	5.55	16.03	75.71	60.73	16.57	82.62	19.79
<i>Terpsiphone bourbonnensis</i>	650148	Source	-	AMNH	3.68	5.62	15.79	70.30	56.49	16.20	77.03	19.65
<i>Terpsiphone bourbonnensis</i>	650150	Source	-	AMNH	3.50	5.29	15.71	71.51	58.49	17.83	68.06	18.20
<i>Terpsiphone m. vulpine</i>	652409	Source	M	AMNH	4.53	5.61	17.92	77.37	63.82	15.45	81.46	17.52
<i>Terpsiphone m. vulpine</i>	652414	Source	F	AMNH	4.47	5.87	17.59	69.83	58.57	15.50	70.55	16.12
<i>Terpsiphone bourbonnensis desolata</i>	650161	Source	-	AMNH	3.94	5.38	16.48	75.74	61.97	16.82	81.43	18.18
<i>Terpsiphone bourbonnensis desolata</i>	650160	Source	-	AMNH	3.95	5.70	16.33	74.03	60.73	16.81	79.46	17.97
<i>Terpsiphone corvina</i>	652441	Source	M	AMNH	4.39	6.51	20.52	89.00	72.32	15.26	111.54	18.74
<i>Terpsiphone corvina</i>	652452	Source	F	AMNH	4.43	6.48	18.74	83.28	67.84	15.12	103.68	18.54
<i>Terpsiphone a. atrocaudata</i>	223878	Source	M	FMNH	5.74	6.30	19.28	92.64	70.07	13.59	137.58	24.36
<i>Terpsiphone a. atrocaudata</i>	74225	Source	F	FMNH	5.25	6.29	18.04	86.16	66.51	13.48	93.47	22.81
<i>Terpsiphone cinnamomea</i>	74003	Source	M	FMNH	5.72	7.59	23.75	90.94	73.21	14.23	101.10	19.50

Species	Accession	Clade	Sex	Museum	BD	BW	BL	WL	SI	Tar-L	Tail	HWI2
<i>Terpsiphone cinnamomea</i>	184417	Source	F	FMNH	6.26	7.31	20.88	80.91	67.41	14.05	82.24	16.68
<i>Terpsiphone p. paradise</i>	242403	Source	M	FMNH	5.26	7.31	24.06	92.31	73.99	14.39	113.48	19.85
<i>Terpsiphone p. paradise</i>	242376	Source	M	FMNH	5.70	7.28	24.22	90.24	72.17	14.42	112.96	20.02
<i>Terpsiphone p. leucogaster</i>	250494	Source	M	FMNH	5.38	7.30	22.83	92.93	75.12	13.97	119.59	19.16
<i>Terpsiphone p. leucogaster</i>	242389	Source	F	FMNH	5.49	6.90	22.60	86.42	69.58	15.18	98.20	19.48
<i>Terpsiphone p. incei</i>	108876	Source	M	FMNH	5.80	6.43	19.94	91.73	73.42	13.02	123.50	19.96
<i>Terpsiphone p. incei</i>	108888	Source	F	FMNH	5.04	5.79	18.88	85.77	62.33	12.06	87.24	27.33
<i>Terpsiphone rufiventer nigriceps</i>	186803	Source	M	FMNH	5.12	6.71	19.38	78.64	66.09	13.75	99.10	15.97
<i>Terpsiphone rufiventer nigriceps</i>	277225	Source	F	FMNH	5.21	6.12	18.74	74.88	63.72	11.31	88.61	14.90
<i>Terpsiphone batesi</i>	272216	Source	M	FMNH	5.45	5.92	19.52	75.92	64.84	12.70	86.54	14.60
<i>Terpsiphone batesi</i>	59217	Source	F	FMNH	4.54	5.87	18.29	73.09	62.16	12.88	86.67	14.95
<i>Terpsiphone viridis ferreti</i>	197817	Source	M	FMNH	4.50	6.36	17.48	77.36	63.89	13.81	102.31	17.41
<i>Terpsiphone viridis ferreti</i>	355982	Source	F	FMNH	4.77	6.03	17.69	77.16	64.26	13.76	87.02	16.72

CHAPTER 3

TESTING THE IMPORTANCE OF DISPERSAL ABILITY TO DIVERSIFICATION OF MALAGASY BIRDS

Summary and discussion of results of objective 1

I investigated how dispersal ability may have influenced diversification of the endemic birds of Madagascar by comparing morphological variation in radiating lineages and non-radiating lineages. Using the hand-wing index 2 (HWI2) as a measure of dispersal ability I compared Malagasy clade to their source clade. I treated each lineage as an independent case study to determine if there was a general pattern, or lack thereof, that explained why some lineages diversified in Madagascar and others did not. I predicted the radiating lineages Malagasy clade to occupy a greater volume of morphological space in a distinct region from source reflecting a morphological shift to the unique Malagasy habitats. I predicted that I will find reduced dispersal ability (lower HWI2) in the Malagasy clade in response to isolation in a smaller range size.

In this chapter, I discuss the results of objective 1: *to examine if Malagasy species shifted in their dispersal ability after colonizing Madagascar*. For this component, I sampled 117 species and took seven morphological measurements of 451 specimens (Table 3 [specimen table]; Table 4). My analyses demonstrate that across all studied groups, dispersal ability (HWI2) does not differ between Malagasy and source clade and was likely not an important factor in the diversification of these Malagasy endemics (Table 5). Additionally, my analyses indicated that

these Malagasy species did not shift in their dispersal ability after colonizing Madagascar. These same patterns hold for radiating and non-radiating lineages.

The detailed results from my analyses of each family are below (see details of results by lineage). Briefly, the results of my study found that within Vangidae, Malagasy species occupied a significantly differed part of morphospace with greater disparity between Malagasy lineages, which likely reflects a phenotypic shift upon colonization of Madagascar (Fig. 12; Fig. 13). The Malagasy clade of Bernieridae and its sister, Locustellidae, similarly differed in the region of morphospace occupancy from source clade, but the disparity between source lineages was greater than Malagasy ones (Fig. 16; Fig. 17; Fig. 20; Fig. 21). The remaining lineages (except *Nelicurvius* males; Fig. 28; Fig. 29) showed a pattern of Malagasy lineages occupying similar morphospace as their source clades (Fig. 24; Fig. 25; Fig. 32; Fig. 35; Fig. 38; Fig. 41; Fig. 42). In summary, dispersal ability, as measured by HWI2, does not appear important to the diversification of Malagasy endemics from their source clades for any of the lineages studied (Fig. 14; Fig. 18; Fig. 22; Fig. 26; Fig. 30; Fig. 33; Fig. 36; Fig. 39; Fig. 43).

Possible explanations for why dispersal ability was not different between island and continental lineages include: selection or adaptation to similar environments in islands and continents, lack of selective pressures to drive shift upon island colonization, phylogenetic conservatism or other constraint is how this phenotype can evolve, or other factors may be contributing to phenotypic differentiation than dispersal ability. It is difficult to test between these possibilities in this current study with only morphometric data.

The lack of morphological differences between Malagasy representatives and close relatives on islands and continents has been demonstrated (Warren et al., 2003). In some cases, these may be explained by the biology of each clade—some lineages (like sunbirds) have a

general ability to disperse easily across landmasses, but rarely demonstrate *in-situ* speciation even in large areas (Warren et al., 2003).

The breadth of variation in HWI2 is greater in the Malagasy clade of Vangidae. In this Malagasy clade there are extreme variants of HWI2 such as *Leptopterus chabert* or *Cyanolanius madagascariensis* that have high HWI2 values compared to the lower HWI values of *Newtonia* species. A recent study sampled more than 99% of avian species to investigate global variation in HWI (Sheard et al., 2020). They found that within assemblages, the hotspots for the highest variability in HWI were in Madagascar, the Saharan and Arabian deserts, the Andes mountains, and the Pacific islands (Sheard et al., 2020). There may be several possibilities for why the Malagasy vangas have such variation in HWI2 such as their foraging behaviors (sallying, probing, and gleaning), habitat use, or climatic conditions. There are close phylogenetic relatives of Malagasy species on nearby islands that vary in island size and provide an opportunity to study island biogeography. Future research on island biogeography should consider comparing the HWI2 values these species to see if HWI2 is associated with island size.

Interestingly, although my results did not show significant differences in HWI2, another trait—tarsus length did show differences in some lineages (Table 5). Tarsus length differed significantly between clades in Vangidae, Bernieridae, and Locustellidae. Wright et al. (2016) similarly found evidence of morphological shifts in tarsus length of island birds compared to their continental relatives. In other studies, tarsus length has been associated with foraging niche and body size (Derryberry et al., 2011; Tobias et al., 2013). Bill size was significantly reduced in the Malagasy clade of Monarchidae. These trait differences suggest that adaptations to ecological conditions other than dispersal ability are driving diversification of birds on Madagascar.

Table 4. Summary table of the number of species and specimens sampled in each family by clade for Objective 1. Source clade species and specimens were the same for Bernieridae and Locustellidae so they were not counted twice in totals. Outliers were omitted from totals.

Family	Malagasy		Source	
	# species	# specimens	# species	# specimens
Vangidae	20	129	7	15
Bernieridae	10	66	23	60
Locustellidae	2	10	23	60
Ploceidae (<i>Foudia</i>)	2	10	11	21
Ploceidae (<i>Nelicurvius</i>)	2	15	9	18
Nectariniidae (<i>C. notata</i>)	1	5	3	8
Nectariniidae (<i>C. sovimanga</i>)	1	10	7	18
Pycnonotidae	1	5	9	20
Monarchidae	1	11	8	27
Total	40	261	77	187

Table 5. Summary of Chapter 3 results for each family. Within each family I compared the morphometric data of Malagasy (M) and source (S) clades to test for differences. For MANOVA, significant differences in the centroids between clades is marked 'M $\hat{=}$ S' with a p-value. For disparity, the greater or less than sign indicates whether Malagasy or source clade occupied a significantly a greater volume of morphospace. There were no significant differences between clades for HWI2. Additional other morphological traits were compared and listed if they significantly differed between clades.

Family	Multivariate		Univariate	
	MANOVA	Disparity	HWI2	Sig. morphometrics
Vangidae	M $\hat{=}$ S (p<0.001)	M>S (p<0.001)	p>0.05	tarsus length (p<0.01)
Bernieridae	M $\hat{=}$ S (p<0.001)	M<S (p<0.001)	p>0.05	tarsus length (p<0.05)
Locustellidae	M $\hat{=}$ S (p<0.05)	–	p>0.05	wing chord length (p<0.05) tarsus length (p<0.05)
Ploceidae (<i>Foudia</i>)	p>0.05	–	p>0.05	none
Ploceidae (<i>Nelicurvius</i>)	M $\hat{=}$ S (p<0.001)	–	p>0.05	none
Nectariniidae (<i>C. notata</i>)	–	–	N/A	none
Nectariniidae (<i>C. souimanga</i>)	p>0.05	–	N/A	none
Pycnonotidae	p>0.05	–	N/A	none
Monarchidae	p>0.05	–	p>0.05	bill depth (p<0.05) bill width (p<0.05) bill length (p<0.05)

Details of results by lineage

Vanginae (Vangidae)

During the data check, I found four individuals in Vangidae were outliers with standard deviations greater than one (*Falculea palliata* (#413666), *Xenopirostris polleni* (#664429 and #664430), *Prionops plumata* (#285944)) and were removed prior to analyses. There was no significant difference between sexes for any of the morphological variables based on our

ANOVA, so I analyzed males and females together. The dataset for this family consisted of 27 species (20 Malagasy and seven source; 147 specimens; Table 4) and eight morphological variables. The principal component analysis resulted in 8 axes of which the first three (Fig. 11) explained ~91% of the variation (Table 6). There is a significant difference in the Malagasy and source occupancy of morphospace (MANOVA $p < 0.001^{***}$, Fig. 12) and the disparity of the Malagasy clade is greater than source ($p < 0.001^{***}$; Fig. 13). The first principal component likely reflects body size. HWI2 had the highest weighting in PC2 and PC3 loadings contributing substantially to variation explained by these PCs (Table 6). There are no significant differences in the means of HWI2 between Malagasy and source (ANOVA $p > 0.05$, Fig. 14). Tarsus length of Malagasy was significantly greater than source (ANOVA $p < 0.01^{**}$; Table 7).

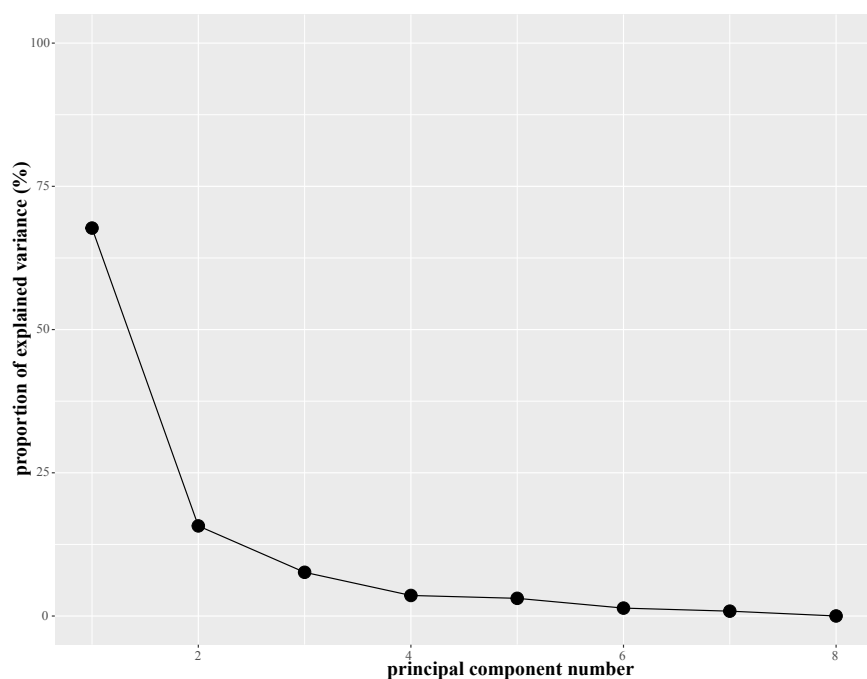


Figure 11. Scree plot of the proportion of explained variance for eight principal components in Vangidae. The first three principal components incorporated greater than 5% variance. Table 6 shows the loadings of these three principal components.

Table 6. Summary of principal components and their loadings in Vangidae. The cumulative proportion of the three principal components is 91.08%. Abbreviations are as follows (BD= bill depth, BW= bill width, BL= bill length, WL= wing chord length, S1= secondary length, Tar-L= tarsus length, Tail-L = tail length, HWI2= hand-wing index 2).

Morphometrics	PC1	PC2	PC3
BD	-0.375	0.072	-0.457
BW	-0.320	0.355	-0.638
BL	-0.372	-0.152	0.145
WL	-0.410	0.073	0.279
S1	-0.408	-0.076	0.213
Tar-L	-0.300	-0.553	0.111
Tail-L	-0.401	-0.102	0.011
HWI2	-0.172	0.718	0.474
Prop. Of Variance	67.72%	15.73%	7.63%

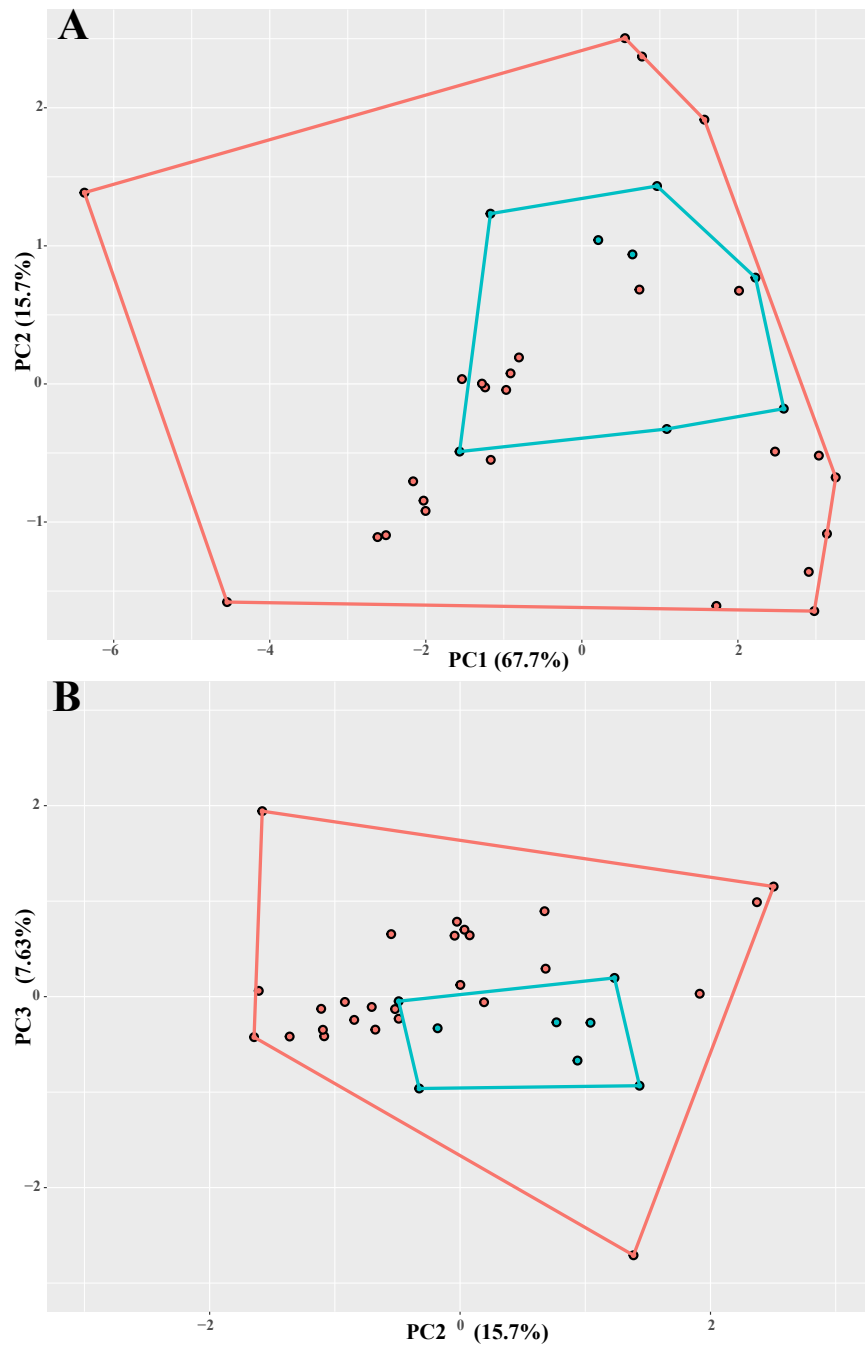


Figure 12. Principal components analysis of morphometric comparisons between clades in Vangidae. (A) Plot of PC1 vs. PC2 (B) Plot PC2 vs. PC3. Each dot represents a single species and is colored by clade (orange = Malagasy; blue = source); disparity of each group is represented as a minimal convex polygon of all species in that group. The centroid of each clade is statistically different (MANOVA $p < 0.001^{***}$).

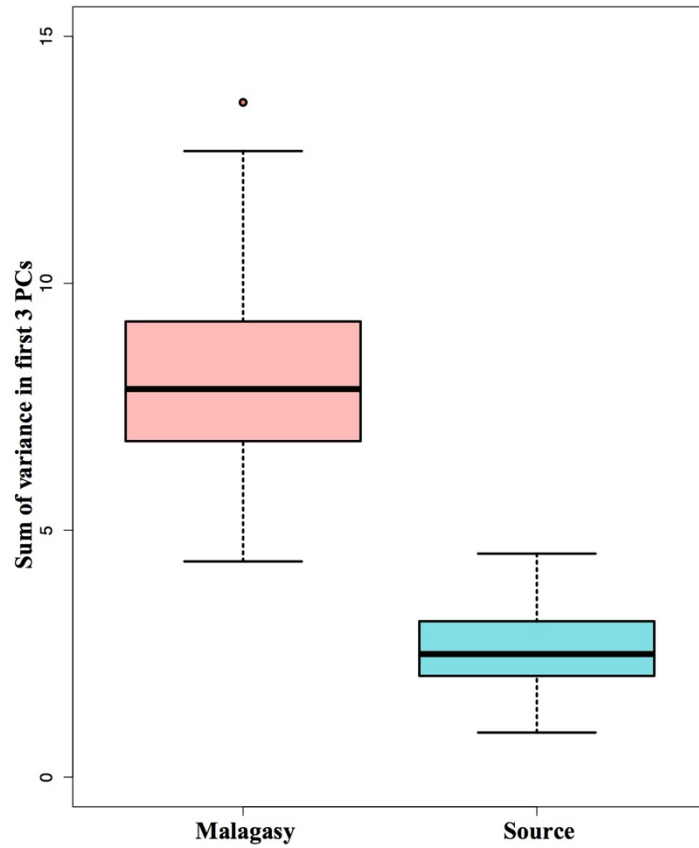


Figure 13. Vangidae plot of disparity between clades. Thick black lines represent the median of the sum of variances in each clade. There is a significant difference in the volume of morphospace occupied between the two clades with Malagasy species occupying a greater area in morphological space than source species (non-parametric Wilcoxon test $W=9999$, $p<0.001^{***}$).

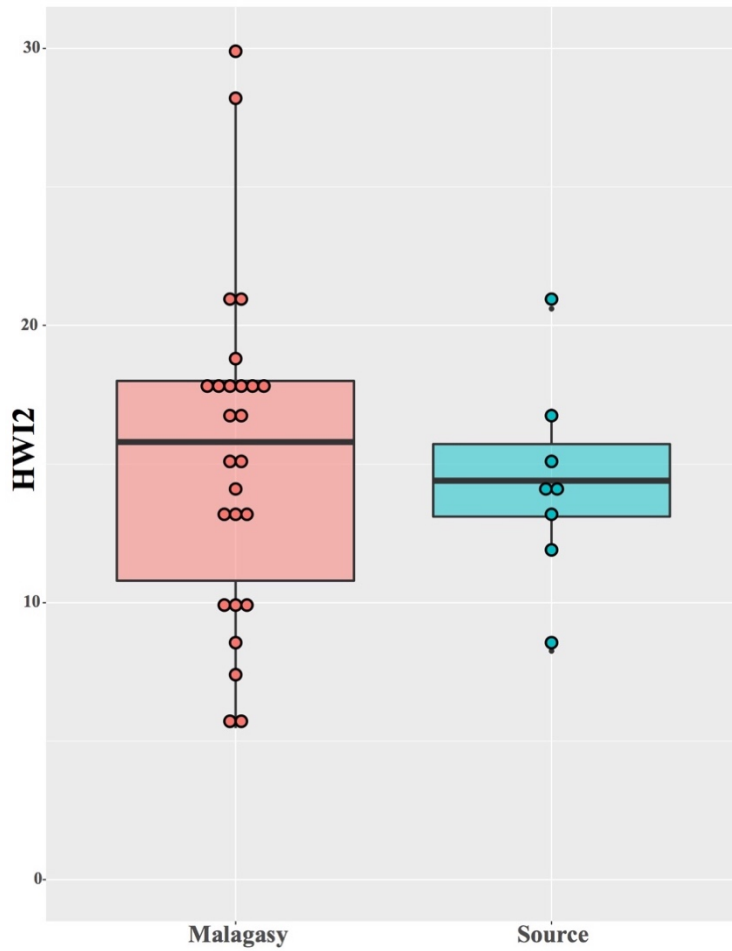


Figure 14. Boxplot of HWI2 between the Malagasy and source clades of Vangidae. Each dot represents a mean value for individual species' HWI2. The Malagasy clade consists of 20 species with the inclusion of six subspecies and the source clade consists of seven species with the inclusion of one subspecies. There are no significant differences in the means of HWI2 between the Malagasy and source clade (ANOVA $p > 0.05$).

Table 7. Summary statistics table of each morphological variable compared between Malagasy and source clade of Vangidae. Only tarsus length was significantly different between the two clades. Significant differences between clades that were uncovered using an ANOVA are shown in bold and asterisk.

Trait	Malagasy (n=20)		Source (n=7)	
	Mean	SD	Mean	SD
BD	7.53	4.47	5.71	1.42
BW	5.48	2.17	6.60	1.22
BL	24.10	11.30	21.00	3.83
WL	95.20	28.70	87.60	20.00
S1	79.80	22.70	74.60	15.50
Tar-L**	19.80	4.06	15.00	3.38
Tail-L	76.00	21.70	69.30	18.00
HWI2	15.40	6.00	14.40	3.60

Bernieridae

There are significant differences between sexes for bill length (ANOVA $p < 0.05$), wing chord length (ANOVA $p < 0.001$), secondary length (ANOVA $p < 0.01$), and tarsus length (ANOVA $p < 0.01$). For this reason, I analyzed males and females of Bernieridae independently. To test for differences between Malagasy and source clade, I used 33 species (10 Malagasy and 23 source; 126 specimens; Table 4). Of the resulting eight principal component, the first three explained ~89% and ~88% of the variation in males and females respectively (Fig. 15; Table 8). For both sexes, there is a significant difference in the Malagasy and source occupancy of morphospace (MANOVA $p < 0.001^{***}$; Fig. 16). The disparity of the source clade is greater than Malagasy ($p < 0.001^{***}$, Fig. 17). The first principal component likely reflects body size. HWI2 did not weigh heavily in the principal component analysis of either sex; tail length was heavily weighted in PC3 for both sexes (Table 8). There were no significant differences in the means of HWI2 between Malagasy and source clade in either sex (ANOVA $p > 0.05$, Fig. 18). Tarsus length of source was significantly greater than Malagasy (ANOVA $p < 0.05^*$; Table 9).

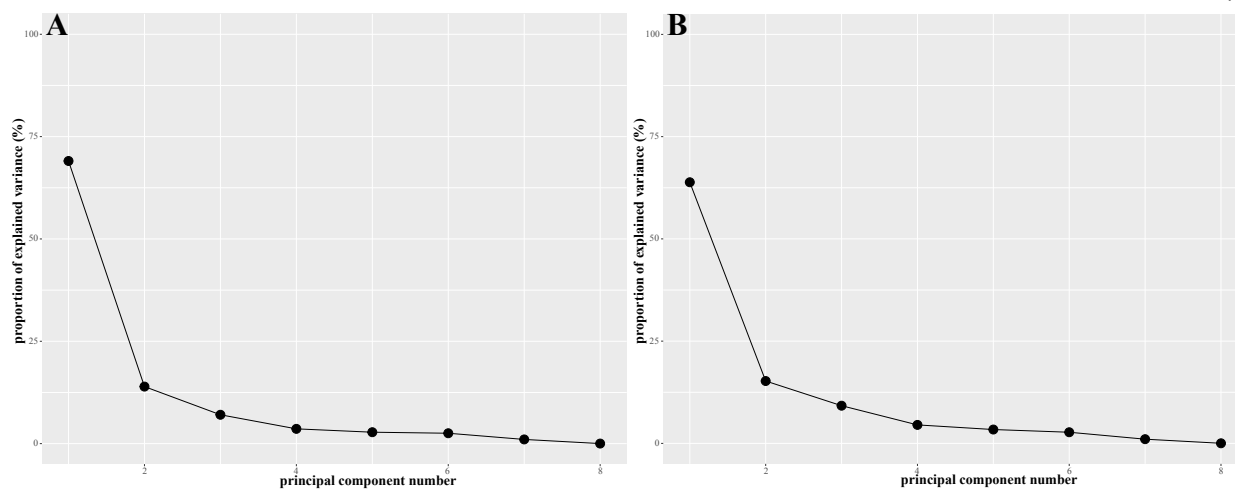


Figure 15. Scree plot of the proportion of explained variance for eight principal components in Bernieridae (A) males and (B) females. The first three principal components incorporated greater than 5% variance in males and females. Table 8 shows the loadings of these three principal components in each sex.

Table 8. Summary of principal components and their loadings in Bernieridae. The cumulative proportion of the three principal components is 90.02% in males and 88.31% in females.

Morphometrics	Males			Females		
	PC1	PC2	PC3	PC1	PC2	PC3
BD	-0.398	0.049	-0.139	-0.407	0.120	-0.144
BW	-0.384	-0.041	-0.002	-0.389	≤0.001	-0.347
BL	-0.350	0.012	-0.656	-0.372	0.088	-0.420
WL	-0.382	-0.303	-0.076	-0.368	-0.431	0.045
S1	-0.400	0.103	-0.127	-0.411	0.109	0.111
Tar-L	-0.366	-0.029	0.456	-0.382	-0.040	0.113
Tail-L	-0.357	0.104	0.563	-0.295	-0.057	0.798
HWI2	0.042	-0.938	0.042	0.072	-0.880	-0.127
Prop. Of Variance	69.05%	13.93%	7.04%	63.85%	15.25%	9.21%

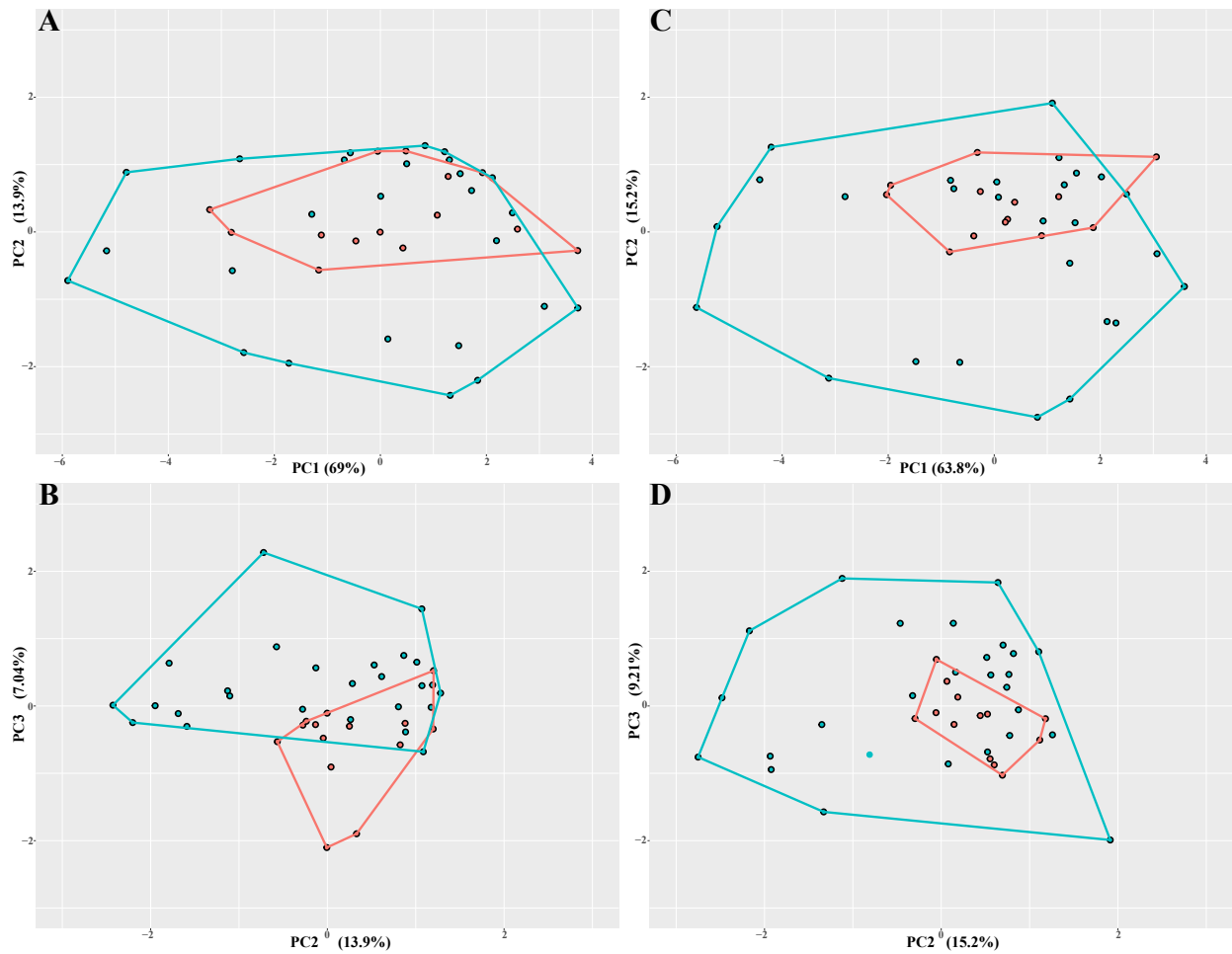


Figure 16. Principal components analysis of morphometric comparisons between clades for males (A,B) and females (C,D) in Bernieridae. Each dot represents a single species and is colored by clade (orange = Malagasy; blue = source); disparity of each group is represented as a minimal convex polygon of all species in that group. The centroid of each clade is statistically different for both sexes (MANOVA $p < 0.001^{***}$).

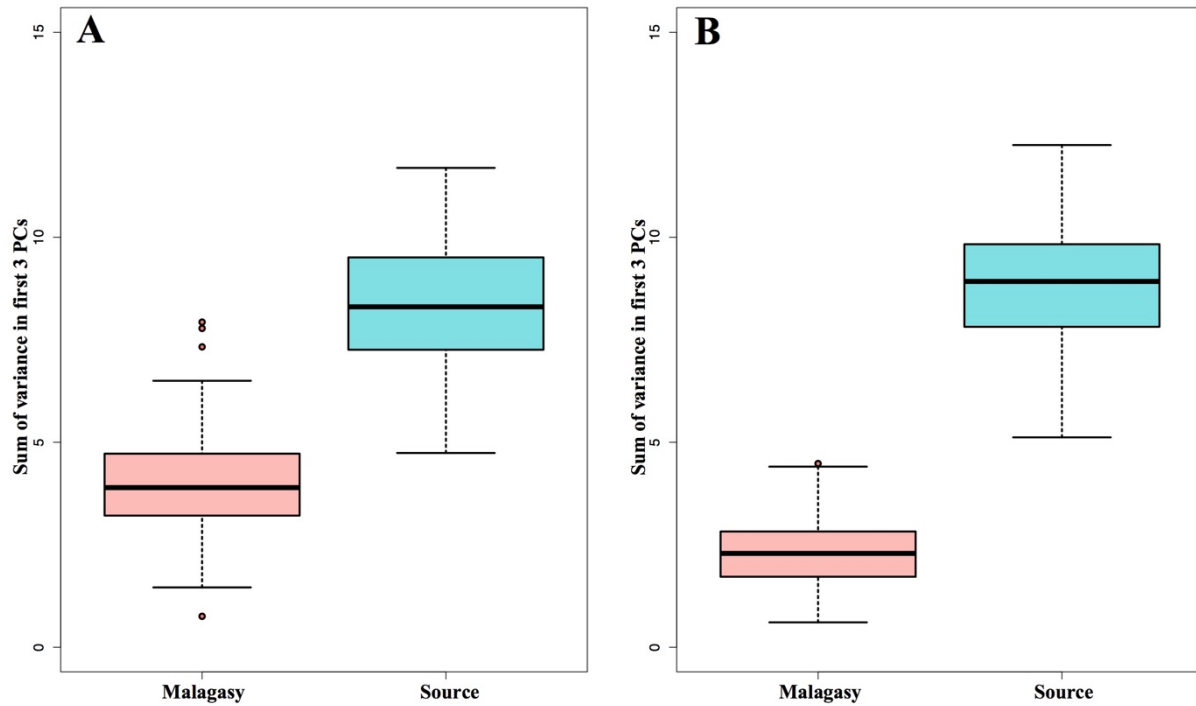


Figure 17. Bernieridae plot of disparity between clades for (A) males and (B) females. There is a significant difference in the volume of morphospace occupied between the two clades with source species occupying a greater area in morphological space than Malagasy species in both sexes (non-parametric Wilcoxon test A) $W=143$, $p<0.001$ ***; B) $W=0$, $p<0.001$ ***).

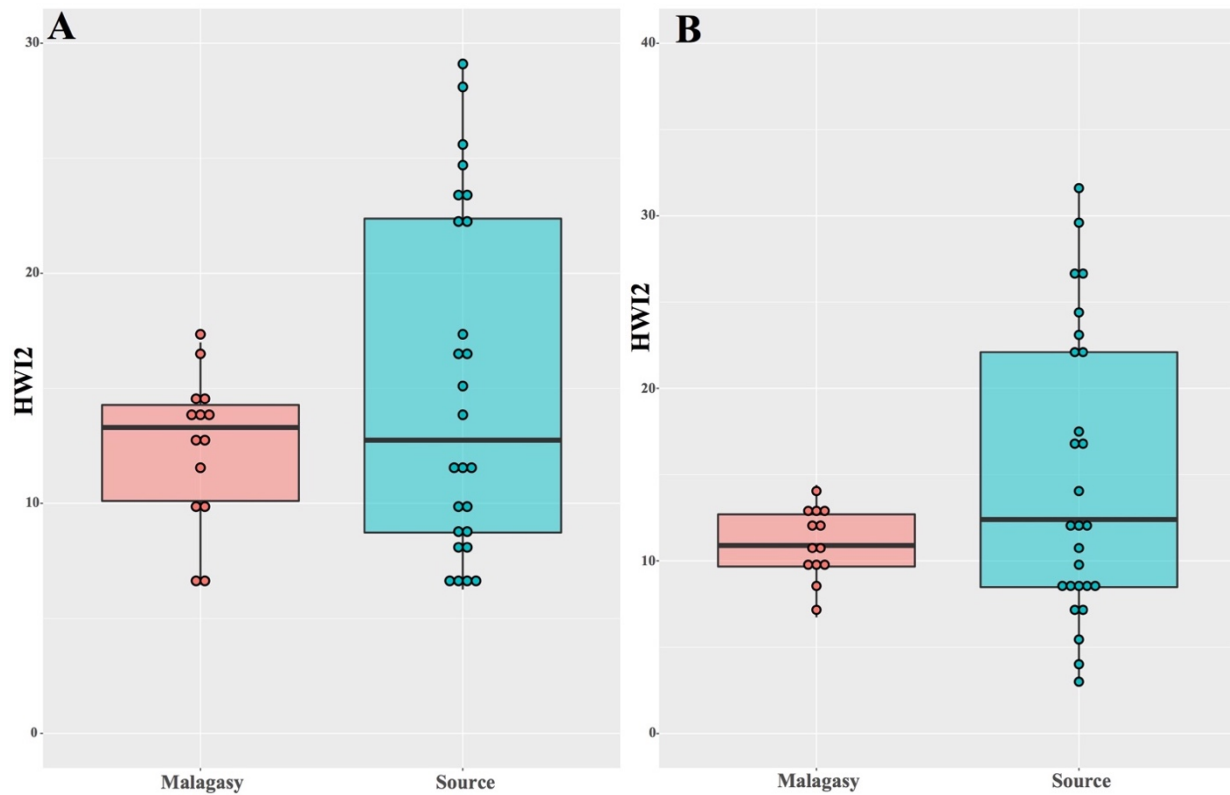


Figure 18. Boxplot of HWI2 between the Malagasy and source clades of Bernieridae in (A) males and (B) females. Each dot represents a mean value for individual species' HWI2. There are no significant differences in the means of HWI2 between Malagasy and source clade (ANOVA $p > 0.05$) in either sex.

Table 9. Summary statistics table of each morphological variable compared between Malagasy and source clade of Bernieridae. Only tarsus length was significantly different between the two clades in males and females. Significant differences between clades that were uncovered using an ANOVA are shown in bold and asterisk with an M and/or F indicating which sex the trait significantly differed in.

Trait	MALE				FEMALE			
	Malagasy (n=10)		Source (n=22)		Malagasy (n=9)		Source (n=23)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
BD	3.81	0.75	3.91	0.87	3.68	0.50	3.72	0.69
BW	3.05	0.40	3.27	0.77	3.15	0.38	3.21	0.67
BL	18.40	4.56	17.00	4.16	17.20	2.69	16.50	3.36
WL	69.80	11.20	68.40	12.40	65.20	5.92	65.70	10.60
S1	61.10	9.50	57.90	10.30	58.00	4.94	55.70	9.03
Tar-L*^{M,F}	19.20	2.75	22.20	4.63	18.80	1.99	21.30	3.64
Tail-L	68.20	10.20	76.30	19.40	64.00	6.23	69.70	17.80
HWI2	12.40	3.22	15.10	7.44	11.00	2.12	14.70	8.27

Locustellidae

There were significant differences between sexes for tail length (ANOVA $p < 0.05^*$). For this reason, I analyzed males and females independently. The dataset for this family consisted of 25 species (two Malagasy and 23 source species; 70 specimens; Table 4). The first three principal components explained ~92% of the variation in males and females respectively (Fig. 19; Table 10). For both sexes, there is a significant difference in the Malagasy and source occupancy of morphospace (MANOVA $p < 0.05^*$, Fig. 20). Disparity of source appears to be greater than Malagasy, but I did not calculate a statistical value to confirm this because of low sample size (two or fewer species) in Malagasy clade (Fig. 21). The first principal component likely reflects body size. HWI2 was not weighted heavily in the principal component analysis of either sex (Table 10). Tail length was heavily weighted in PC2 for both sexes (Table 10). There were no significant differences in the means of HWI2 between Malagasy and source clade in either sex (ANOVA $p > 0.05$, Fig. 22). No other morphological variables significantly differed

between clades in males. For females, wing chord length (ANOVA $p < 0.05^*$) and tarsus length (ANOVA $p < 0.05^*$) was significantly greater in source than Malagasy (Table 11).

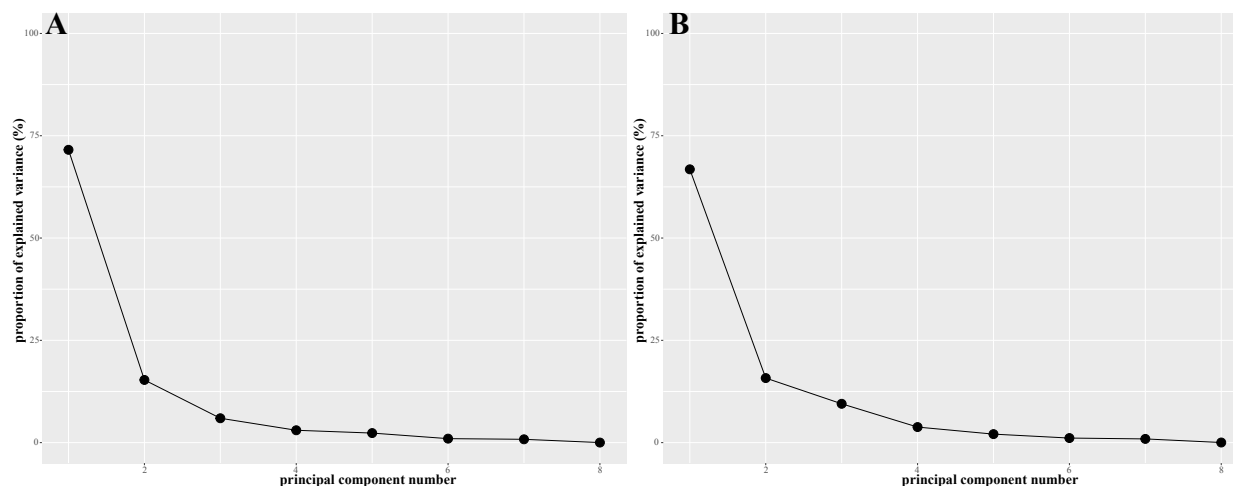


Figure 19. Scree plot of the proportion of explained variance for eight principal components in Locustellidae (A) males and (B) females. Only the first three principal components incorporated greater than 5% variance in males and females. Table 10 shows the loadings of these three principal components in each sex.

Table 10. Summary of principal components and their loadings in Locustellidae. The cumulative proportion of the first three principal components is 92.83% in males and 92.07% in females.

Morphometrics	Males			Females		
	PC1	PC2	PC3	PC1	PC2	PC3
BD	0.397	0.040	-0.003	0.405	0.093	0.051
BW	0.392	-0.015	-0.229	0.387	-0.050	0.286
BL	0.359	-0.051	-0.570	0.386	-0.041	0.342
WL	0.377	-0.327	0.177	0.367	-0.402	-0.183
S1	0.403	0.081	0.022	0.412	0.107	-0.056
Tar-L	0.392	-0.032	-0.017	0.405	0.008	0.086
Tail-L	0.315	0.312	0.732	0.255	0.246	-0.847
HWI2	-0.015	-0.884	0.231	-0.040	-0.867	-0.188
Prop. Of Variance	71.56%	15.32%	5.95%	66.80%	15.78%	9.49%

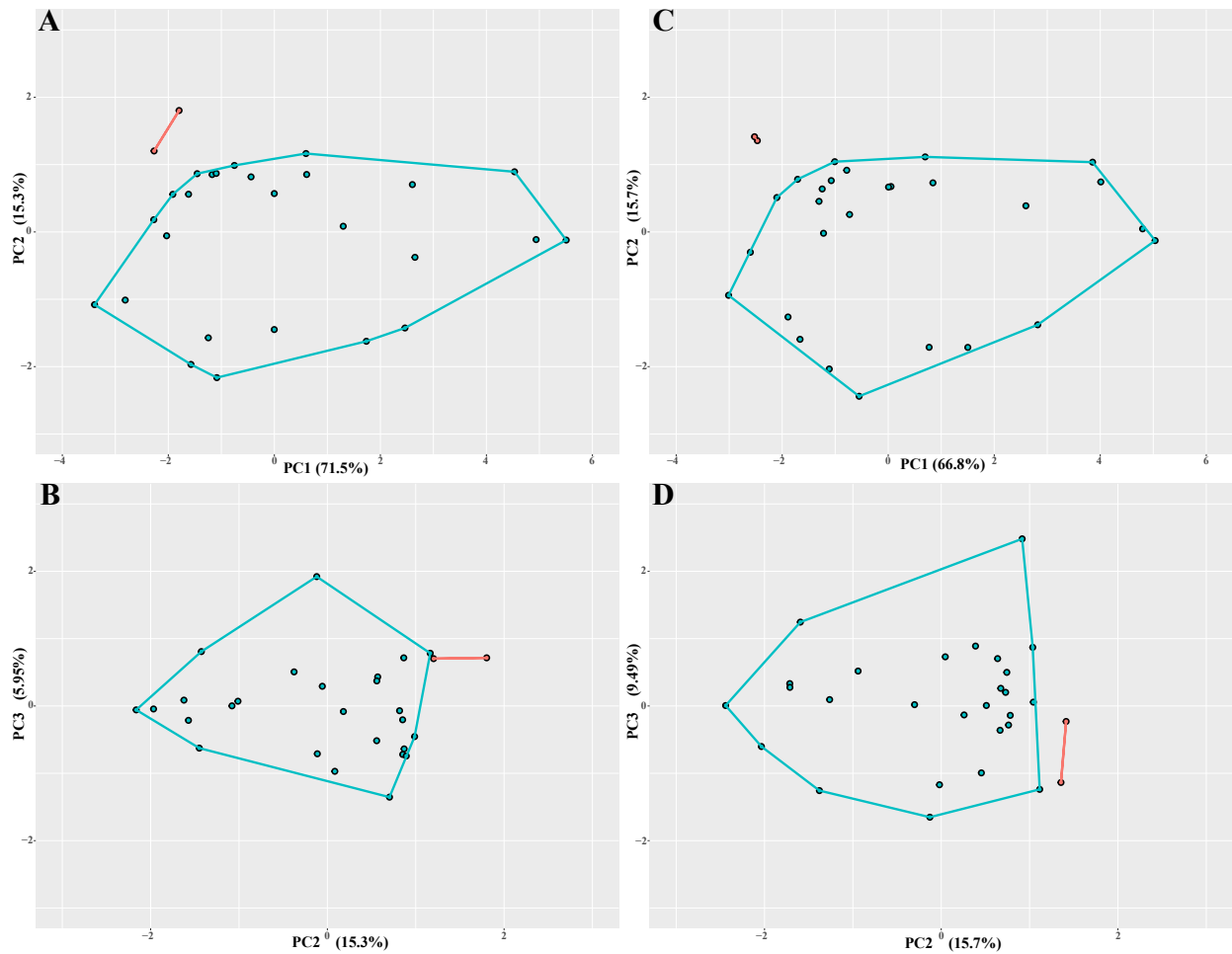


Figure 20. Principal components analysis of morphometric comparisons between clades in Locustellidae (A, B) males and (C, D) females. Each dot represents a single species and is color coded by clade (orange = Malagasy; blue = source); disparity of each group is represented as a minimal convex polygon of all species in that group. The centroid of each clade is statistically different for both sexes (MANOVA $p < 0.05^*$).

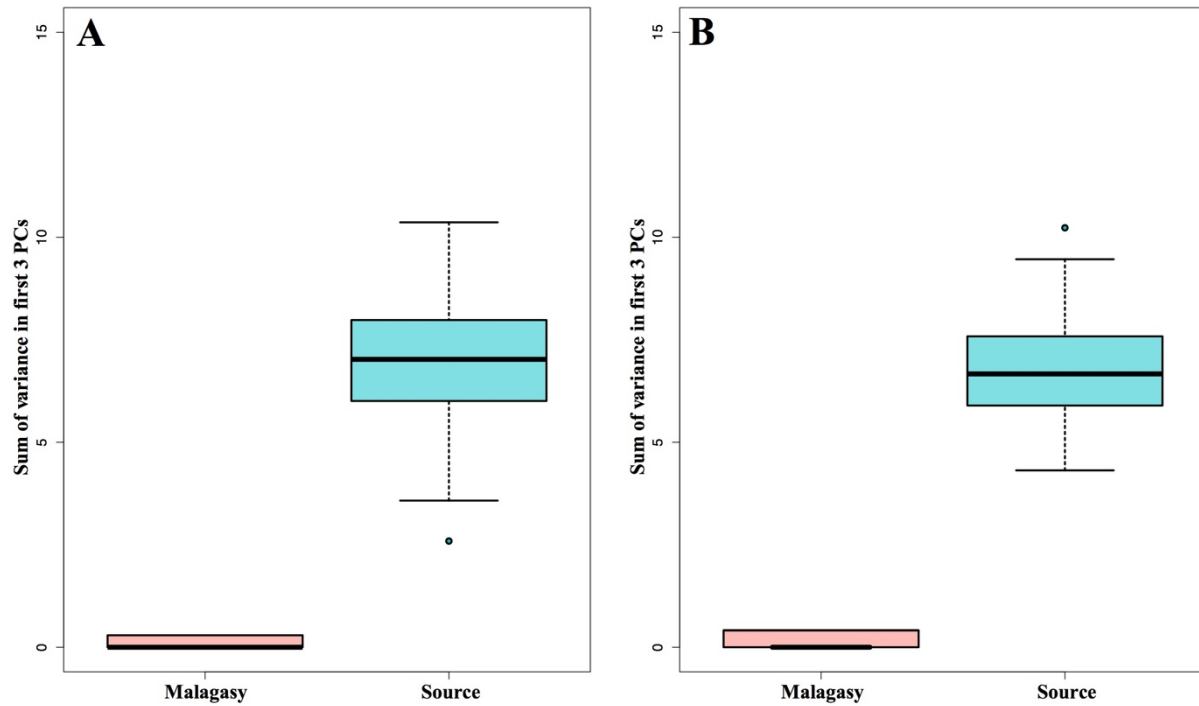


Figure 21. Locustellidae plot of disparity between clades for (A) males and (B) females. Source appears to occupy a greater area in morphological space than Malagasy, but I did not calculate a statistical value of disparity to confirm this because of low sample size in Malagasy clade.

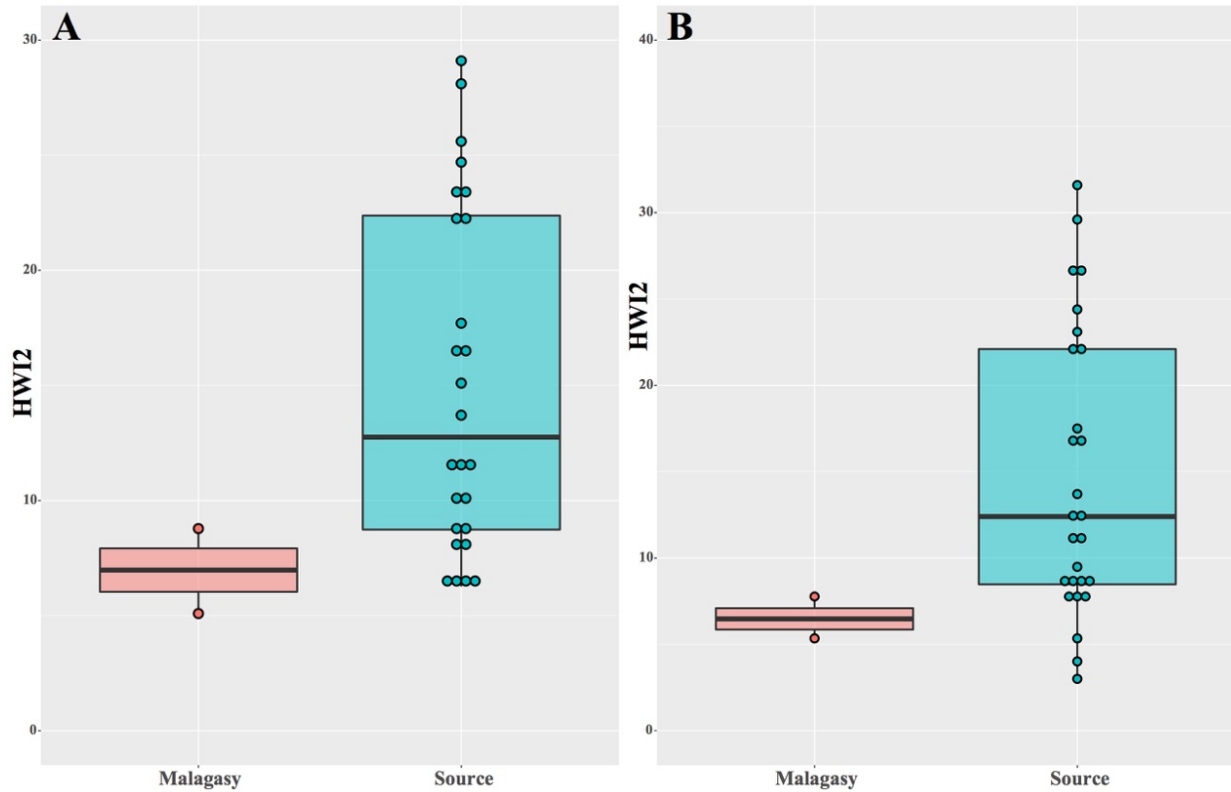


Figure 22. Boxplot of HWI2 between the Malagasy and source clades of Locustellidae in (A) males and (B) females. Each dot represents an individual species' HWI2 value. There are no significant differences in the means of HWI2 between Malagasy and source clade (ANOVA $p > 0.05$) in either sex.

Table 11. Summary statistics table of each morphological variable compared between Malagasy and source clade of Locustellidae. No significant differences between Malagasy and source male species were recovered. Wing chord length and tarsus length were significantly greater in female source species than Malagasy species. Significant differences between clades that were uncovered using an ANOVA are shown in bold and asterisk with an M and/or F indicating which sex the trait significantly differed in.

Trait	MALE				FEMALE			
	Malagasy (n=2)		Source (n=22)		Malagasy (n=2)		Source (n=23)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
BD	3.20	0.10	3.91	0.87	3.10	0.27	3.72	0.69
BW	2.64	0.36	3.27	0.77	2.51	0.24	3.21	0.67
BL	12.90	0.00	17.00	4.16	12.50	0.28	16.50	3.36
WL*^F	50.60	1.48	68.40	12.40	48.50	1.27	65.70	10.60
S1	47.00	0.07	57.90	10.30	45.20	0.35	55.70	9.03
Tar-L*^F	16.50	1.70	22.20	4.63	15.90	1.27	21.30	3.64
Tail-L	89.60	5.87	76.30	19.40	77.90	8.98	69.70	17.80
HWI2	6.98	2.67	15.10	7.44	6.47	1.74	14.70	8.27

***Foudia* clade (Ploceidae)**

There were significant differences between sexes for bill depth (ANOVA $p < 0.05$), bill width (ANOVA $p < 0.05$), wing chord length (ANOVA $p < 0.05$), secondary length (ANOVA $p < 0.01$), and tarsus length (ANOVA $p < 0.01$). For this reason, I analyzed males and females independently. The dataset for this family consisted of 13 species (two Malagasy and 11 source species; 31 specimens; Table 4). The first two principal components (Fig. 23) explained ~89% of the variation in males (Fig. 23; Table 12). The first three principal components explained ~93% of the variation in females (Fig. 23; Table 12). For both sexes, the two clades reside in a similar region of morphospace. The centroid of each clade did not statistically differ in either sex (MANOVA $p > 0.05$, Fig. 24). The disparity of the source clade species appears to be greater than Malagasy species, but I did not calculate a statistical value to confirm this because of low sample size (two or fewer species) in Malagasy clade (Fig. 25). The first principal component likely reflects body size. HWI2 weighted heavily in PC2 and PC3 of males but did not in the principal

component analysis for females (Table 12). There were no significant differences in the means of HWI2 between Malagasy and source clade in either sex (ANOVA $p > 0.05$, Fig. 26). No other morphological variables significantly differed between clades in either sex (Table 13).

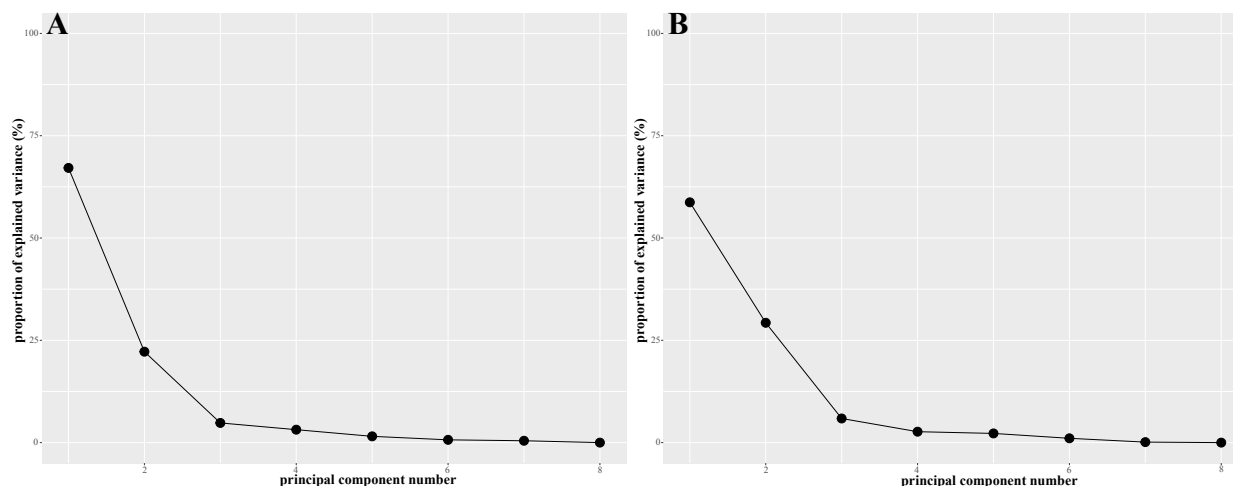


Figure 23. Scree plot of the proportion of explained variance for eight principal components in *Foudia* (A) males and (B) females. The first two and three principal components in males and females incorporated greater than 5% variance. Table 12 shows the loadings of these principal components.

Table 12. Summary of principal components and their loadings in *Foudia*. The cumulative proportion of the two principal components in males is 89.35% and three principal components in females is 93.91%.

Morphometrics	Males			Females		
	PC1	PC2	PC3	PC1	PC2	PC3
BD	0.323	0.426	-0.458	0.204	-0.548	-0.380
BW	0.267	0.544	-0.348	0.195	-0.586	0.038
BL	0.411	-0.008	0.134	0.400	-0.049	0.620
WL	0.406	≤0.001	0.446	0.443	-0.044	-0.229
S1	0.401	-0.219	0.162	0.433	0.149	-0.272
Tar-L	0.388	-0.112	0.041	0.408	0.081	0.471
Tail-L	0.405	-0.186	-0.011	0.405	0.134	-0.252
HWI2	-0.110	0.652	0.649	-0.206	-0.551	0.234
Prop. Of Variance	67.13%	22.22%	4.81%	58.73%	29.29%	5.89%

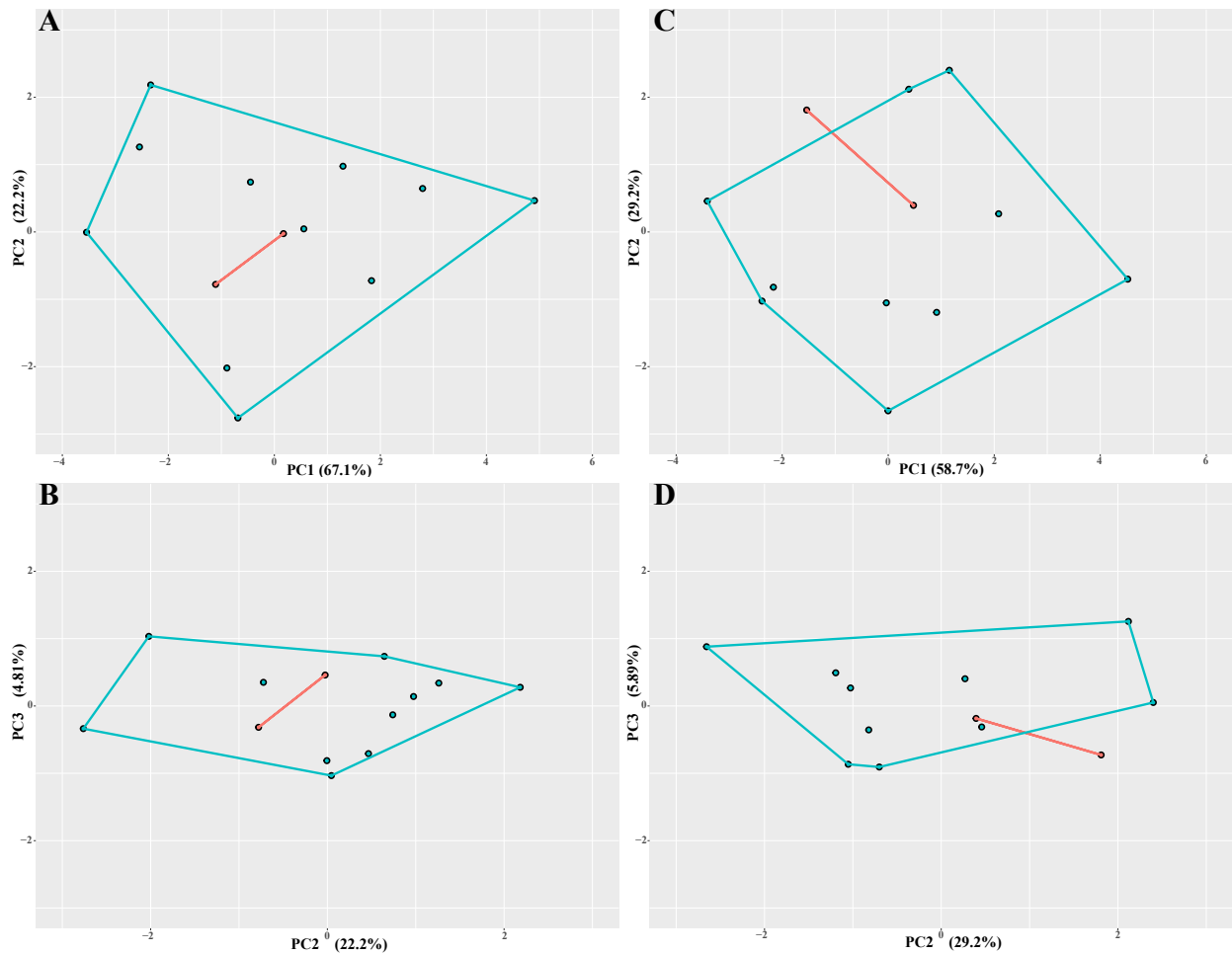


Figure 24. Principal components analysis of morphometric comparisons between clades in *Foudia* (A, B) males and (C, D) females. Each dot represents a single species and is colored by clade (orange = Malagasy; blue = source); disparity of each group is represented as a minimal convex polygon of all species in that group. The centroid of each clade is not statistically different (MANOVA $p > 0.05$) in either sex.

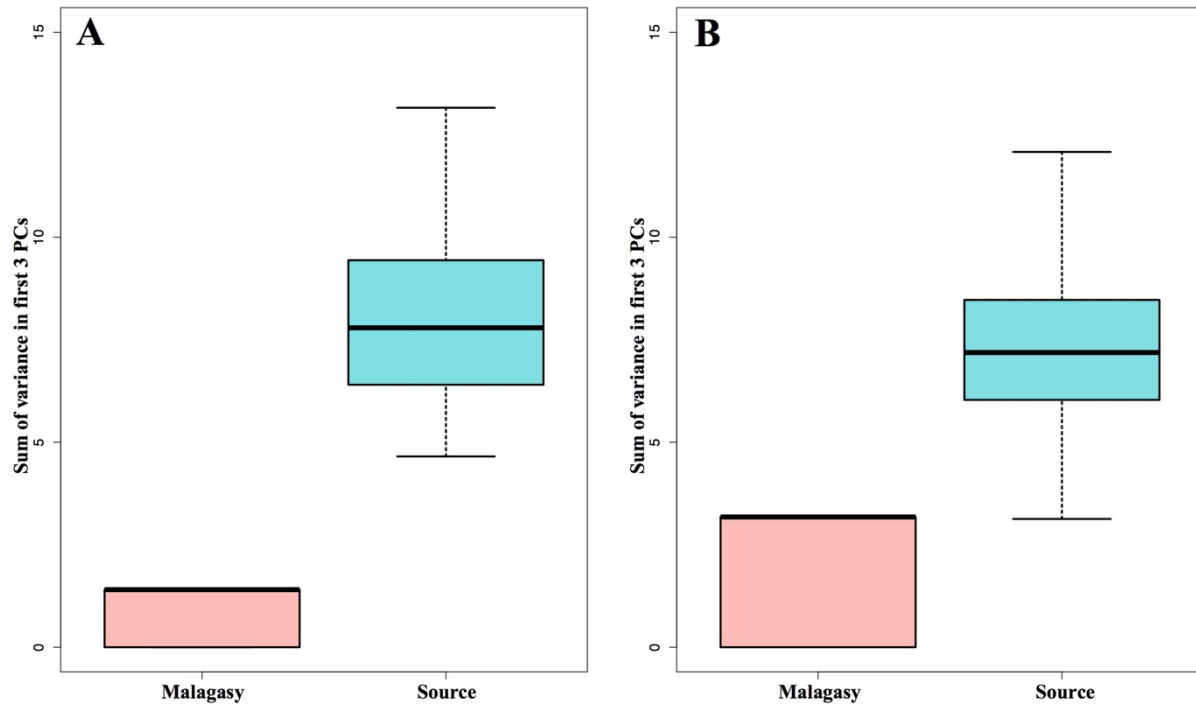


Figure 25. *Foudia* plot of disparity between clades for (A) males and (B) females. Source appears to occupy a greater area in morphological space than Malagasy, but I did not calculate a statistical value of disparity to confirm this because of low sample size in Malagasy clade.

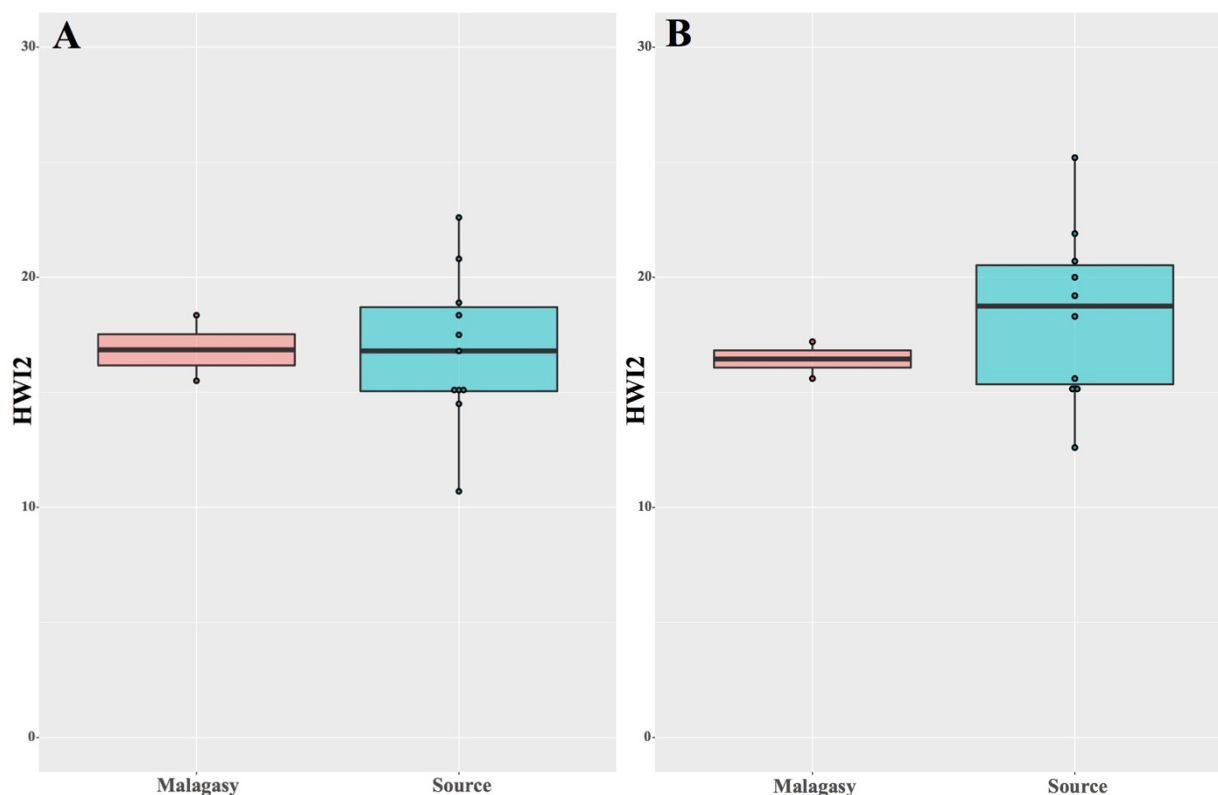


Figure 26. Boxplot of HWI2 between the Malagasy and source clades of *Foudia* in (A) males and (B) females. Each dot represents a mean value for individual species' HWI2. There are no significant differences in the means of HWI2 between Malagasy and source clade (ANOVA $p > 0.05$) in either sex.

Table 13. Summary statistics table of each morphological variable compared between Malagasy and source clade of *Foudia*. No significant differences between Malagasy species and source species were recovered using ANOVA.

Trait	MALE				FEMALE			
	Malagasy (n=2)		Source (n=11)		Malagasy (n=2)		Source (n=10)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
BD	8.38	0.41	8.88	1.44	7.76	0.72	8.34	1.04
BW	6.04	0.24	6.46	0.84	5.59	0.48	6.19	0.56
BL	15.30	0.84	17.20	3.10	14.80	2.12	16.20	2.09
WL	67.90	4.03	69.90	6.92	63.60	4.45	66.90	7.15
S1	56.40	2.05	58.20	6.52	53.00	3.04	54.70	7.47
Tar-L	17.60	1.13	17.30	2.35	16.00	0.77	16.60	1.66
Tail-L	51.60	1.70	48.10	9.34	50.70	1.27	45.10	7.62
HWI2	16.80	1.91	16.90	3.29	16.40	1.06	18.40	3.80

***Nelicurvius* clade (Ploceidae)**

There were significant differences between sexes for wing chord length (ANOVA $p < 0.01$), secondary length (ANOVA $p < 0.01$), tarsus length (ANOVA $p < 0.01$), and tail length (ANOVA $p < 0.05$). For this reason, I analyzed males and females independently. The dataset for this family consisted of 11 species (two Malagasy and nine source species; 33 specimens; Table 4). The principal component analysis resulted in eight axes of which, the first three explained more than 95% of the variation in males and females (Fig. 27; Table 14). There is a significant difference in the Malagasy and source occupancy of morphospace (Fig. 28). However, only in males did the centroids of each clade statistically differ (MANOVA $p < 0.001^{***}$, Fig. 28). Disparity of source appears to greater than Malagasy, but I did not calculate a statistical value to confirm this because of low sample size (two or fewer species) in Malagasy clade (Fig. 29). The first principal component likely reflects body size. HWI2 was weighted heavily in PC2 for males and in PC2 and PC4 in females (Table 14). There were no significant differences in the means of HWI2 between Malagasy and source clade in either sex (ANOVA $p > 0.05$, Fig. 30). No other morphological variables significantly differed between clades in either sex (Table 15).

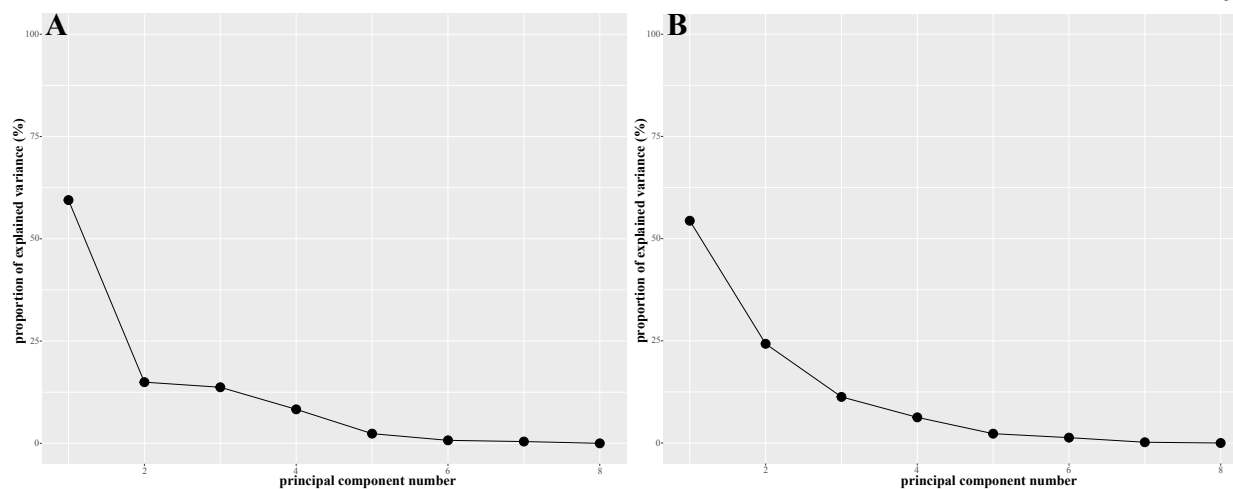


Figure 27. Scree plot of the proportion of explained variance for eight principal components in *Nelicurvius* (A) males and (B) females. The first four principal components incorporated greater than 5% variance. Table 14 shows the loadings of these four principal components in each sex.

Table 14. Summary of principal components and their loadings in *Nelicurvius*. The cumulative proportion of the first four principal components in males is 96.45% and 96.21% in females.

Morphometric	Males				Females			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
BD	-0.289	-0.574	0.159	-0.474	0.301	-0.453	-0.136	0.468
BW	-0.407	-0.212	0.004	-0.368	0.408	-0.297	0.178	-0.013
BL	-0.360	0.397	-0.235	-0.411	0.380	0.185	0.515	0.292
WL	-0.400	0.414	0.113	0.070	0.396	0.390	-0.073	0.158
S1	-0.416	0.255	-0.249	0.143	0.459	0.183	0.067	-0.047
Tar-L	-0.351	-0.305	0.314	0.461	0.290	-0.252	-0.709	0.030
Tail-L	-0.401	-0.100	0.061	0.440	0.341	0.337	-0.236	-0.596
HWI2	0.045	0.354	0.860	-0.191	-0.167	0.555	-0.338	0.557
Prop. Of Variance	59.47%	14.96%	13.71%	8.31%	54.38%	24.27%	11.28%	6.28%

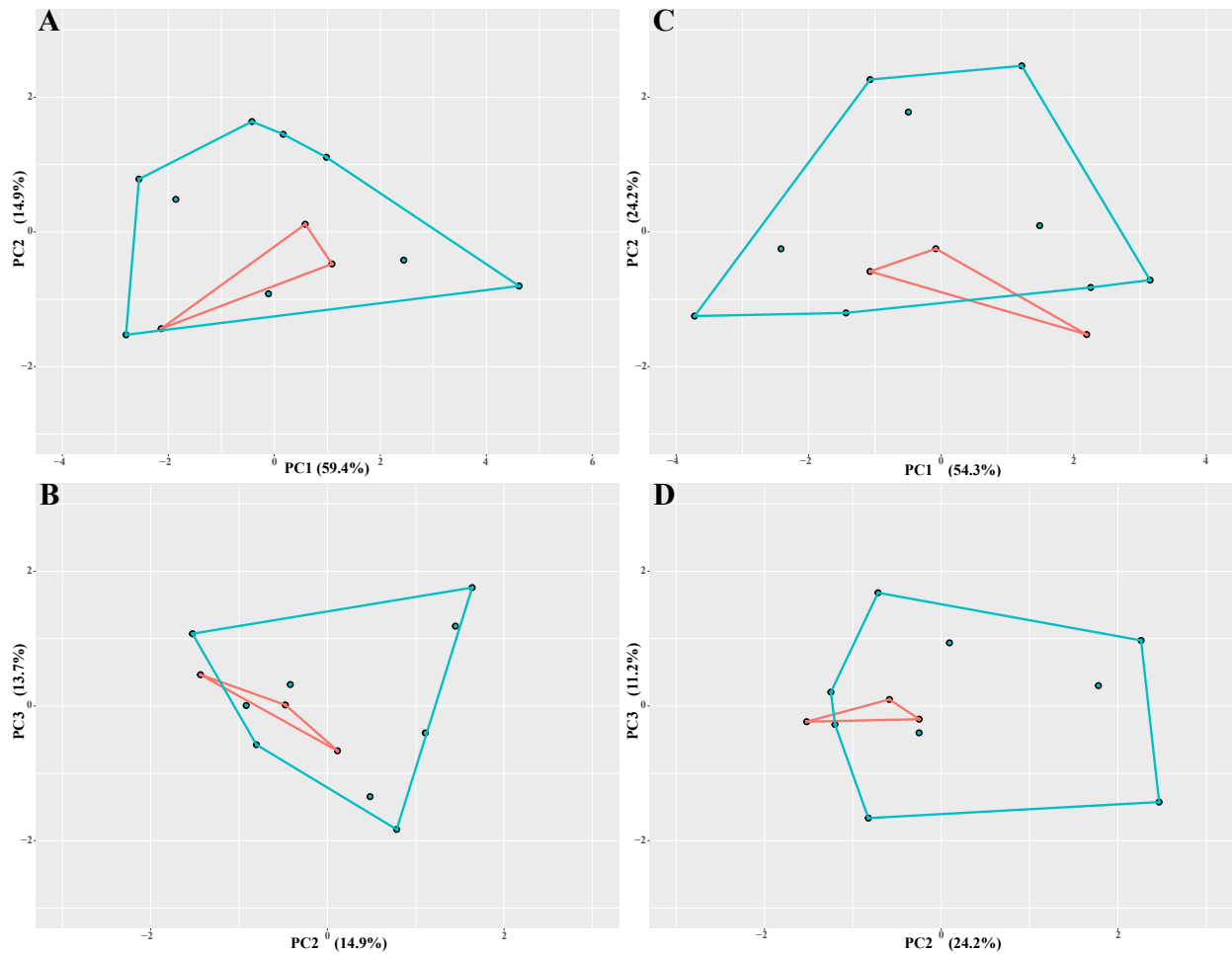


Figure 28. Principal components analysis of morphometric comparisons between clades in *Nelicurvius* (A, B) males and (C, D) females. Each dot represents a single species and is colored by clade (orange = Malagasy; blue = source); disparity of each group is represented as a minimal convex polygon of all species in that group. The centroid of each clade is statistically different in males, but not in females (MANOVA $p < 0.001$ ***, $p > 0.05$).

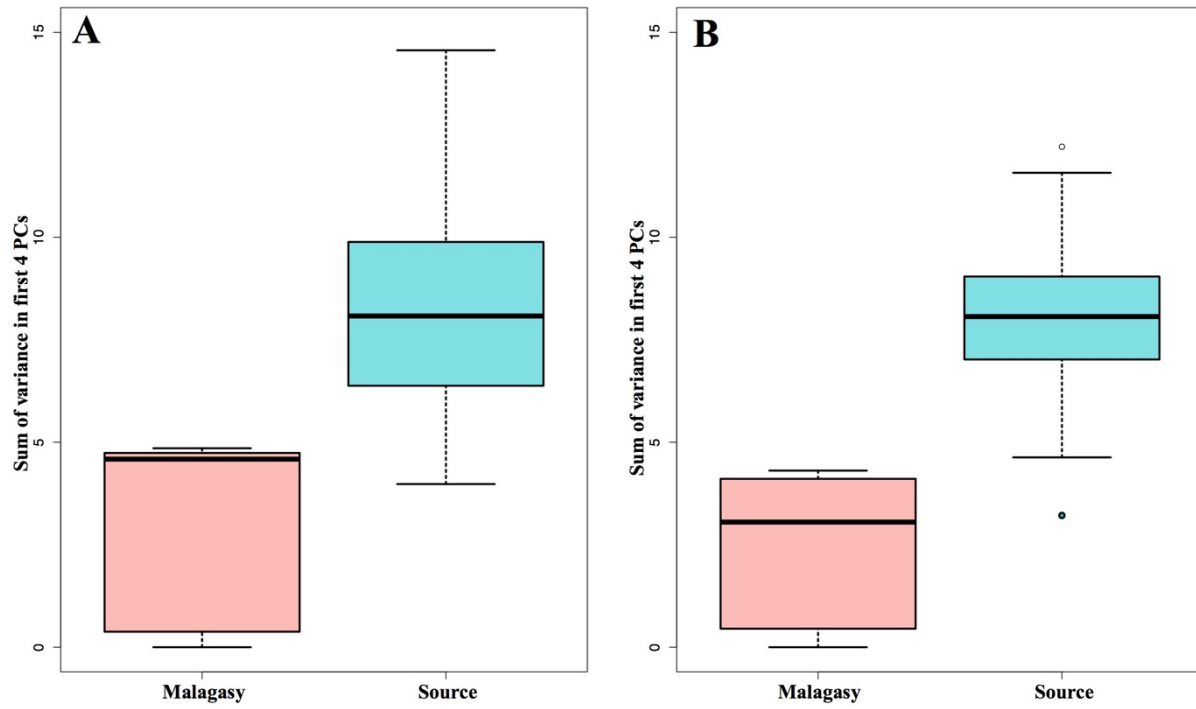


Figure 29. *Nelicurvius* plot of disparity between clades for (A) males and (B) females. Source appears to occupy a greater area in morphological space than Malagasy, but I did not calculate a statistical value of disparity to confirm this because of low sample size in Malagasy clade.

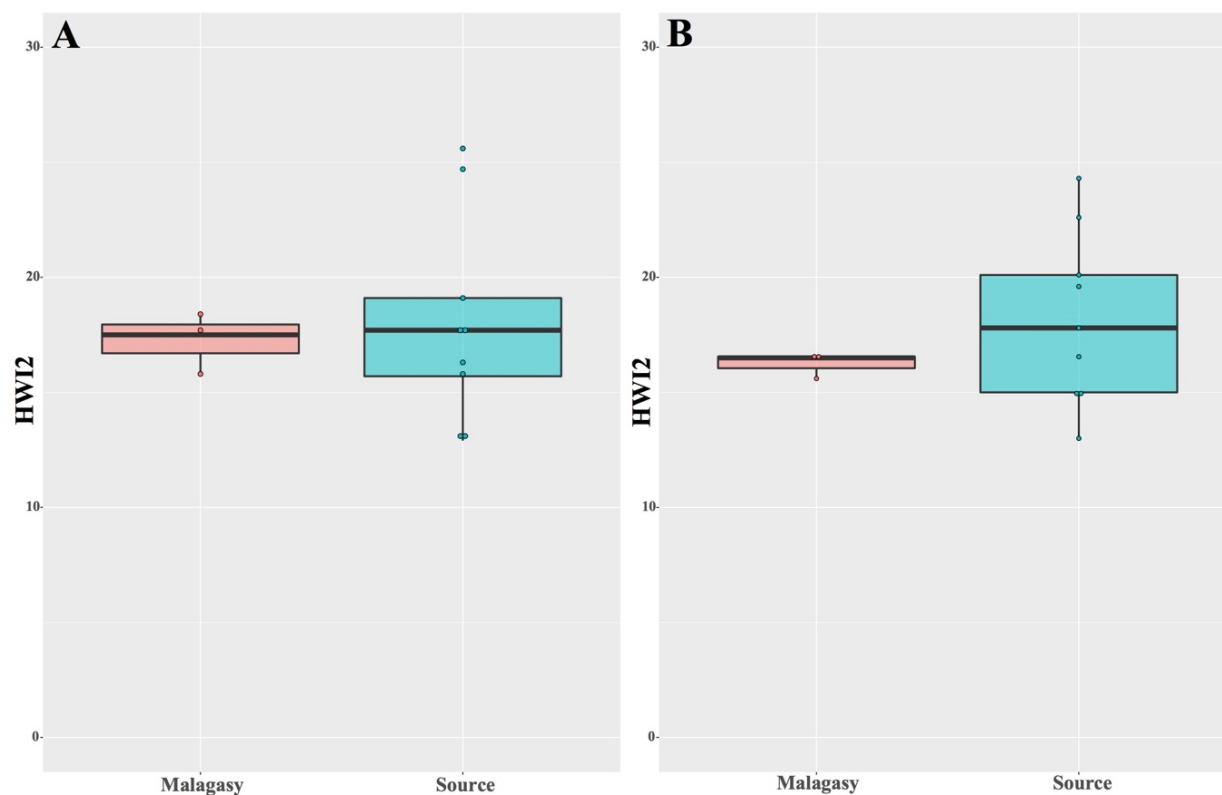


Figure 30. Boxplot of HWI2 between the Malagasy and source clades of *Nelicurvius* (A) males and (B) females. Each dot represents a mean value of individual species' HWI2. There are no significant differences in the means of HWI2 between the Malagasy and source clade (ANOVA $p > 0.05$) in either sex.

Table 15. Summary statistics table of each morphological variable compared between Malagasy and source clade of *Nelicurvius*. No significant differences between Malagasy species and source species were recovered.

Trait	MALE				FEMALE			
	Malagasy (n=2)		Source (n=9)		Malagasy (n=2)		Source (n=9)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
BD	8.77	1.36	7.52	0.78	8.49	1.29	7.43	0.71
BW	6.26	0.77	6.17	0.46	6.13	0.68	6.08	0.61
BL	17.90	1.56	17.50	2.98	17.00	1.60	17.30	3.17
WL	77.40	3.56	79.50	10.90	73.40	4.25	74.40	10.20
S1	64.10	2.46	65.00	9.21	61.50	3.51	60.70	8.29
Tar-L	17.70	0.85	17.90	2.18	17.00	1.07	16.40	1.98
Tail-L	52.70	3.55	54.60	8.03	49.90	2.37	51.40	8.41
HWI2	17.30	1.27	18.10	4.47	16.20	0.55	18.20	3.76

***Cinnyris notata* clade (Nectariniidae)**

There were significant differences between sexes for HWI2 (ANOVA $p < 0.001$), wing chord length (ANOVA $p < 0.001$), secondary length (ANOVA $p < 0.001$), and tail length (ANOVA $p < 0.001$). For this reason, I analyzed males and females independently. The dataset for this family consisted of four species (one Malagasy and three source; 13 specimens; Table 4). The principal component analysis resulted in five axes of which the first two and three explained more than 97% of the variation in males and females respectively (Fig. 31; Table 16). No MANOVA or test of disparity was calculated for either sex due to the small sample size of the clades. Based on visual interpretations of PCA polygons, there does not appear to be a difference in morphology, but I did not calculate statistical values to confirm this (Fig. 32). The first principal component likely reflects body size. HWI2 was weighted heavily in PC2 for females, but not for any principal components in males (Table 16). There are no significant differences in the means of HWI2 between Malagasy and source clade in either sex (ANOVA $p > 0.05$, Fig. 33). No other morphological variables significantly differed between clades in either sex (Table 17).

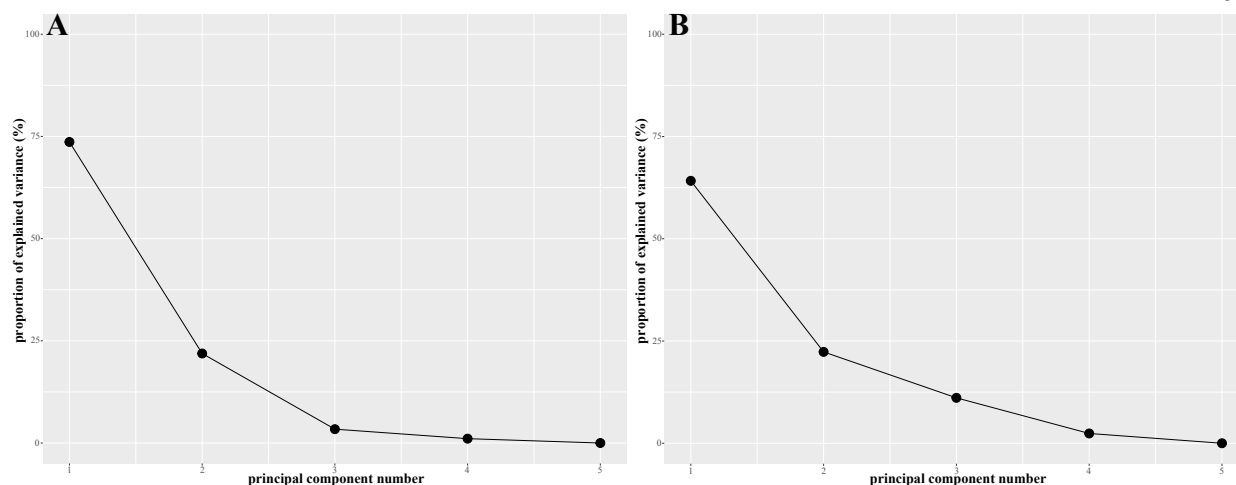


Figure 31. Scree plot of the proportion of explained variance for five principal components in *Cinnyris notata* (A) males and (B) females. The first two principal components for males and three principal components for females incorporated greater than 5% variance. Table 16 shows the loadings of their principal components.

Table 16. Summary of principal components and their loadings in *Cinnyris notata*. The cumulative proportion of the two principal components in males is 95.54% and three principal components in females is 97.61%.

Morphometrics	Males			Females		
	PC1	PC2	PC3	PC1	PC2	PC3
BD	-0.381	-0.130	-0.599	-0.344	0.148	-0.628
BW	-0.369	-0.241	0.572	-0.419	-0.023	0.303
BL	-0.390	-0.181	0.355	-0.435	0.063	0.004
WL	-0.405	-0.068	-0.210	-0.402	0.298	0.029
S1	-0.397	0.171	-0.136	-0.430	0.080	0.100
Tar-L	-0.400	0.118	0.179	-0.369	-0.254	0.326
Tail-L	-0.284	0.537	-0.152	-0.169	-0.551	-0.588
HWI2	-0.041	-0.744	-0.261	0.050	0.713	-0.221
Prop. Of Variance	73.64%	21.90%	3.39%	64.17%	22.34%	11.10%

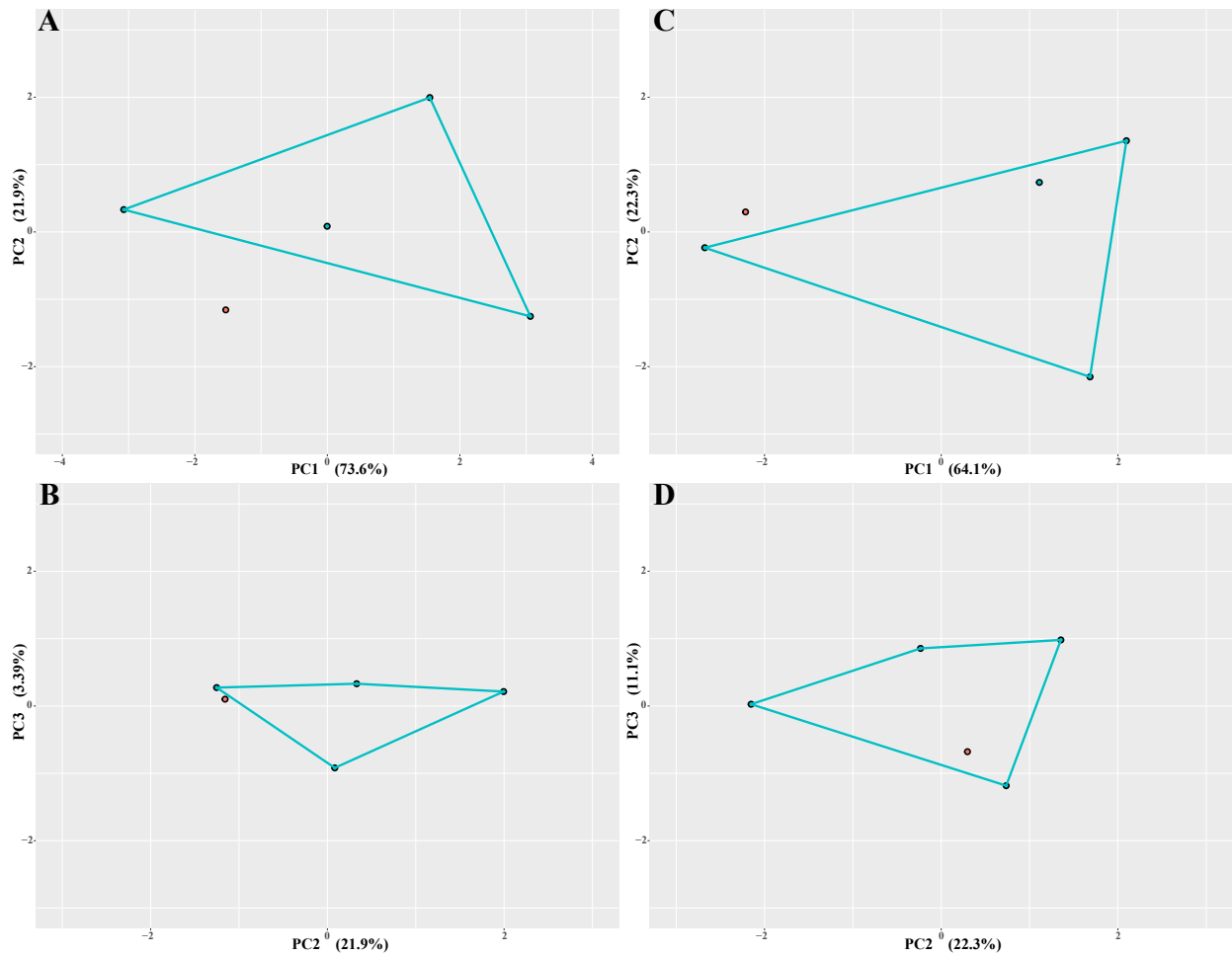


Figure 32. Principal components analysis of morphometric comparisons between clades in *Cinnyris notata* (A, B) males and (C, D) females. Each dot represents a single species and is colored by clade (orange = Malagasy; blue = source); disparity of each group is represented as a minimal convex polygon of all species in that group. No MANOVA test was calculated due to the small sample size of the Malagasy clade for both sexes.

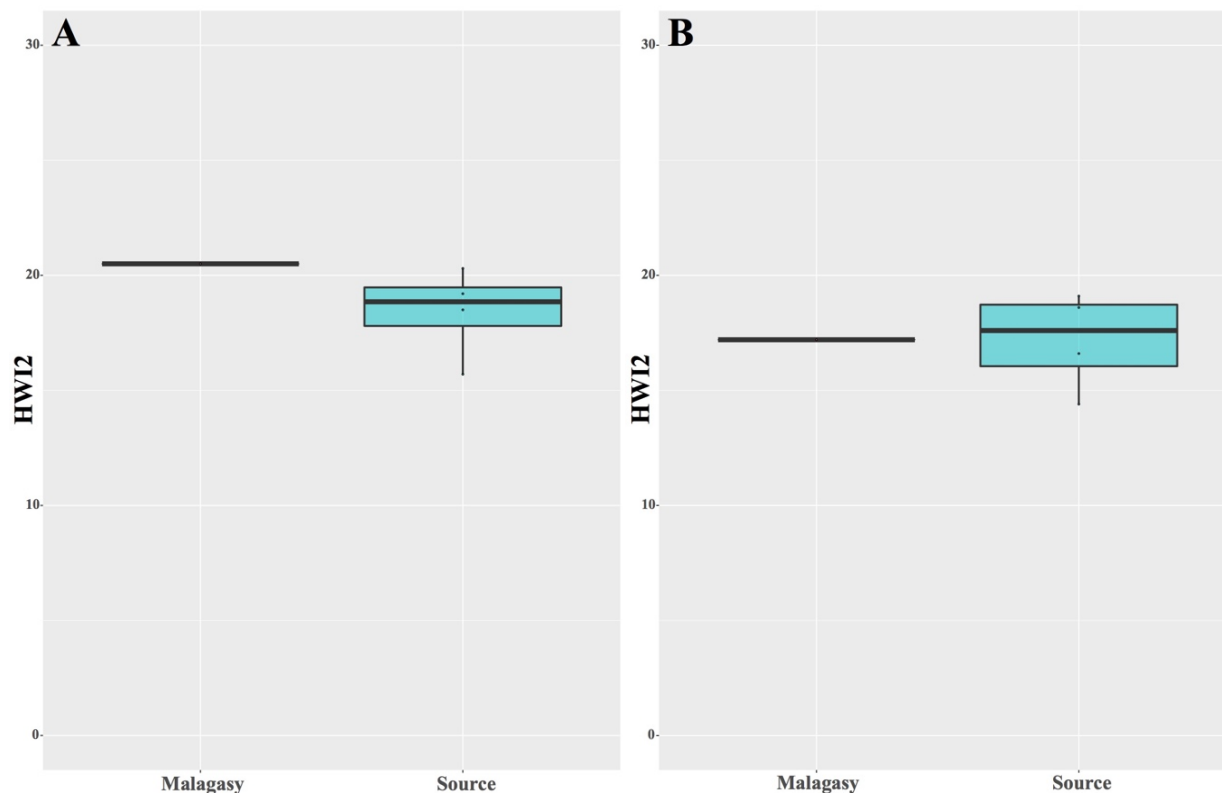


Figure 33. Boxplot of HWI2 between the Malagasy and source clades of *Cinnyris notata* (A) males and (B) females. Each dot represents an individual species' HWI2 value. There are no significant differences in the means of HWI2 between Malagasy and source clade (ANOVA $p > 0.05$) in either sex.

Table 17. Summary statistics table of each morphological variable compared between Malagasy and source clade of *Cinnyris notata*. No significant differences between Malagasy species and source species were recovered.

Trait	MALE				FEMALE			
	Malagasy (n=1)		Source (n=3)		Malagasy (n=1)		Source (n=3)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
BD	3.86	NA	3.46	0.38	3.99	NA	3.32	0.34
BW	4.41	NA	3.92	0.38	4.22	NA	3.70	0.48
BL	31.80	NA	24.00	6.09	30.20	NA	23.50	6.87
WL	69.00	NA	65.80	5.17	64.40	NA	58.90	3.74
S1	54.90	NA	53.70	4.29	53.40	NA	48.70	3.00
Tar-L	15.30	NA	14.80	1.43	14.60	NA	14.40	1.71
Tail-L	52.20	NA	52.60	7.26	47.10	NA	44.40	4.17
HWI2	20.50	NA	18.40	1.96	17.20	NA	17.20	2.14

***Cinnyris sovimanga* clade (Nectariniidae)**

There were significant differences between sexes for bill depth (ANOVA $p < 0.001$), bill length (ANOVA $p < 0.001$), wing chord length (ANOVA $p < 0.001$), secondary length (ANOVA $p < 0.001$), tarsus length (ANOVA $p < 0.05$), and tail length (ANOVA $p < 0.001$). For this reason, I analyzed males and females independently. The dataset for this family consisted of eight species (one Malagasy and seven source; 28 specimens; Table 4). Of the resulting eight principal components, the first five and three principal components explained more than 90% of the variation in males and females (Fig. 34; Table 18). No MANOVA (except for males) or test of disparity was calculated for either sex due to the small sample size of the clades. The centroid of each clade did not statistically differ (MANOVA $p > 0.05$) in males (Fig. 35). Based on visual interpretations of PCA polygons, females appear to not differ in centroids between clades, but I did not calculate a statistical value to confirm this. Based on visual interpretation, disparity of the source clade appears to be greater than Malagasy, but I did not calculate a statistical value of disparity to confirm this due to small sample size in the Malagasy clade (Fig. 35). The first principal component likely reflects body size. HWI2 was weighted heavily in PC3 for males but not for any principal components of females (Table 18). There were no significant differences in the means of HWI2 between Malagasy and source clade in either sex (ANOVA $p > 0.05$, Fig. 36). No other morphological variables significantly differed between clades in either sex (Table 19).

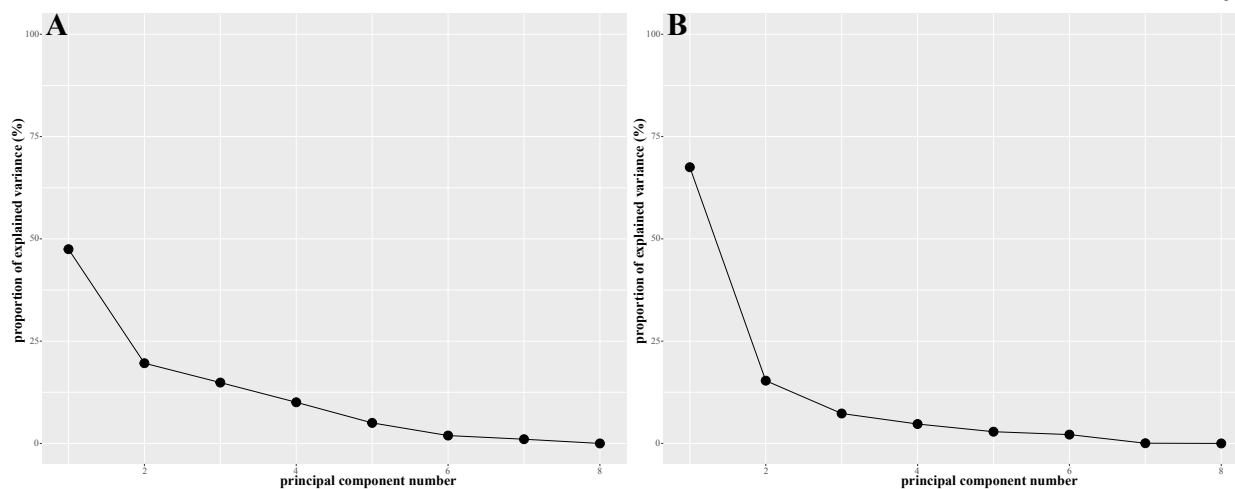


Figure 34. Scree plot of the proportion of explained variance for eight principal components in *Cinnnyris sovimanga* (A) males and (B) females. The first five principal components of males and three of females incorporated greater than 5% variance. Table 18 shows the loadings of these principal components.

Table 18. Summary of principal components and their loadings in *Cinnnyris sovimanga*. The cumulative proportion of the five principal components in males is 97.04% and three principal components is 90.16% in females.

Morphometric	Males					Females		
	PC1	PC2	PC3	PC4	PC5	PC1	PC2	PC3
BD	-0.237	0.413	-0.532	0.207	-0.561	-0.294	0.183	0.898
BW	-0.319	0.490	0.262	-0.120	0.470	-0.337	-0.458	-0.129
BL	-0.375	0.369	-0.162	-0.426	-0.033	-0.352	-0.224	-0.136
WL	-0.479	-0.074	0.263	0.133	0.002	-0.415	-0.153	-0.112
S1	-0.491	-0.188	0.013	0.028	0.139	-0.418	0.131	-0.187
Tar-L	-0.290	-0.435	0.265	-0.459	-0.511	-0.386	0.008	0.113
Tail-L	-0.362	-0.265	-0.084	0.658	0.076	-0.395	0.172	-0.124
HWI2	0.110	0.387	0.688	0.311	-0.419	0.147	-0.796	0.285
Prop. Of Variance	47.47%	19.61%	14.88%	10.06%	5.02%	67.51%	15.34%	7.31%

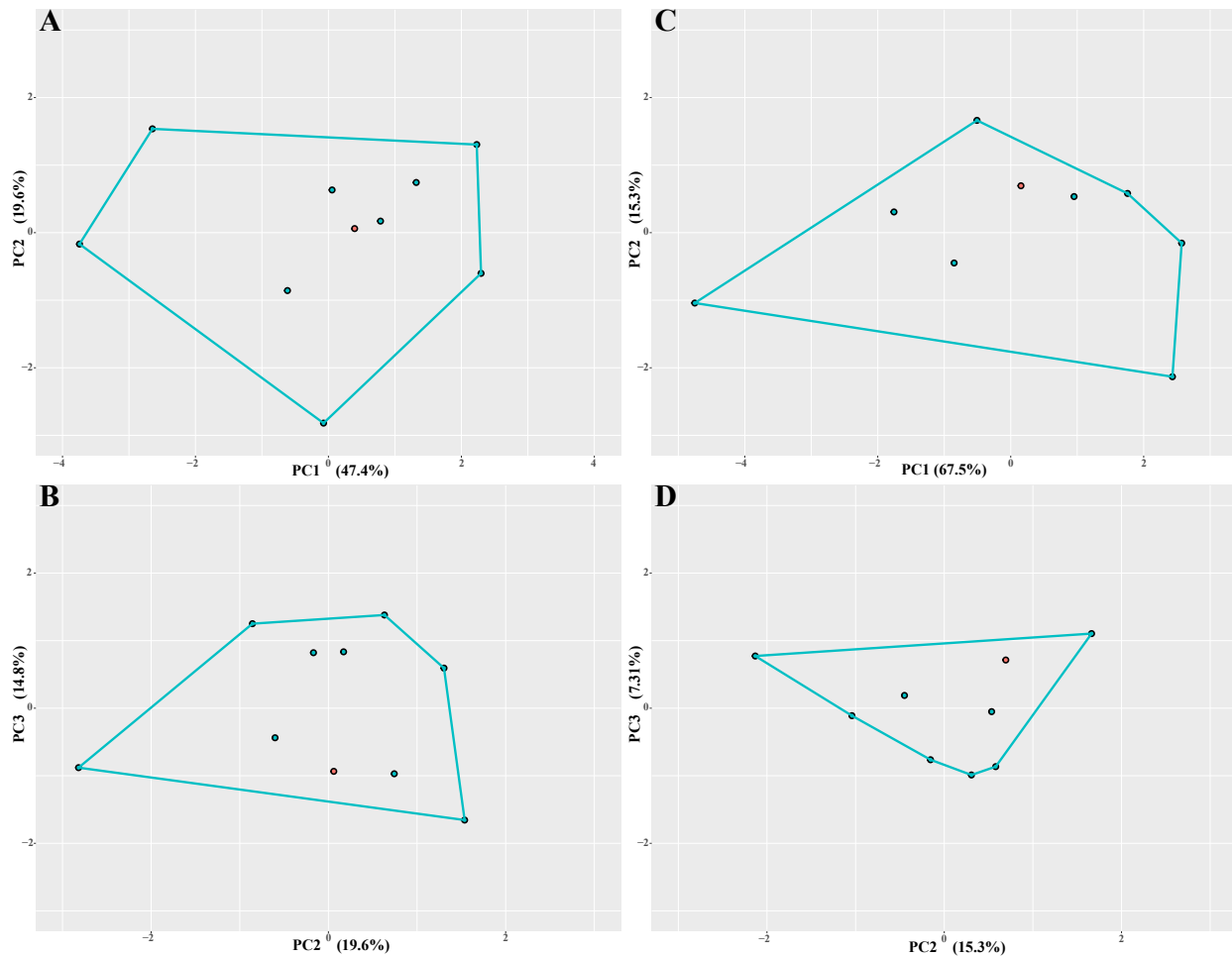


Figure 35. Principal components analysis of morphometric comparisons between clades in *Cinnyris sovimanga* (A, B) males and (C, D) females. Each dot represents a single species and is colored by clade (orange = Malagasy; blue = source); disparity of each group is represented as a minimal convex polygon of all species in that group. The centroid of each clade is not statistically different (MANOVA $p > 0.05$) in males (no MANOVA is reported for females due to sample size).

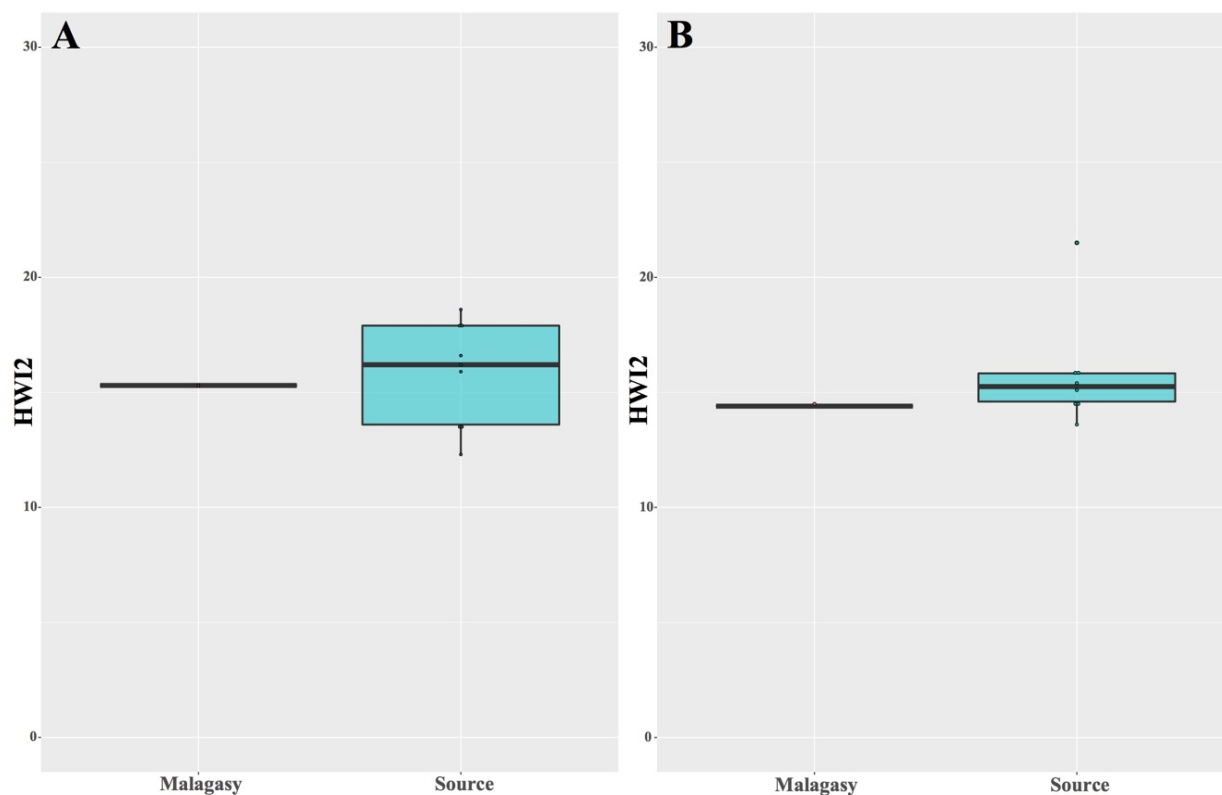


Figure 36. Boxplot of HWI2 between the Malagasy and source clades of *Cinnyris sovimanga* (A) males and (B) females. Each dot represents an individual species' HWI2 value. There are no significant differences in the means of HWI2 between the Malagasy and source clade (ANOVA $p > 0.05$) in either sex.

Table 19. Summary statistics table of each morphological variable compared between Malagasy and source clade of *Cinnyris sovimanga*. No significant differences between Malagasy species and source species were recovered.

Trait	MALE				FEMALE			
	Malagasy (n=1)		Source (n=7)		Malagasy (n=1)		Source (n=6)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
BD	3.26	NA	3.10	0.23	3.13	NA	2.88	0.23
BW	3.32	NA	3.51	0.21	3.26	NA	3.40	0.34
BL	21.30	NA	21.10	2.08	20.30	NA	19.40	1.75
WL	53.80	NA	55.10	4.10	49.00	NA	50.70	3.76
S1	45.60	NA	46.40	3.68	41.90	NA	42.70	3.60
Tar-L	13.70	NA	14.10	0.89	13.20	NA	13.80	0.87
Tail-L	43.10	NA	42.70	5.18	37.00	NA	37.50	4.60
HWI2	15.30	NA	15.80	2.24	14.40	NA	15.80	2.42

Pycnonotidae

There were no significant differences between sexes for any of the morphological variables. For this reason, I analyzed males and females together. The dataset for this family consisted of 10 species (one Malagasy and nine source; 25 specimens; Table 4). The first three principal components explained ~92% of the variation (Fig. 37; Table 20). The centroids of the two clades do not statistically differ (MANOVA $p > 0.05$, Fig. 38) indicating no substantial differences in morphology. Disparity of source appears to be greater than Malagasy, but I did not calculate a statistical value of disparity to confirm this because of low sample size (two or fewer species) in the Malagasy clade (Fig. 38). The first principal component likely reflects body size. HWI2 did not weight heavily in this principal component analysis (Table 20). There were no significant differences in the means of HWI2 between Malagasy and source clade (ANOVA $p > 0.05$, Fig. 39). No other morphological variables significantly differed between clades (Table 21).

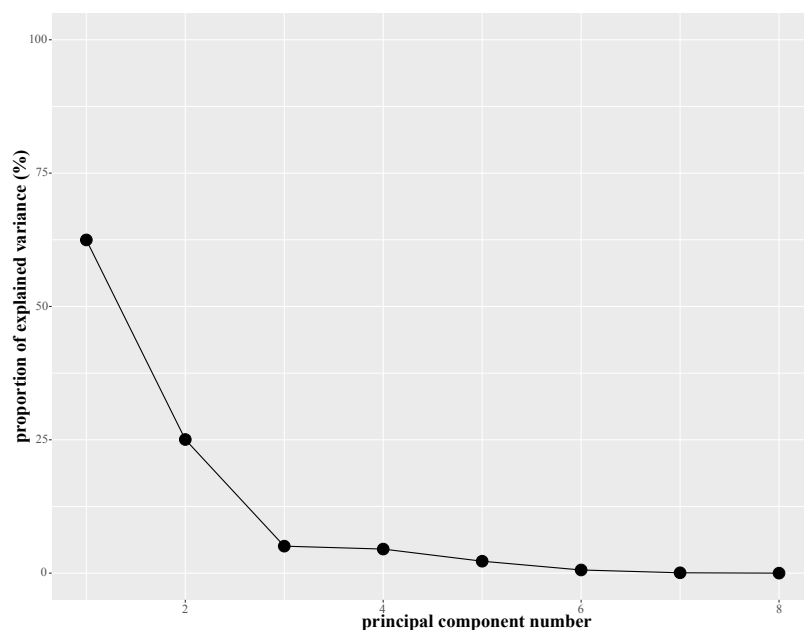


Figure 37. Scree plot of the proportion of explained variance for eight principal components in Pycnonotidae. The first three principal components incorporated greater than 5% variance. Table 20 shows the loadings of these three principal components.

Table 20. Summary of principal components and their loadings in Pycnonotidae. The cumulative proportion of the three principal components is 92.58%.

Morphometric	PC1	PC2	PC3
BD	0.342	0.385	0.229
BW	0.328	0.417	0.117
BL	0.433	0.028	0.196
WL	0.372	-0.366	0.242
S1	0.417	-0.132	0.272
Tar-L	0.368	0.108	-0.828
Tail-L	0.371	-0.323	-0.274
HWI2	0.014	-0.639	0.025
Prop. Of Variance	62.47%	25.05%	5.06%

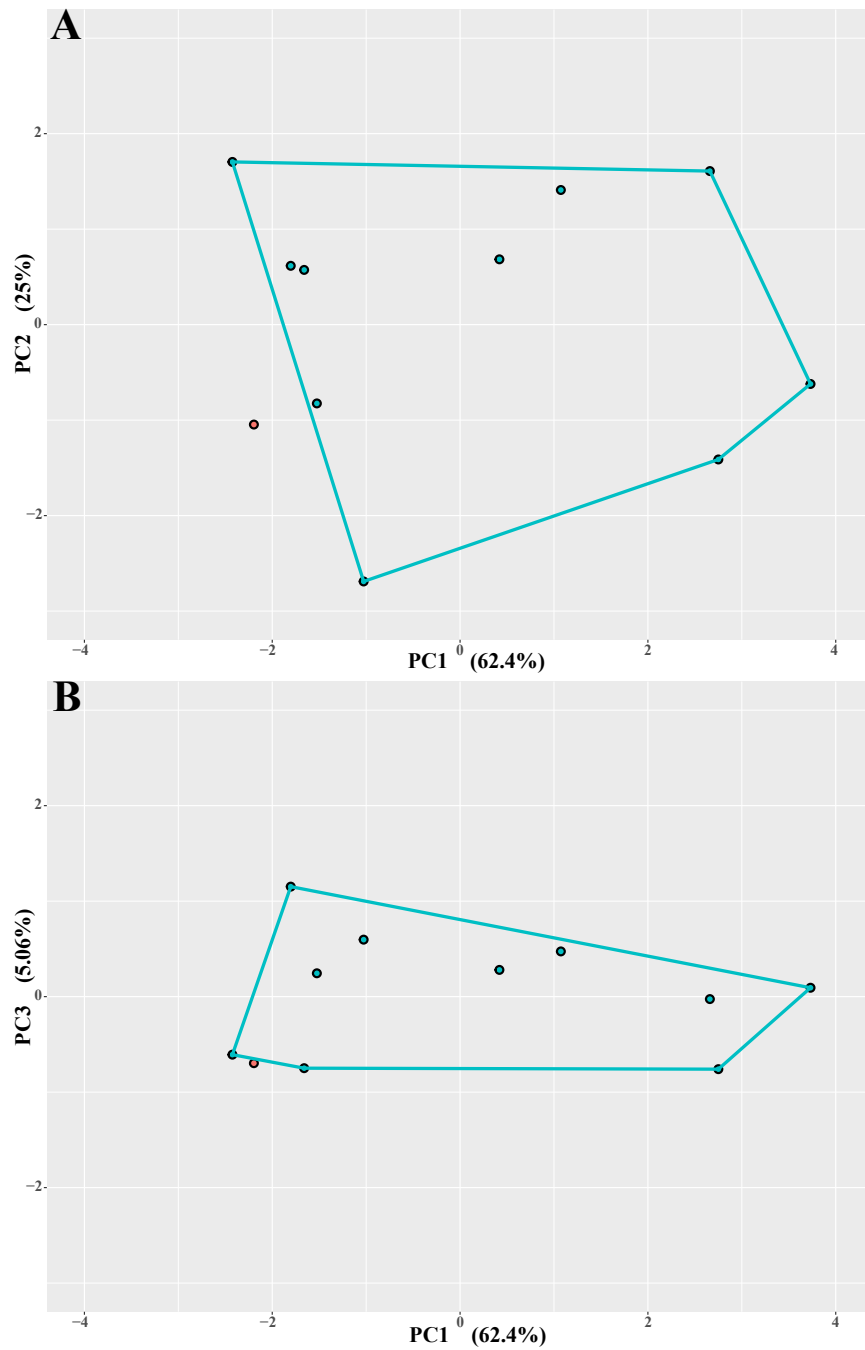


Figure 38. Principal components analysis of morphometric comparisons between clades in Pycnonotidae. Each dot represents a single species and is color coded by clade (orange = Malagasy; blue = source); disparity of each group is represented as a minimal convex polygon of all species in that group. The centroid of each clade is not statistically different (MANOVA $p > 0.05$).

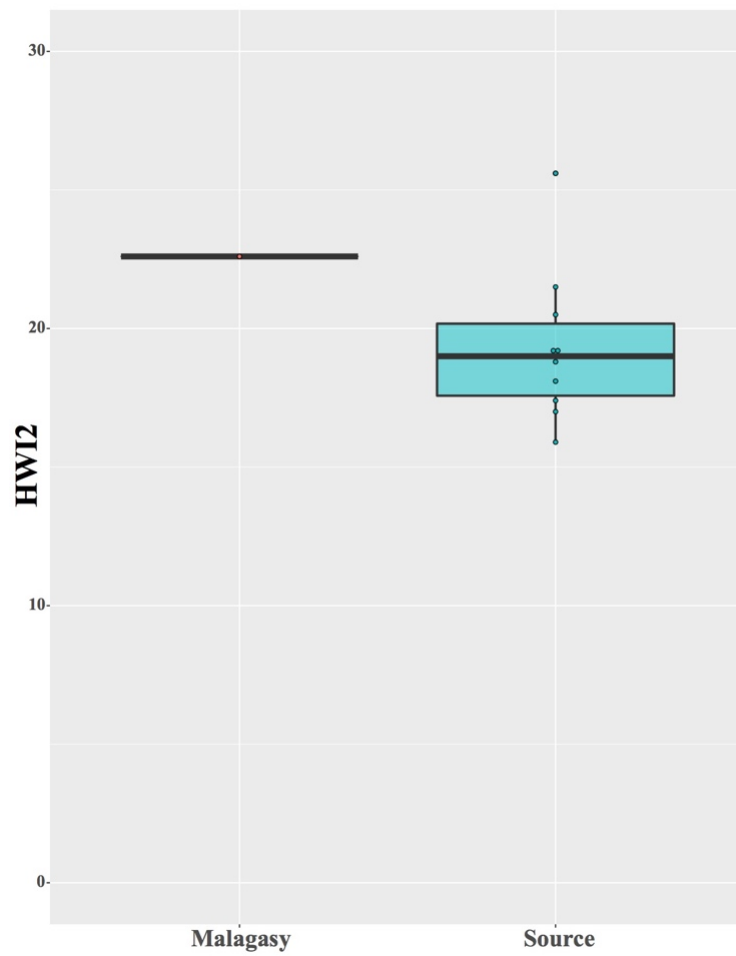


Figure 39. Boxplot of HWI2 between the Malagasy and source clades of Pycnonotidae. Each dot represents an individual species' HWI2 value. There are no significant differences between the means of HWI2 between Malagasy and source clade (ANOVA $p > 0.05$).

Table 21. Summary statistics table of each morphological variable compared between Malagasy and source clade of Pycnonotidae. No significant differences between Malagasy and source species were recovered.

Trait	Malagasy (n=1)		Source (n=9)	
	Mean	SD	Mean	SD
BD	5.94	NA	6.85	0.86
BW	5.01	NA	5.62	0.45
BL	24.70	NA	27.20	1.64
WL	105.00	NA	110.00	10.00
S1	81.00	NA	88.80	6.75
Tar-L	16.80	NA	17.00	1.72
Tail-L	95.90	NA	103.00	9.27
HWI2	22.60	NA	19.30	2.75

Monarchidae

There were significant differences between sexes for wing chord length (ANOVA $p < 0.01$), secondary length (ANOVA $p < 0.001$), and tail length (ANOVA $p < 0.001$). For this reason, I analyzed males and females independently. The dataset for this family consisted of nine species (one Malagasy and eight source; 38 specimens; Table 4). The first three and four principal components explained more than 93% of the variation in males and females respectively (Fig. 40; Table 22). For both sexes, there is a significant difference in the Malagasy and source occupancy of morphospace (Fig. 41). The centroids of the two clades do not statistically differ (MANOVA $p > 0.05$, Fig. 41) indicating no substantial differences in morphology for either sex. Disparity of the source clade appears to be greater than Malagasy, but I did not calculate a statistical value to confirm this because of low sample size (two or fewer species) in Malagasy clade (Fig. 42). The first principal component likely reflects body size. HWI2 was weighted heavily in PC3 for males and in PC2 and PC4 for females (Table 22). There were no significant differences in the means of HWI2 between Malagasy and source clade

(ANOVA $p > 0.05$, Fig. 43) in either sex. Bill depth, width, and length were significantly greater in source than Malagasy (ANOVA $p < 0.05^*$) in both sexes (Table 23).

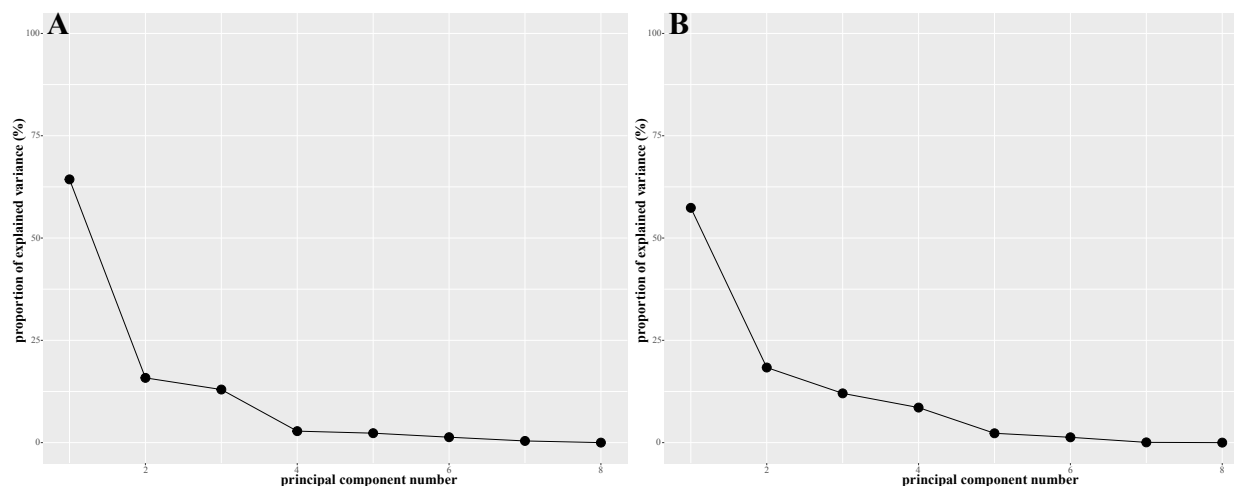


Figure 40. Scree plot of the proportion of explained variance for eight principal components in Monarchidae (A) males and (B) females. The first three and four principal components in males and females incorporated greater than 5% variance. Table 22 shows the loadings of these principal components.

Table 22. Summary of principal components and their loadings in Monarchidae. The cumulative proportion of the three principal components in males is 93.15% and four principal components in females is 96.33%.

Morphometrics	Males			Females			
	PC1	PC2	PC3	PC1	PC2	PC3	PC4
BD	0.345	-0.321	-0.351	0.372	-0.143	0.560	0.153
BW	0.368	0.235	-0.339	0.418	-0.304	0.128	0.020
BL	0.383	0.269	-0.345	0.417	-0.190	0.162	0.083
WL	0.429	-0.002	0.163	0.408	0.361	-0.108	0.122
S1	0.422	0.109	-0.040	0.430	-0.071	-0.135	-0.290
Tar-L	0.075	0.780	0.392	0.141	-0.448	-0.681	0.489
Tail-L	0.371	-0.286	0.308	0.326	0.268	-0.383	-0.585
HWI2	0.300	-0.254	0.603	0.180	0.664	-0.034	0.535
Prop. Of Variance	64.34%	15.83%	12.98%	57.38%	18.35%	12.04%	8.56%

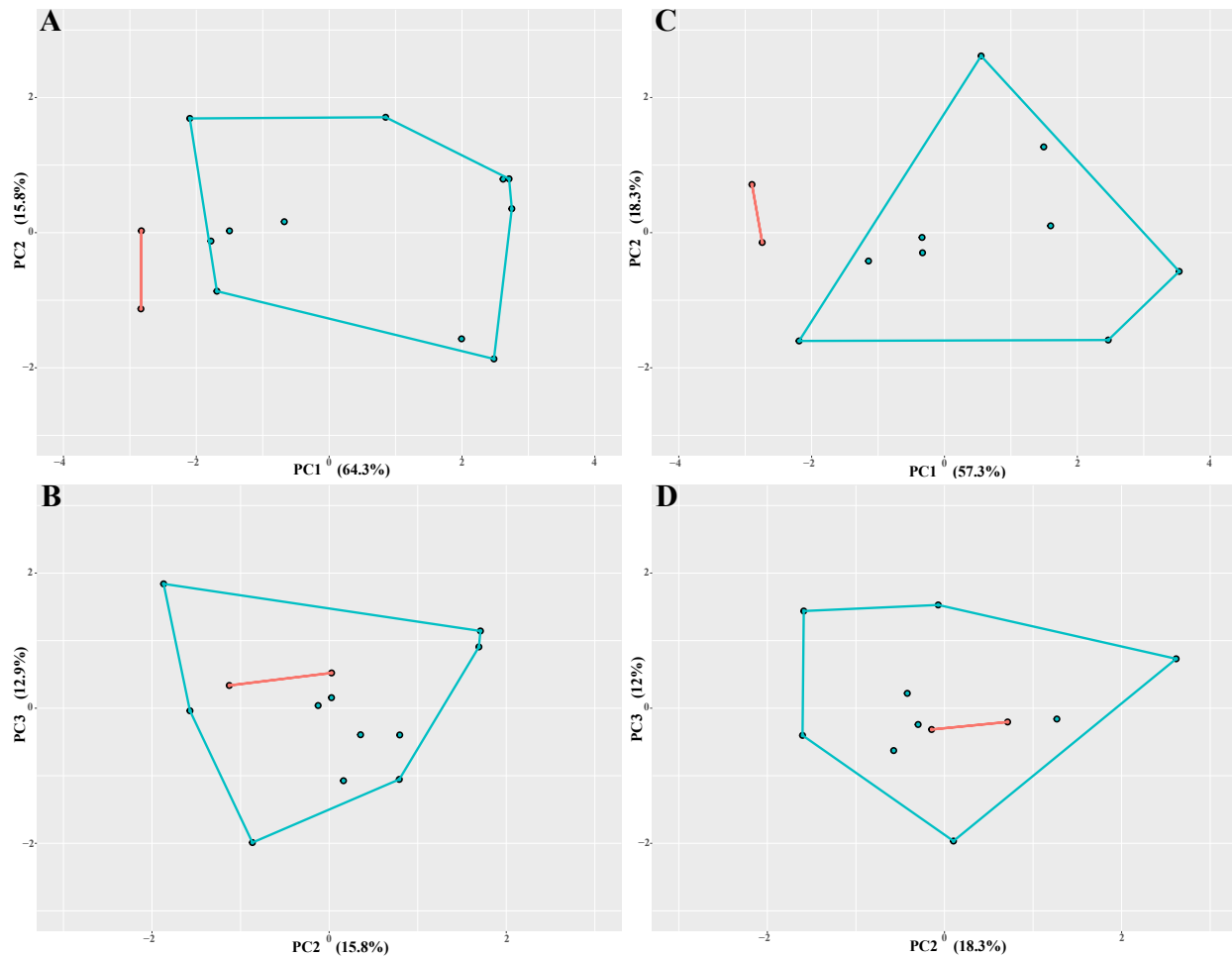


Figure 41. Principal components analysis of morphometric comparisons between clades in Monarchidae (A, B) males and (C, D) females. Each dot represents a single species and is colored by clade (orange = Malagasy; blue = source); disparity of each group is represented as a minimal convex polygon of all species in that group. The centroid of each clade is not statistically different (MANOVA $p > 0.05$) in either sex.

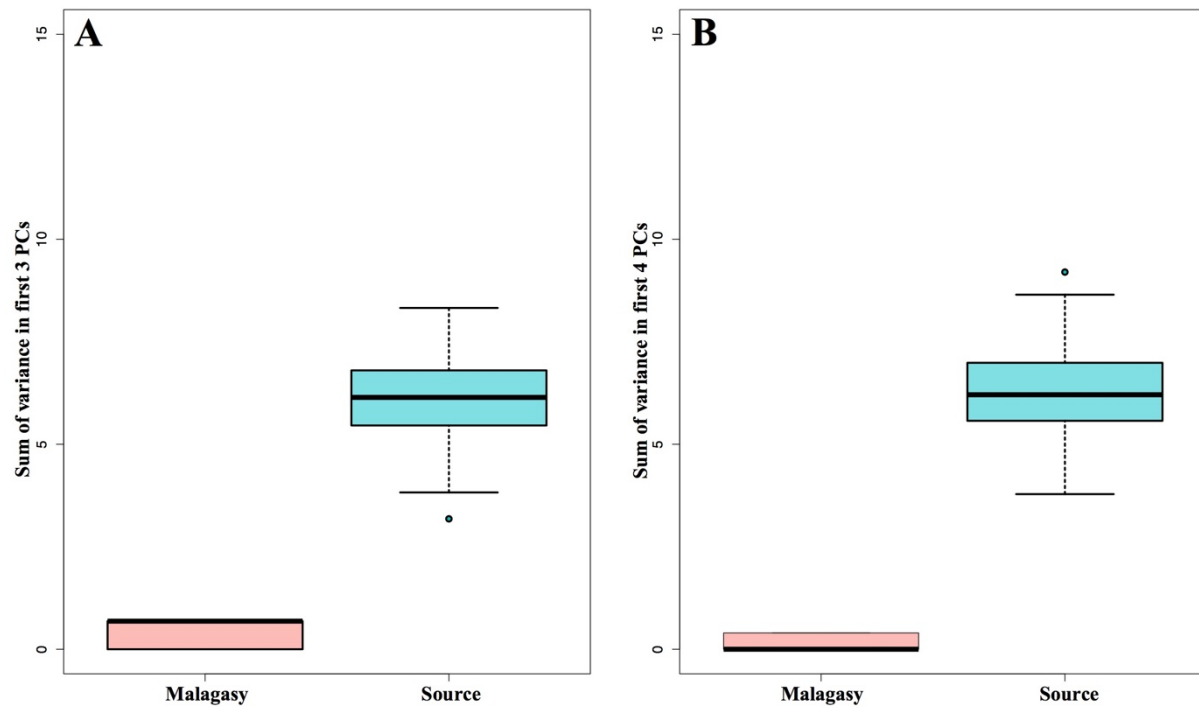


Figure 42. Monarchidae plot of disparity between clades for (A) males and (B) females. Source appears to occupy a greater area in morphological space than Malagasy, but I did not calculate a statistical value of disparity to confirm this because of low sample size in Malagasy clade.

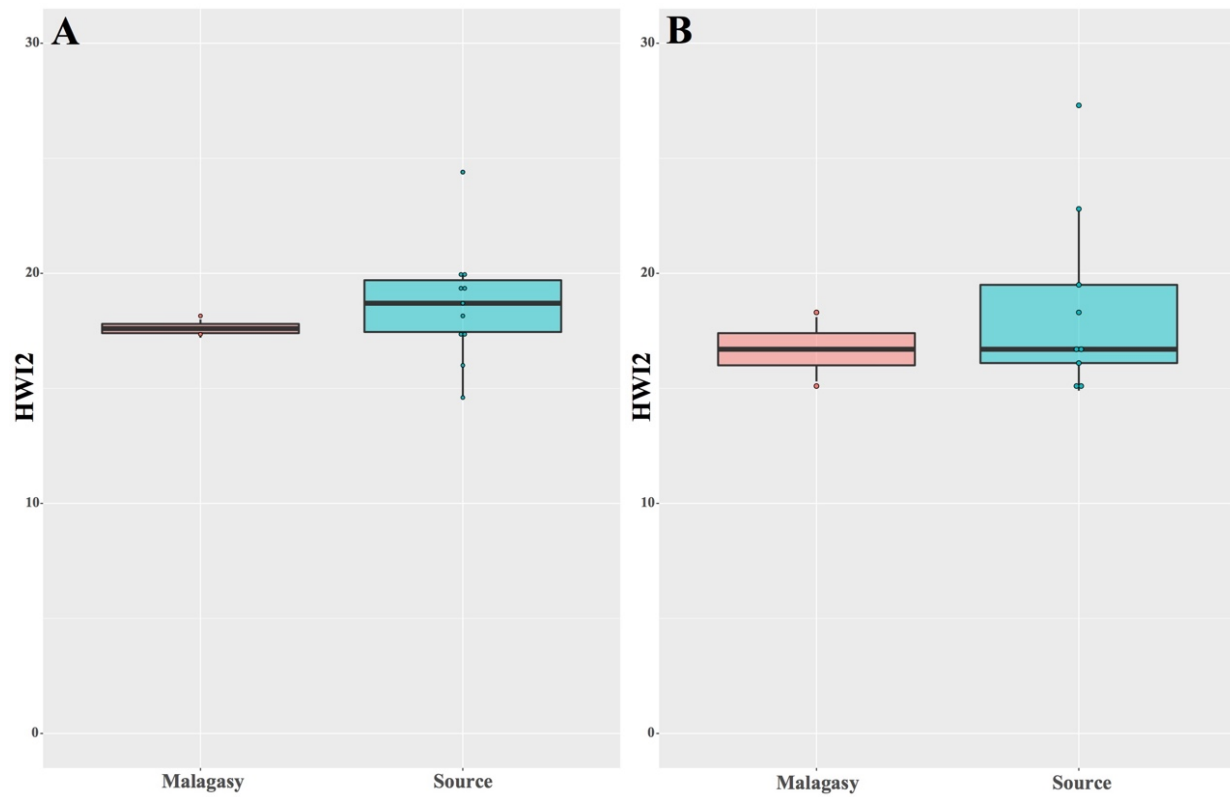


Figure 43. Boxplot of HWI2 between the Malagasy and source clades of Monarchidae (A) males and (B) females. Each dot represents an individual species' HWI2 value. There are no significant differences in the means of HWI2 between Malagasy and source clade (ANOVA $p > 0.05$) in either sex.

Table 23. Summary statistics table of each morphological variable compared between Malagasy and source clade of Monarchidae. Bill shape was significantly different between the two clades in males and females. Significant differences between clades that were uncovered using an ANOVA are shown in bold and asterisk with an M and/or F indicating which sex the trait significantly differed in.

Trait	MALE				FEMALE			
	Malagasy (n=1)		Source (n=8)		Malagasy (n=1)		Source (n=8)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
BD * ^{M,F}	4.27	0.02	5.16	0.55	4.05	0.07	5.05	0.59
BW * ^{M,F}	5.44	≤0.01	6.57	0.60	5.25	0.15	6.30	0.51
BL * ^{M,F}	16.20	0.07	20.20	2.41	15.50	0.14	19.00	1.65
WL	76.00	0.56	85.00	7.40	72.40	1.34	79.70	6.22
S1	62.60	0.84	69.00	4.62	60.30	2.55	64.70	3.44
Tar-L	13.30	0.70	14.00	0.85	13.00	0.49	13.70	1.44
Tail-L	86.80	3.89	106.00	17.60	79.60	5.87	88.70	9.53
HWI2	17.60	0.56	18.70	2.53	16.70	1.98	18.60	4.10

CHAPTER 4

INVESTIGATING VARIATION IN DISPERSAL ABILITY IN WIDESPREAD SPECIES

MACROHABITATS

Summary and discussion of results of objective 2

The second goal of this study was to examine variation in dispersal ability associated with the three macrohabitats of Madagascar. I investigated widespread Malagasy species and their subspecies restricted to habitat types – East (E; closed wet forest), West (W; closed dry forest), and Southwest (SW; open spiny desert). In this chapter, I treated each species occupying more than one of three macrohabitats in the island as an independent case study to identify whether there was an overall pattern of morphological differentiation in response to ecological variation across Madagascar.

The detailed results from my analyses of each widespread species are below. In summary, my results indicate that some Malagasy species exhibit local adaptation while others do not (Table 24). When analyzing all eight morphological variables in a multivariate framework, two of my case studies (*Schetba rufa*, *Coua ruficeps*) showed no significant differences in morphospace occupancy between macrohabitats (Fig. 45; Fig. 51), while the other two case studies (*Coua cristata*, *Terpsiphone mutata*) showed significant differences in morphospace occupancy between macrohabitats (Table 24). *Coua cristata* has populations in all three macrohabitats, but only the SW was distinctly separated from the E and W, which

overlapped in morphospace (Fig. 48; Table 24). *Terpsiphone mutata* has subspecies in the W and E that were separated in morphospace (Fig. 54; Table 24).

Hand-wing index 2 differed significantly between macrohabitats in three of my four case studies (Table 24). The SW populations of *Coua ruficeps* had a significantly greater HWI2 than W (Fig. 52). *Coua cristata* had a significantly greater HWI2 in the SW population than E or W populations. HWI2 did not differ between populations of *Coua cristata* living in closed (E or W) habitat classes (Fig. 48). *Terpsiphone mutata* had a significantly greater HWI2 in the W population than E (Fig. 55). However, in contrast to the results of *Terpsiphone mutata*, *Schetba rufa* did not significantly differ in HWI2 between W and E macrohabitats (Fig. 46). In all four cases, other morphological trait(s) significantly differed between macrohabitats supporting the idea that these traits evolved in response to local conditions (Table 24).

The results of my study provide support for differential dispersal ability evolving in open versus closed habitats. In particular, forest had lower HWI2 than the SW spiny desert. In a study of the Galapagos medium ground finch (*Geospiza fortis*) populations of this species similarly varied in their wing aspect ratios (HWI2 is a simple index of aspect ratio) according to open arid versus closed humid habitats (Vanhooydonck et al., 2009). A global study of avian dispersal ability recently found that across all birds, high HWI is associated with open habitats, this finding is still supported when comparisons of habitat type are restricted to passerines alone (Sheard et al., 2020). It is interesting that dispersal ability evolves differently for birds in open versus closed habitats and this pattern is consistent whether compared at a global scale or at a local scale of the populations within a species.

The results of this study highlighted that within widespread species there are significant morphological differences between populations restricted to these macrohabitats. These

populations that are morphologically diverging in different habitats could potentially be different species. The phylogenetic relationships of *Coua* still remain unclear (Johnson et al., 1999) and populations within widespread species have not been tested for genetic divergence. To test if these morphologically distinct populations of a widespread species are indeed unrecognized new species, DNA samples of each population should be sequenced and compared. The results of my study highlight the need for additional phylogenetic studies of widespread species populations because the true biodiversity of birds in Madagascar is likely underestimated. Understanding the true biodiversity in each of these macrohabitats is of upmost importance as deforestation in Madagascar is an ever-growing concern and little is known about these species ability to adapt or persist in fragmented habitats.

Future research should focus on studying these lineages via ecological niche modeling with factors such as foraging behavior, foraging strata, elevational data, precipitation, and diet accounted for as influencing variables. The role of micro-habitats, habitat patchiness, and elevational variability may reveal more fine-scale patterns. Additional case studies of widespread species with populations in the W and E should be sampled to further understand and clarify whether there is a general pattern of populations evolving differently between the closed forest macrohabitats of the W and E. There are research opportunities to see if my findings of morphological divergence of widespread species populations in different macrohabitats is similarly observed in mammals, reptiles, or bats in Madagascar.

Table 24. Summary of Chapter 4 results for each widespread species. Within each widespread species I compared the morphometric data of their populations restricted to macrohabitats. For MANOVA, significant differences in the centroids between macrohabitat populations is marked ‘SW $\hat{=}$ W $\hat{=}$ E’ with a p-value.

Widespread species	Multivariate MANOVA	HWI2	Univariate Sig. morphometrics
<i>Schetba rufa</i>	p>0.05	p>0.05	wing chord length (p<0.05) tail length (p<0.001)
<i>Coua cristata</i>	SW $\hat{=}$ W $\hat{=}$ E (p<0.01)	p<0.001	bill length (p<0.01) wing chord length (p<0.001) secondary length (p<0.001)
<i>Coua ruficeps</i>	–	p<0.05	bill depth (p<0.05) tail length (p<0.05)
<i>Terpsiphone mutata</i>	–	p<0.05	tarsus length (p<0.01)

Details of results by species

Vangidae *Schetba rufa*

In *Schetba rufa*, I compared *Schetba r. occidentalis* (W) and *Schetba r. rufa* (E; five specimens for each subspecies; Table 26). The first five principal components (Fig. 44) explained ~95% of the variation (Table 25). There were no significant differences in the W and E occupancy of morphospace (MANOVA p>0.05, Fig. 45). HWI2 had the highest weighting in PC3 loadings contributing substantially to variation explained by this PC (Table 25). There were no significant differences in the means of HWI2 between the W and E (ANOVA p>0.05, Fig. 46). The wing chord length and tail length of the W subspecies was significantly greater than E (p<0.05, p<0.001; Table 26).

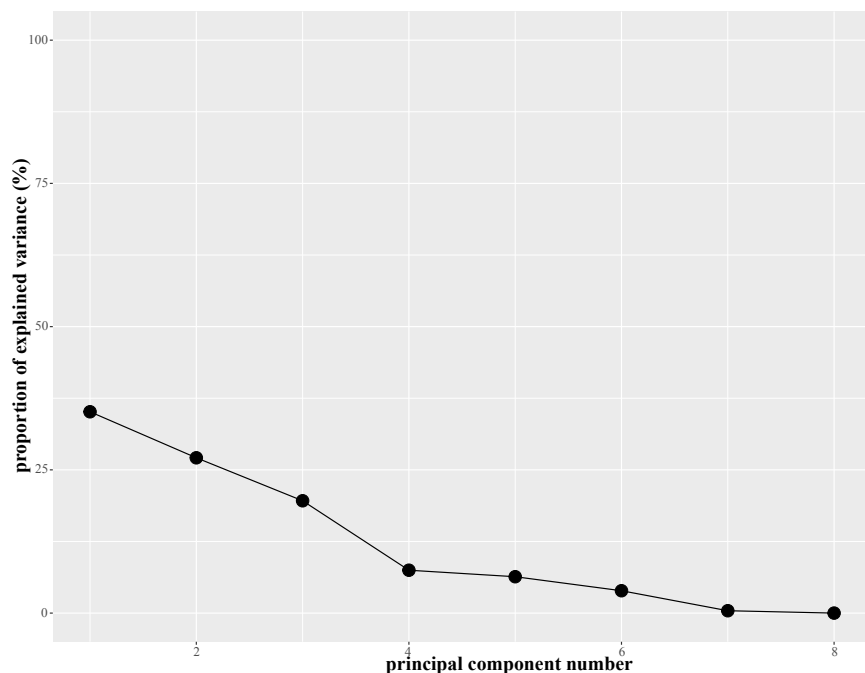


Figure 44. Scree plot of the proportion of explained variance for eight principal components in *Schetba rufa* subspecies. The first five principal components incorporated greater than 5% variance. Table 25 shows the loadings of these five principal components.

Table 25. Summary of principal components and their loadings in *Schetba rufa* subspecies. The cumulative proportion of the five principal components is 95.68%. Abbreviations are as follows (BD= bill depth, BW= bill width, BL= bill length, WL= wing chord length, S1= secondary length, Tar-L= tarsus length, Tail-L = tail length, HWI2= hand-wing index 2).

Morphometrics	PC1	PC2	PC3	PC4	PC5
BD	≤0.001	0.556	0.097	-0.031	0.758
BW	0.047	0.632	0.031	0.036	-0.142
BL	-0.328	0.403	-0.002	0.581	-0.454
WL	-0.551	-0.121	0.133	0.012	0.145
S1	-0.416	0.030	-0.548	-0.166	0.069
Tar-L	-0.345	0.216	0.317	-0.739	-0.316
Tail-L	-0.535	-0.206	-0.021	0.211	0.256
HWI2	-0.077	-0.149	0.754	0.199	0.071
Prop. Of Variance	35.14%	27.11%	19.60%	7.48%	6.35%

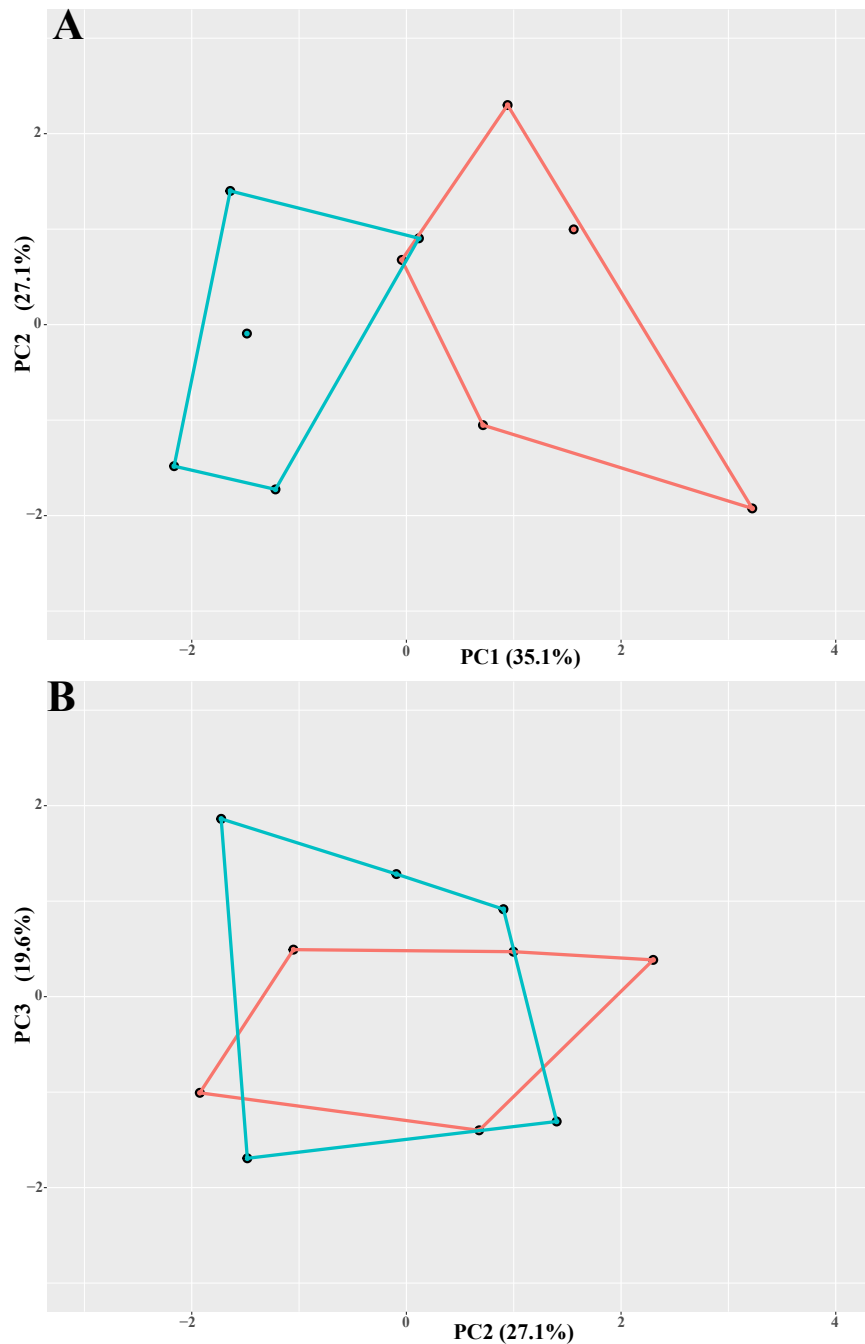


Figure 45. Principal components analysis of morphometric comparisons between subspecies macrohabitats in *Schetba rufa*. (A) Plot of PC1 vs. PC2 (B) Plot PC2 vs. PC3. Each dot represents a single specimen and is colored by macrohabitat (orange = E, blue = W); polygons were drawn as a minimum convex of all specimens in that macrohabitat. The centroid of each macrohabitat is not statistically different (MANOVA $p > 0.05$).

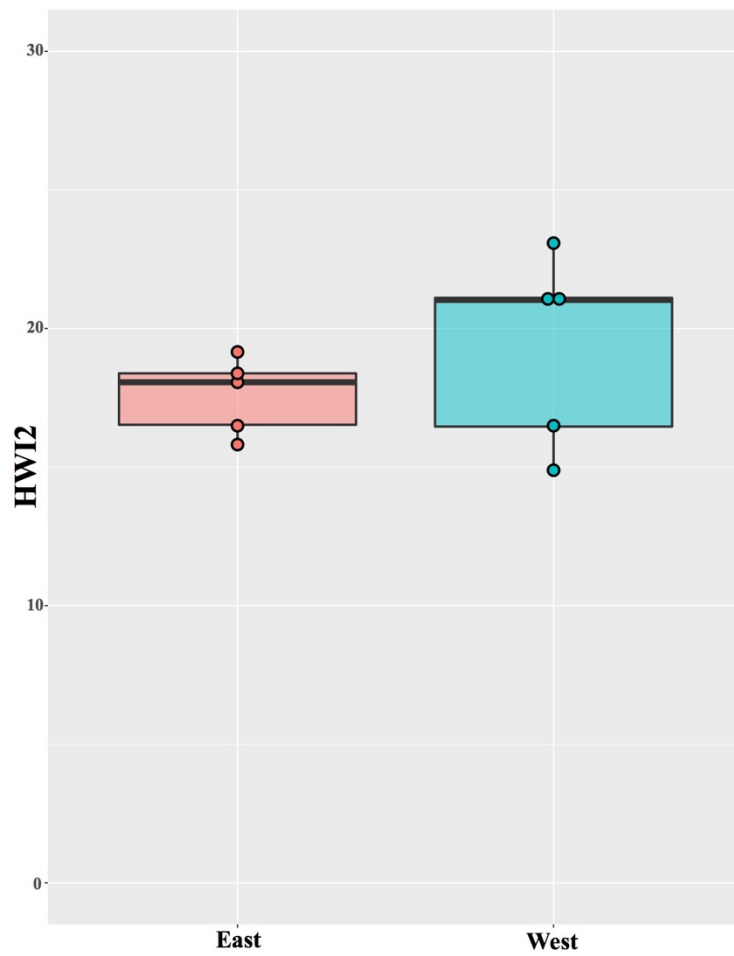


Figure 46. Boxplot of HWI2 between the subspecies of *Schetba rufa* inhabiting E and W. Each dot represents an individual specimens' HWI2 value. There are no significant differences in the means of HWI2 between the W and E (ANOVA $p > 0.05$).

Table 26. Summary statistics table of each morphological variable compared between E and W subspecies of *Schetba rufa*. Only wing chord length and tail length were significantly different between the two subspecies with W being greater. Significant differences between macrohabitats that were uncovered using an ANOVA are shown in bold and asterisk.

Trait	West (n=5)		East (n=5)	
	Mean	SD	Mean	SD
BD	8.23	0.48	8.23	0.70
BW	6.59	0.24	6.78	0.45
BL	25.00	1.12	23.80	0.92
WL*	105.00	2.18	101.00	2.61
S1	85.10	3.71	83.00	2.43
Tar-L	21.60	0.69	21.20	0.82
Tail-L***	90.60	3.53	79.00	2.70
HWI2	19.30	3.47	17.60	1.38

Cuculidae *Coua cristata*

In *Coua cristata*, I compared *Coua c. cristata* (E), *Coua c. dumonti* (W), and *Coua c. pyropyga* (SW; four specimens in SW and five specimens each in W and E; Table 28). The first four principal components explained ~93% of the variation (Fig. 47; Table 27). There were significant differences in the occupancy of morphospace between these macrohabitats (MANOVA $p < 0.01$, Fig. 48). The SW occupied a distinct region of morphospace from the E and W, which shared a similar region of morphospace. HWI2 had the highest weighting in PC3 loadings contributing substantially to variation explained by this PC (Table 27). There were significant differences in the means of HWI2 between macrohabitats overall (ANOVA $p < 0.001$, Fig. 49). The HWI2 mean of the SW was significantly greater than E or W (pairwise t-tests: $p_{SW,E} < 0.001$, $p_{SW,W} < 0.01$). There were no significant differences in the means of HWI2 between E and W (pairwise t-test $p_{E,W} > 0.05$). Similarly, the wing chord length and secondary length were significantly greater in the SW population than E or W ($p < 0.001$) with no differences between E

and W. Bill length was significantly greater in the E than W ($p < 0.01$; Table 28), but neither E or W differed from SW.

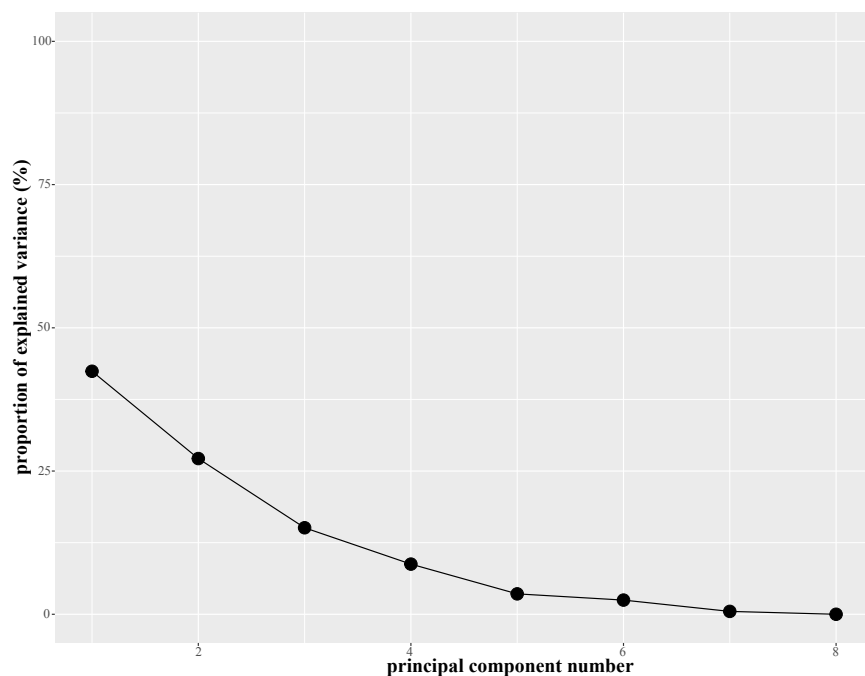


Figure 47. Scree plot of the proportion of explained variance for eight principal components in *Coua cristata* subspecies. The first four principal components incorporated greater than 5% variance. Table 27 shows the loadings of these four principal components.

Table 27. Summary of principal components and their loadings in *Coua cristata* subspecies. The cumulative proportion of the four principal components is 93.45%.

Morphometrics	PC1	PC2	PC3	PC4
BD	-0.051	-0.553	-0.305	-0.344
BW	0.088	-0.613	-0.108	0.314
BL	0.070	0.080	-0.869	-0.106
WL	-0.530	≤ -0.001	-0.002	-0.221
S1	-0.508	0.056	-0.095	-0.192
Tar-L	-0.280	0.438	-0.317	0.461
Tail-L	-0.370	-0.321	0.006	0.644
HWI2	-0.478	-0.110	0.169	-0.239
Prop. Of Variance	42.42%	27.18%	15.10%	8.75%

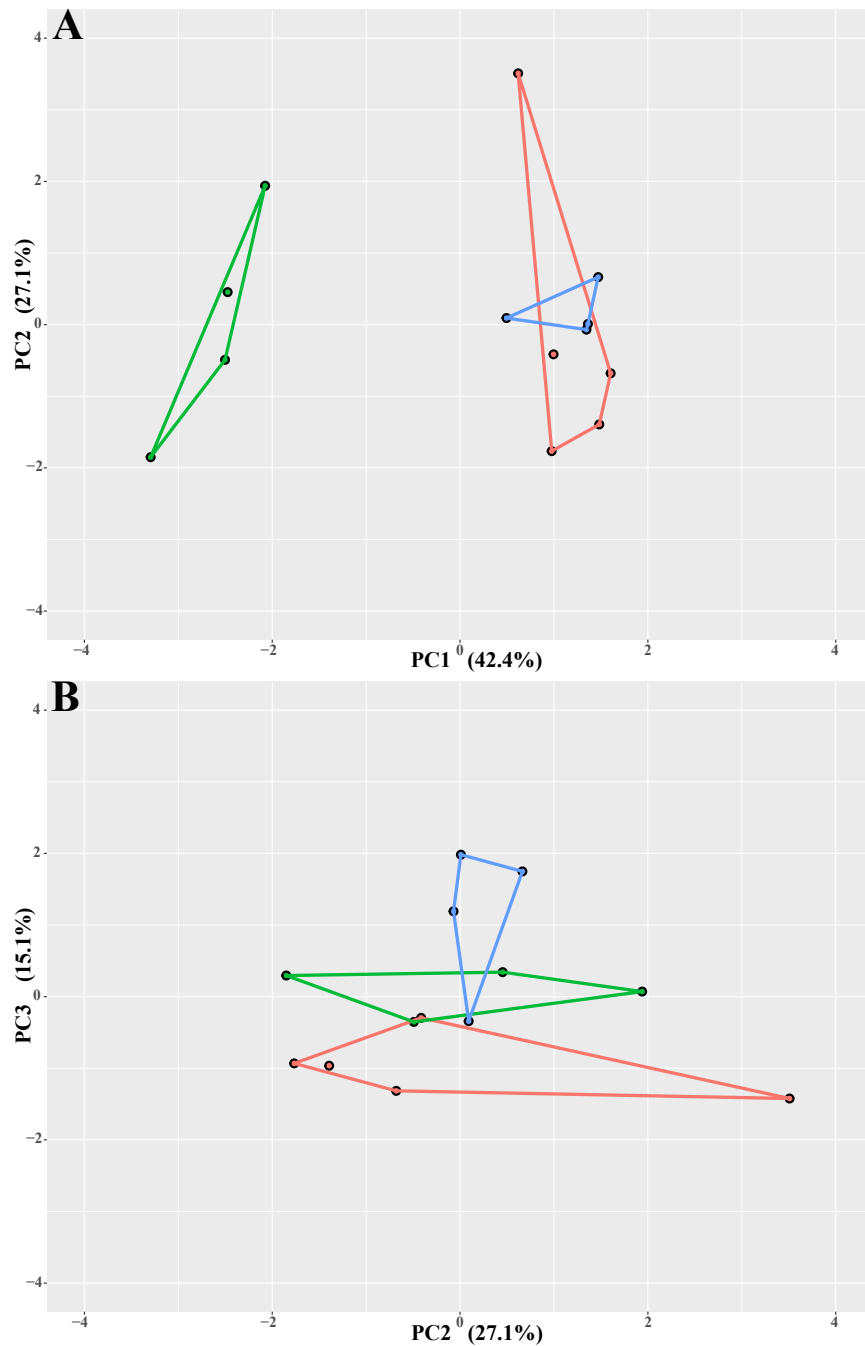


Figure 48. Principal components analysis of morphometric comparisons between subspecies macrohabitats in *Coua cristata*. (A) Plot of PC1 vs. PC2 (B) Plot PC2 vs. PC3. Each dot represents a single specimen and is colored by macrohabitat (orange = E; blue = W; green = SW); polygons were drawn as a minimum convex of all specimens in that macrohabitat. The centroids of the macrohabitats were statistically different (MANOVA $p < 0.01^{**}$).

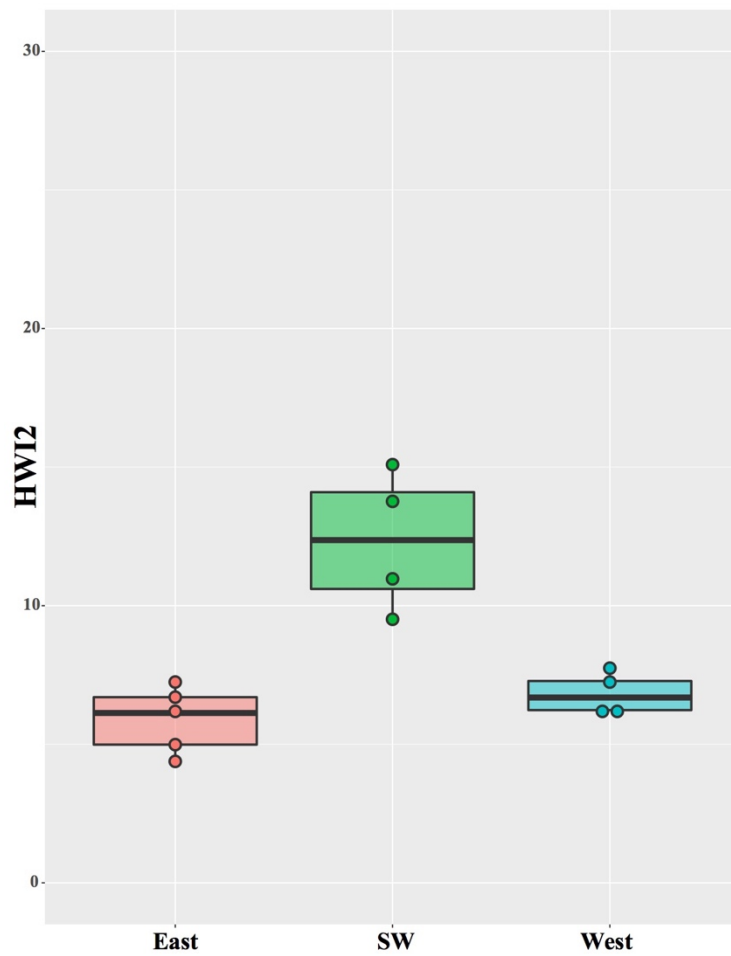


Figure 49. Boxplot of HWI2 between the subspecies of *Coua cristata* inhabiting the E, SW, and W macrohabitats. Each dot represents an individual specimens' HWI2 value. There were significant differences in the means of HWI2 between the macrohabitats (ANOVA $p < 0.001^{***}$). The HWI2 mean of the SW was significantly different from E or W, but there were no differences between E and W (pairwise t-tests: $p_{SW,E} < 0.001^{***}$, $p_{SW,W} < 0.01^{**}$, $p_{E,W} > 0.05$).

Table 28. Summary statistics table of each morphological variable compared between macrohabitats of *Coua cristata* subspecies. HWI2, bill length, wing chord length, and secondary length all significantly differed between macrohabitats. HWI2, wing length, and secondary length were all significantly greater in SW than E or W, but did not differ between E and W. Bill length was significantly greater in the E than W but did not differ otherwise. Significant differences between macrohabitats that were uncovered using an ANOVA are shown in bold and asterisk.

Trait	Southwest (n=4)		West (n=4)		East (n=5)	
	Mean	SD	Mean	SD	Mean	SD
BD	9.62	0.29	9.33	0.27	9.70	0.56
BW	7.89	1.16	8.02	0.54	8.47	1.28
BL**	23.20	0.54	22.40	1.37	24.90	0.77
WL***	161.00	5.20	132.00	3.39	132.00	2.50
S1***	141.00	5.19	123.00	2.32	125.00	2.78
Tar-L	33.90	2.63	30.00	1.24	31.80	3.53
Tail-L	216.00	15.10	203.00	3.06	203.00	5.19
HWI2***	12.30	2.55	6.83	0.74	5.91	1.22

Cuculidae *Coua ruficeps*

In *Coua ruficeps*, I compared *Coua r. olivaceiceps* (SW) and *Coua r. ruficeps* (W; five specimens for SW and four for W; Table 30). The first five principal components explained ~98% of the variation (Fig. 50; Table 29). No MANOVA test was reported due to a residual rank issue. There appears to be no significant difference in morphospace occupancy of the SW and W populations as they occupy similar regions of morphospace, but I do not have a statistical value to confirm their centroids are similar. The only separation in morphospace between macrohabitats is observed in the PC1 axis (Fig. 51). HWI2 had the highest weighting in PC1 loadings (Table 29). The HWI2 of the SW was significantly greater than W (ANOVA $p < 0.05$, Fig. 52). Tail length was significantly greater in the SW population than W (ANOVA $p < 0.05$). Bill depth was significantly greater in the W than SW (ANOVA $p < 0.05$; Table 30).

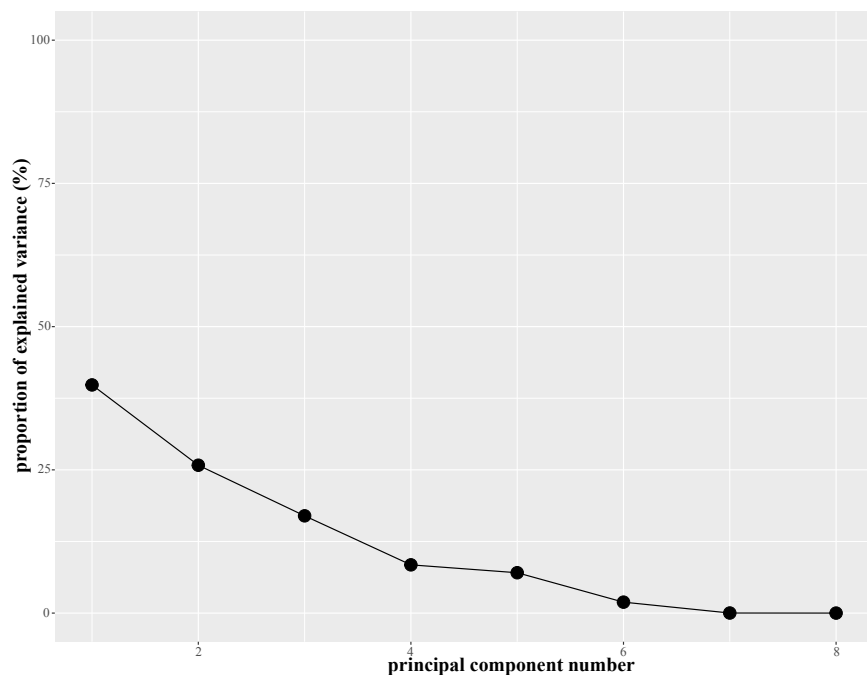


Figure 50. Scree plot of the proportion of explained variance for eight principal components in *Coua ruficeps* subspecies. The first five principal components incorporated greater than 5% variance. Table 29 shows the loadings of these five principal components.

Table 29. Summary of principal components and their loadings in *Coua ruficeps* subspecies. The cumulative proportion of the five principal components is 98.07%.

Morphometrics	PC1	PC2	PC3	PC4	PC5
BD	-0.523	0.022	-0.056	0.165	0.142
BW	-0.482	-0.300	-0.036	-0.140	0.159
BL	-0.406	-0.192	0.413	0.350	0.371
WL	0.018	-0.559	-0.428	-0.359	0.157
S1	-0.388	0.141	-0.570	-0.146	-0.189
Tar-L	0.093	0.510	-0.121	-0.311	0.785
Tail-L	0.243	-0.088	-0.529	0.751	0.237
HWI2	0.330	-0.520	0.142	-0.128	0.287
Prop. Of Variance	39.82%	25.81%	16.98%	8.42%	7.04%

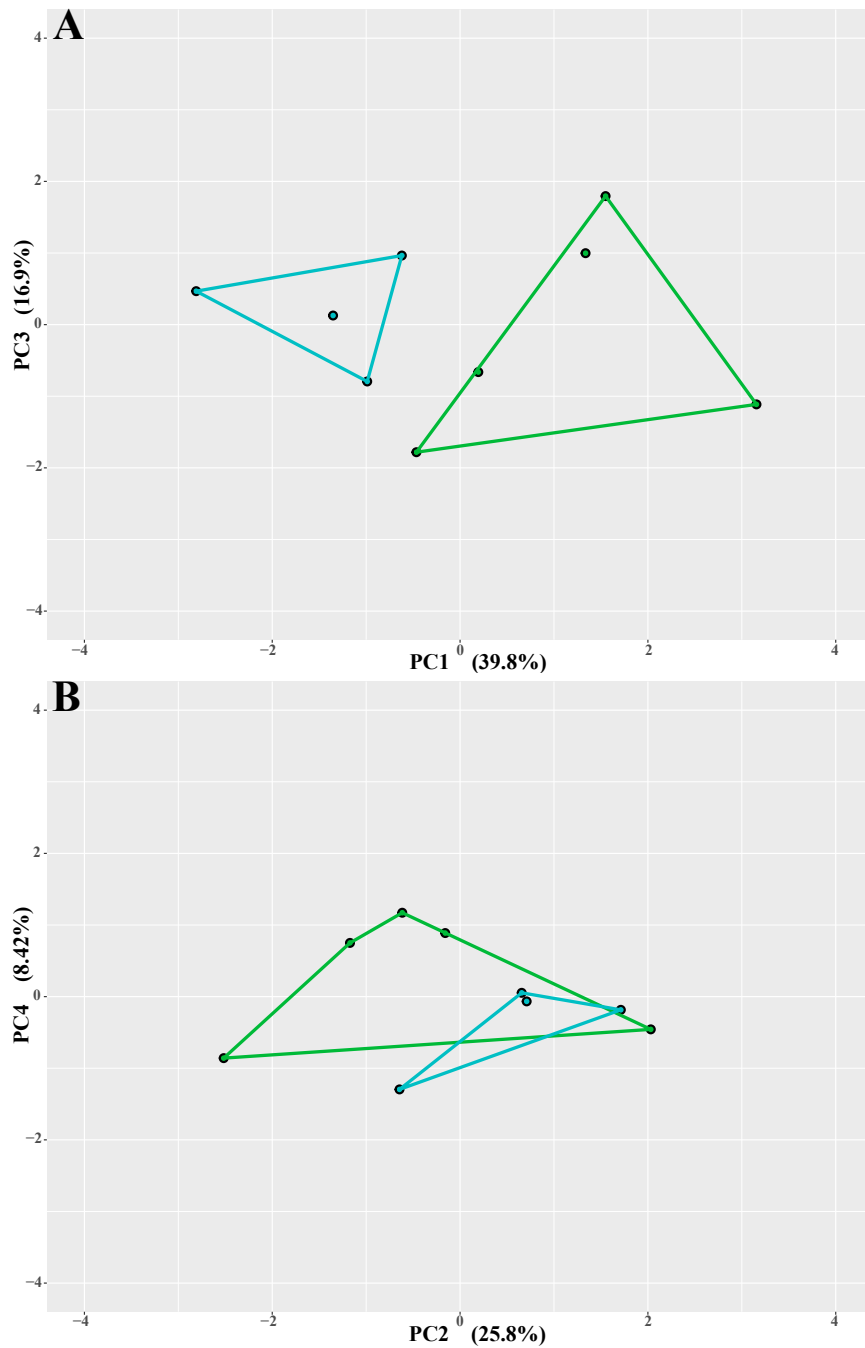


Figure 51. Principal components analysis of morphometric comparisons between subspecies macrohabitats in *Coua ruficeps*. (A) Plot of PC1 vs. PC3 (B) Plot PC2 vs. PC4. Each dot represents a single specimen and is colored by macrohabitat (blue = W; green = SW); polygons were drawn as a minimum convex of all specimens in that macrohabitat. No MANOVA test was reported due to a residual rank issue.

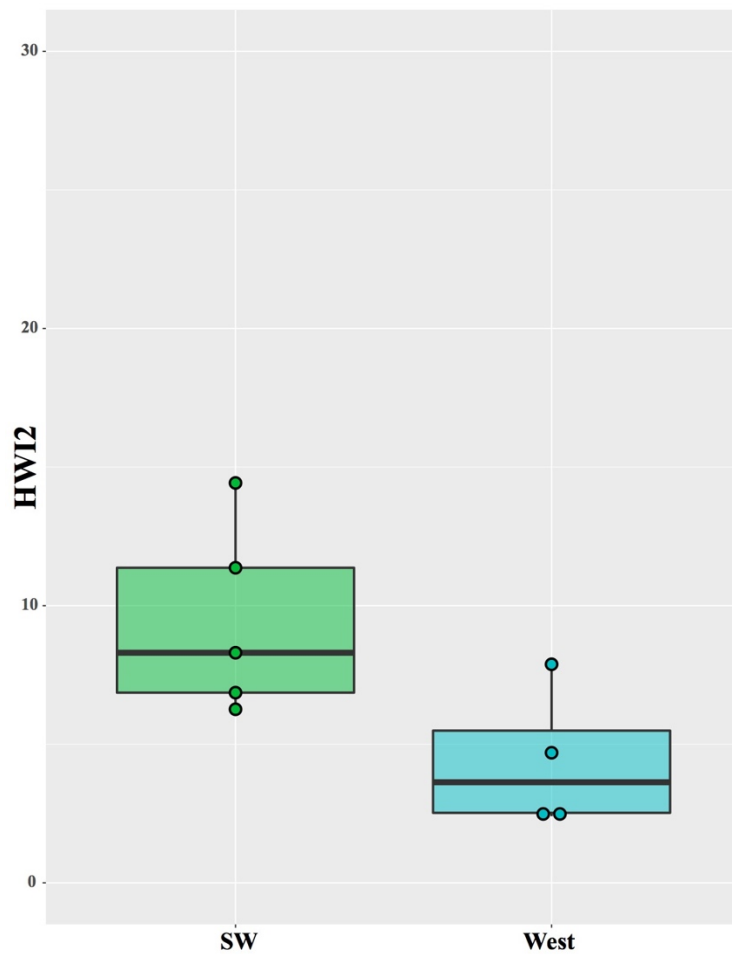


Figure 52. Boxplot of HWI2 between the subspecies of *Coua ruficeps* inhabiting the SW and W macrohabitats. Each dot represents an individual specimens' HWI2 value. There are significant differences in the means of HWI2 between the SW and W (ANOVA $p < 0.05^*$).

Table 30. Summary statistics table of each morphological variable compared between macrohabitats occupied by subspecies of *Coua ruficeps*. Tail length and HWI2 were significantly greater in SW than W, but bill depth was greater in W compared to SW. Significant differences between macrohabitats that were uncovered using an ANOVA are shown in bold and asterisk.

Trait	Southwest (n=5)		West (n=4)	
	Mean	SD	Mean	SD
BD*	9.74	0.40	10.40	0.42
BW	8.12	0.99	9.03	0.60
BL	27.80	1.53	28.70	0.87
WL	164.00	4.78	161.00	5.59
S1	148.00	5.82	154.00	1.91
Tar-L	44.20	3.81	45.50	0.32
Tail-L*	221.00	34.40	167.00	6.95
HWI2*	9.44	3.41	4.39	2.55

Monarchidae *Terpsiphone mutata*

In *Terpsiphone mutata*, I compared *Terpsiphone m. mutata* (E) and *Terpsiphone m. singetra* (W; five specimens for each subspecies; Table 32). The first four principal components explained ~93% of the variation (Fig. 51; Table 31). No MANOVA test was reported due to a residual rank issue. There appears to be a significant difference in morphospace occupancy of the W and E populations as they overall occupy distinct regions of morphospace, but due to a residual rank issue I cannot confirm their centroids statistically differ (Fig. 54). HWI2 had the highest weighting in the loadings of PC2 contributing substantially to variation explained by this PC (Table 31). There HWI2 of the W was significantly greater than the E macrohabitats (ANOVA $p < 0.05$, Fig. 55). Tarsus length was significantly greater in the E population than W (ANOVA $p < 0.01$; Table 32).

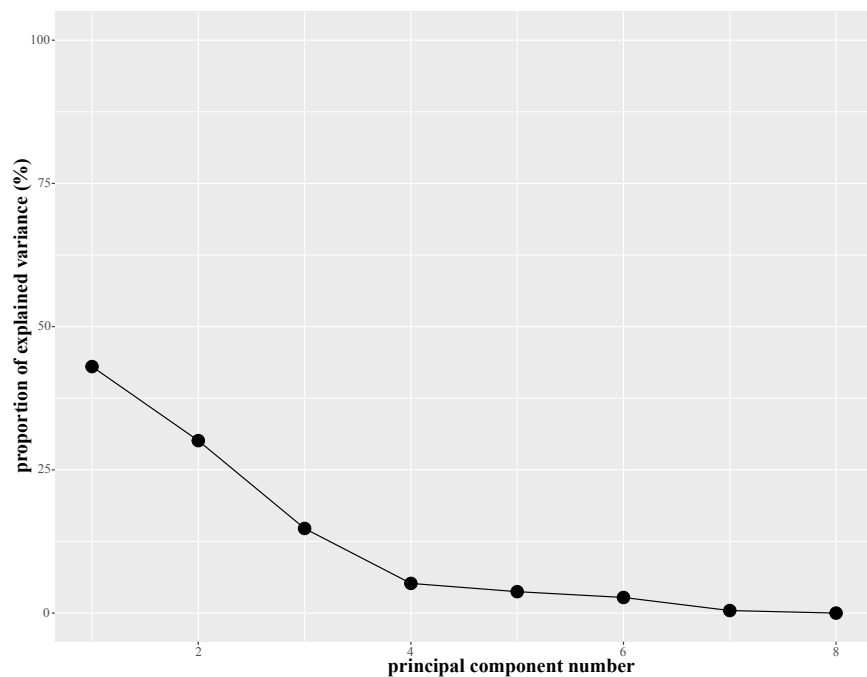


Figure 53. Scree plot of the proportion of explained variance for eight principal components in *Terpsiphone mutata* subspecies. The first four principal components incorporated greater than 5% variance. Table 31 shows the loadings of these four principal components.

Table 31. Summary of principal components and their loadings in *Terpsiphone mutata* subspecies. The cumulative proportion of the four principal components is 93.08%.

Morphometrics	PC1	PC2	PC3	PC4
BD	-0.328	0.206	-0.571	0.550
BW	-0.299	0.350	-0.449	-0.487
BL	-0.496	0.012	-0.077	≤ 0.001
WL	-0.468	-0.250	0.210	-0.032
S1	-0.356	-0.459	0.066	0.140
Tar-L	-0.197	-0.522	-0.113	-0.400
Tail-L	-0.319	0.256	0.531	0.350
HWI2	-0.262	0.470	0.349	-0.394
Prop. Of Variance	43.03%	30.10%	14.77%	5.18%

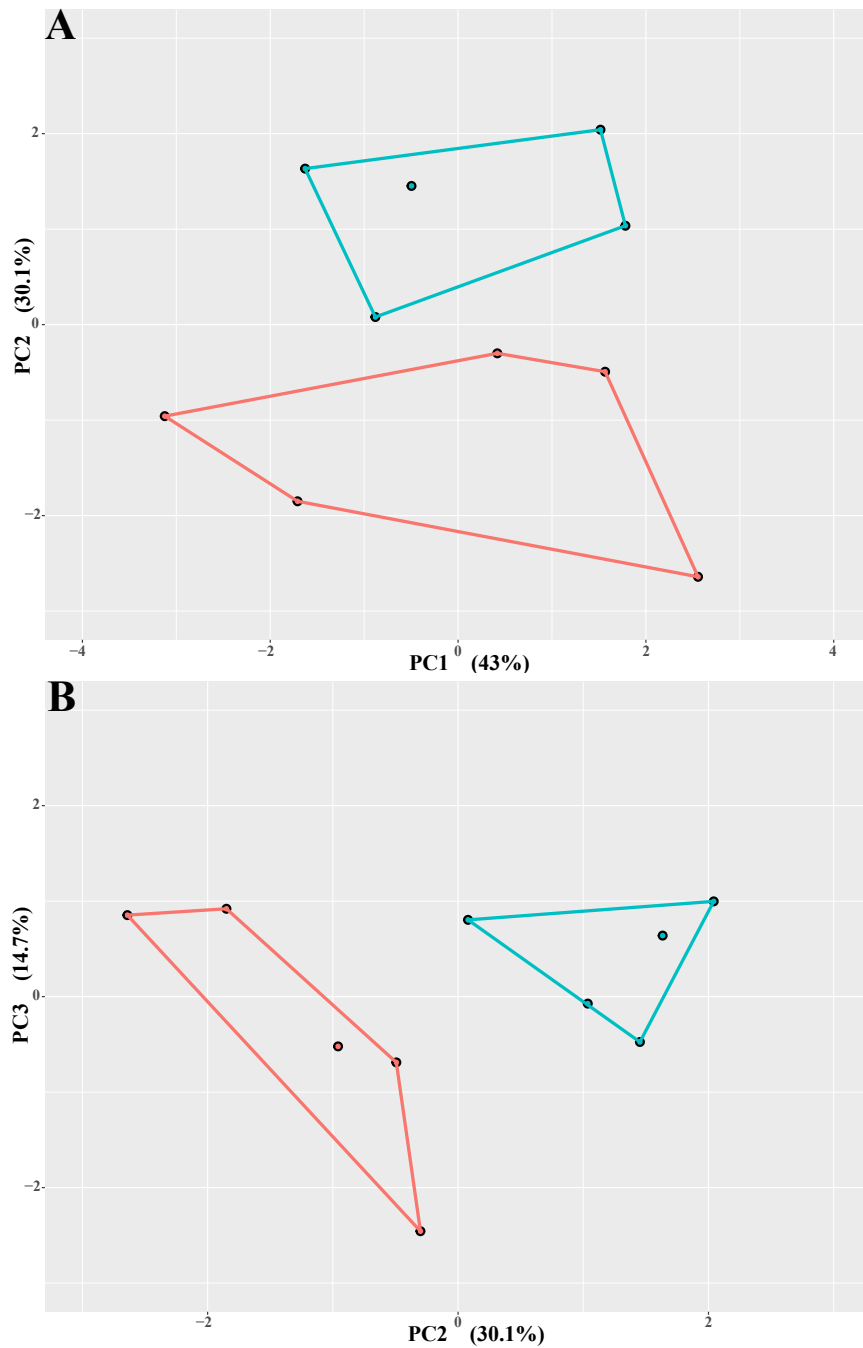


Figure 54. Principal components analysis of morphometric comparisons between subspecies macrohabitats in *Terpsiphone mutata*. (A) Plot of PC1 vs. PC2 (B) Plot PC2 vs. PC3. Each dot represents a single specimen and is colored by macrohabitat (orange = E; blue = W); polygons were drawn as a minimum convex of all specimens in that macrohabitat. No MANOVA test was reported due to a residual rank issue.

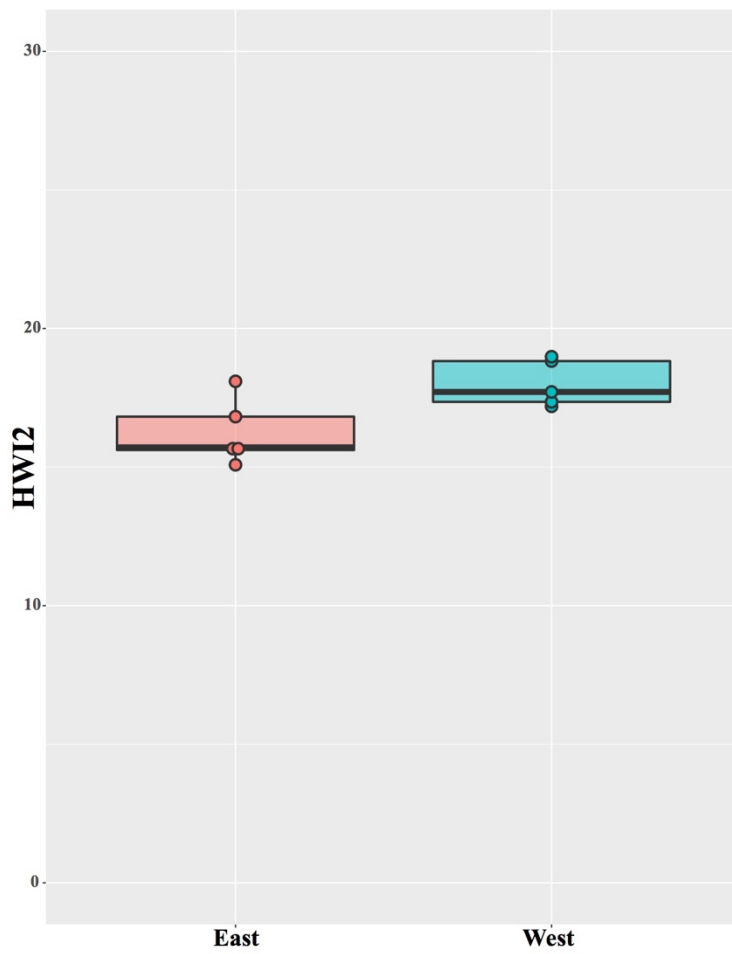


Figure 55. Boxplot of HWI2 between the subspecies of *Terpsiphone mutata* inhabiting the E and W macrohabitats. Each dot represents an individual specimens' HWI2 value. There are significant differences in the means of HWI2 between macrohabitats (ANOVA $p < 0.05^*$).

Table 32. Summary statistics table of each morphological variable compared between macrohabitats occupied by subspecies of *Terpsiphone mutata*. HWI2 was significantly greater in W than E, but tarsus length was significantly greater in E than W. Significant differences between macrohabitats that were uncovered using an ANOVA are shown in bold and asterisk.

Trait	West (n=5)		East (n=5)	
	Mean	SD	Mean	SD
BD	4.18	0.18	4.15	0.26
BW	5.41	0.06	5.29	0.35
BL	15.90	0.59	16.00	0.86
WL	73.90	2.36	75.40	3.26
S1	60.60	2.01	63.10	1.95
Tar-L**	12.80	0.36	13.60	0.36
Tail-L	87.20	4.20	80.30	6.40
HWI2*	18.00	0.83	16.30	1.20

CHAPTER 5

CONCLUSION

In this study, I focused on whether dispersal ability, as measured by hand-wing index 2, influenced diversification in the birds of Madagascar at a large regional scale and smaller local scale within Madagascar. The first objective of my study (chapter 3) assessed whether dispersal ability (HWI2) influenced diversification of the birds of Madagascar by comparing hand-wing index 2 of the Malagasy and source clades of radiating and non-radiating lineages. The second objective of my study (chapter 4) investigated dispersal ability, at a smaller local scale of macrohabitats within Madagascar, to examine whether variation in dispersal ability (HWI2) within widespread Malagasy species differed between populations restricted to macrohabitats reflecting local adaptation and divergence across macrohabitats.

When comparing between Malagasy and source clades, my study showed that Malagasy species did not shift in their dispersal ability after colonizing Madagascar. Dispersal ability (as estimated by HWI2) is not critical to the diversification of Malagasy endemics from source clade, in radiating or non-radiating lineages.

However, when examining variation in dispersal ability at a smaller local scale of Malagasy macrohabitats, three out of four case studies had significant differences in hand-wing index 2 between the macrohabitats and habitat classes of subspecies on Madagascar. In these cases, it is likely that this morphological change is due to local adaptations to macrohabitats. In particular, the results of this study support dispersal ability evolving differently in open (SW)

versus closed (W or E) habitat classes. However, HWI2 was not the only trait contributing to morphological diversification across macrohabitats and habitat classes. Traits such as tail length, bill length, bill depth, and tarsus length significantly differed between macrohabitats further supporting the idea these traits evolved in response to local conditions.

This study adds to our knowledge of dispersal ability and diversification patterns in Malagasy avifauna. My study contributed to the growing field of research investigating the relationship of avian dispersal ability and diversification such as in a South American radiation of woodcreepers (Claramunt et al., 2012), multiple families in the Australasian archipelagos (Weeks and Claramunt, 2014), and Corvides (Kennedy et al., 2016) using museum specimen collections; further emphasizing the importance and ongoing contribution museum specimen collections provide. This is the first study to investigate Malagasy endemic birds' dispersal ability (HWI2) in the context of phylogeny at a broad continental scale and smaller local scale of macrohabitats. In particular, dispersal ability has not been studied in populations of widespread Malagasy species categorized by their macrohabitats. This study also contributed a large morphometric data set to an ongoing large-scale research project investigating phylogeographic structure of Madagascar avifauna across habitats (Reddy Lab). The results of my study agree with another study in the Reddy lab that concluded there is evidence of sexual dimorphism (Bonfitto in prep.). The Malagasy vangas are a truly remarkable radiation with considerable morphological variation yet they are still overlooked in recent publications discussions despite being sampled (Navalon et al., 2020), a missed opportunity. The methods of this study can be applied to other studies of isolated large islands, macrohabitats, and lineages of birds (Claramunt and Wright, 2017). I do not believe the dispersal ability results of my first objective (chapter 3)

are generalizable to other islands because of the unique size and habitat richness of Madagascar.

My data suggests that the results of dispersal ability and macrohabitats in this study are generalizable to other avian species within Madagascar.

My findings of populations of widespread species diverging in different macrohabitats highlights the possibility of potential new species and the need for additional phylogenetic studies to test this. This is a leading step towards additional studies to investigate the impact of potential geographic barriers to dispersal ability in the birds of this region and could provide further insights into diversification patterns. In particular, studies of the effectiveness of rivers as barriers to dispersal ability in species could be insightful. Rivers have been known to act as effective barriers to some birds in South America (Moore et al., 2008), but we do not know for certain how effective they are within Madagascar. Furthermore, over the past 50 years deforestation and habitat fragmentation in Madagascar has become a growing threat (Harper et al., 2007). Little is known about the Madagascan birds' minimum habitat patch size requirements and their ability to adapt to these environmental changes. Previous and recent global studies have found species on islands and/or tropical habitats near the equator have greater difficulty overcoming habitat gaps and barriers (Moore et al., 2008; Bregman, Sekercioglu, and Tobias, 2014; Sheard et al., 2020). In my study, I found the Malagasy vangas have broad variation in HWI2 and thus, their potential ability to overcome barriers such as habitat gaps. Future research should be conducted to understand the effects of habitat fragmentation on gene flow among populations of these endemic species, phenotypic adaptations, and impact on biodiversity.

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