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Exploring The Biogeography Of South American Rainforest Understory Birds Using Morphological Variation In The Wedge-Billed Woodcreeper (glyphorynchus Spirurus)

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EXPLORING THE BIOGEOGRAPHY OF SOUTH AMERICAN RAINFOREST UNDERSTORY BIRDS USING MORPHOLOGICAL VARIATION IN THE WEDGE-BILLED WOODCREEPER (*GLYPHORYNCHUS SPIRURUS*)

Gregory Tito

198 Pages

Tropical rainforests in the Amazon Basin show an extraordinarily high degree of biodiversity, the reasons for which are poorly understood. A number of biogeographical models have been proposed to account for the variation present within and among species, including birds. This study tests the predictive ability of six major historical vicariant biogeographical models (Andean uplift, marine incursion, Amazonian lake, river barrier, refuge, and river refuge) using a large data set of morphological characters in the Wedge-billed Woodcreeper (*Glyphorynchus spirurus*), a small understory songbird found mostly in terra firme tropical rain forest. It also characterizes variation in key morphological characters and tests the validity of the fourteen current subspecies in this species. Canonical discriminant analyses paired with cluster analyses and goodness-of-fit tests were used to test the biogeographical models, and discriminant function analyses were used in the subspecies revision. In all cases, measures were taken to address geographic uncertainty. We discovered that none of the six tested models fully predicted the observed morphological patterns in this species, that the marine incursion, lake, and Andean uplift models could be excluded entirely, and that the river barrier, refuge, and river refuge models showed predictive power in limited locations but not across the entire range. We also found that extensive clinal variation exists in the characters under study, and that at a diagnosability level of 95% only one current subspecies remained valid, but that several more exist as distinct entities at 90% and 75% levels of diagnosability. The use of a very high diagnosability level may impede the recognition of existing geographic variation and should be carefully considered. Various sources of geographic uncertainty were not found to have any effect on the trends discovered, but sparse sampling in some areas remains a problem. These results corroborate recent genetic studies which have questioned the current subspecies rankings, but they fail to recover the same biogeographical patterns found in other studies. Morphological variation in this species captures such a complex history that no single biogeographical model can be distinguished, a phenomenon which we name the palimpsest model.

KEYWORDS: Amazonia, Biogeography, Glyphorynchus, Refugia, Subspecies

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CHAPTER I: INTRODUCTION

This research addresses three interrelated questions concerning the evolutionary history, particularly in the fields of historical biogeography and systematics, of the Neotropical avian species *Glyphorynchus spirurus*, the Wedge-billed Woodcreeper. First, what are the patterns of geographic variation in key external morphological characters? Second, are those patterns predicted by one or more of the major historical vicariance biogeographical models purporting to explain the diversification of the Amazonian biota? Third, do those patterns support the current subspecies rankings within this species? In this introduction, I discuss concepts from both biogeography and systematics as they relate to the three questions outlined above, and then introduce my chosen study organism.

Introduction to Biogeography

Biogeography is the study of the processes that determine the distributions of organisms. It consists of two branches: ecological and historical. Ecological biogeography is concerned with the effects of current biotic and abiotic factors on an organism's distribution. Historical biogeography focuses on how past geographical and climatic processes and conditions have affected the distribution and evolutionary history of organisms, and is further subdivided into dispersalist and vicariant branches. The dispersalist branch concentrates on how these processes and conditions affected the past dispersal patterns of organisms, while the vicariant branch addresses the ways in which specific vicariance events (e.g. mountain orogeny, marine incursion) have shaped the distributions of groups of organisms. Much debate exists over both the relative contributions of ecological and historical (both dispersalist and vicariant) biogeographic approaches to explaining biotic distributions, and to what extent species distributions tend to be idiosyncratic or reflect processes affecting a broader taxon and/or area (Endler 1982b).

Knowledge of the biogeographic processes affecting a species is critical both for understanding the speciation process, for which allopatric speciation models are most commonly used, and for improving species-level conservation focused on evolutionarily significant units. It enables us to discover how a particular species interacts with its geographical environment, how it will interact with anthropogenic barriers to dispersal and gene flow, and which areas have been historically important in the divergence of its populations due to geological or other reasons, and may be important again (as emphasized in the "conserving the stage" approach to conservation biology; Anderson and Ferree 2010).

Within the overall purview of Neotropical biogeography, Amazonian biogeography is a particularly contentious field because of the number of competing hypotheses proposed for the origin of Amazonian diversity and the paucity of data to support them (Haffer 2008). The Amazon Basin currently is a comparatively homogeneous expanse of various forms of lowland tropical rainforest, but despite this it houses far greater amounts of biological diversity, especially in numbers of similar species and in beta diversity, than would be expected based on its size and level of homogeneity (Haffer 2008). Most contemporary biogeographic research concentrates on historical vicariance biogeographic explanations as the most fruitful areas of investigation. At least eight such explanations have been proposed to explain biotic distributional patterns across Amazonia. To some extent their appeal is that, potentially, they can be applied to many Amazonian taxa, although the extent of such application does vary among the mechanisms, especially in relation to the overall dispersal capability of the taxa involved. In many cases these mechanisms, which have also been variously labeled "models" or "hypotheses", are not mutually exclusive. Some of them are known from direct geological evidence to have occurred, although the impact on specific biota and the geographic extent of their occurrence are debated, whereas others, specifically the refuge and river-refuge models, are inferred from other types of data. In most cases, the timing and span of effectiveness of these events are only crudely known, so more than one has the potential for sequential impacts on a particular species. In other cases, different mechanisms might operate simultaneously in different parts of the range. Following is a brief review of the major historical vicariance biogeographic models or hypotheses relevant to this study

Andean Uplift Model

Although not specifically focused on Amazonia, this model is important to organisms ranging from Central America into Amazonia. The Andean uplift hypothesis states that as the Andes arose during the Miocene, the ranges of organisms spanning them were slowly bisected, with divergence and speciation frequently resulting. The northernmost portions of the range were the last to arise and appear to have fragmented the ranges of organisms formerly spanning the northern parts of Colombia, although in at least one aberrant case a population west of the Andes appears more closely related to populations south of the Amazon than to those north of the Amazon, probably due to a dispersal event across the central Andes (Fernandes et al. 2014). Support for the predictions made under this model has been found for certain groups including frogs (Vallinoto et al. 2010) and a number of birds (e.g. Weir and Price 2011).

Marine Incursion Model

Another hypothesis based on paleogeography is the marine incursion (also known as the island or marine transgression) model, which proposes that sea level fluctuations during and after the Miocene drowned large areas of central and northwestern Amazonia and left the higher ground as several huge islands (corresponding mainly to the current geologic shields) on which organisms then diverged before expanding and establishing secondary contact once sea level dropped (Hoorn et al. 1995, Nores 1999). Authors have proposed incursions from the Atlantic (Nores 1999), but also from the Caribbean and the Pacific (Hoorn et al. 1995).

Atlantic incursions are believed to have followed the present course of the Amazon (Nores 1999, Hubert and Renno 2006) and must have either been of exceptional size (as described in Nores 1999 but not supported in recent literature as explained below) or taken place after the Amazon's course had developed, due to geological barriers at earlier time periods (Caputo and Amaral 2016). The existence of such east-west incursions is disputed in Rossetti et al. (2005). Caribbean incursions are believed to have flowed down the current course of the Orinoco and from Maracaibo and along the eastern slopes of the proto-Andes during much of the Miocene (Hoorn et al. 1995, Hoorn et al. 2010, Villegas et al. 2016), and may have had fairly low salinity, resulting in small changes to the vegetation community (Villegas et al. 2016). A recent study (Jaramillo et al. 2017) using sedimentological, palynological, and seismic data from Colombia and Brazil has clarified details regarding the duration of Caribbean incursions, but the exact extent of such incursions and the existence of incursions from other bodies of water remain uncertain. Jaramillo et al. (2017) found support for two Miocene flooding events in western Amazonia between 18.1 and 17.2 million years ago and between 16.1 and 12.4 million years ago.

Pacific incursions are believed to have been small and to have come in through Ecuador in the early Miocene before the Andes had finished rising (Hoorn et al. 1995). Researchers finding support for the importance of incursions from the Atlantic and Caribbean include Hubert and Renno (2006; freshwater fish), while Vallinoto et al. (2010; frogs), and Cooke et al. (2012; marine-derived fish) found support for the importance of Caribbean incursions only.

Amazonian Lake Model

Another paleogeography model, the lake model, states that tectonic activity caused a downwarping of part of the Amazon Basin, resulting in a large lake covering much of the western and central portions of Amazonia and having at various times an outlet either to the north through the Orinoco River or to the east through the current mouth of the Amazon (Frailey et al. 1988). The current outlet and east-west orientation of the Amazon is believed to have arisen only at the end of the Miocene (Figueiredo et al. 2009, Caputo and Amaral 2016). Such a lake would have separated the Brazilian and Guianan Shields in the east, made up of Precambrian rock, from the newly raised Andes in the west for much of the Miocene, with lakes or seas separating the two shields as well, resulting in differentiation of organisms in all three areas (Aleixo and Rossetti 2007). In its original exposition by Frailey et al. (1988), the lake was presumed to date from the Pleistocene, while current authors push its age further back to the Miocene (Aleixo and Rossetti 2007). One recent study proposed two different lake systems sequentially replacing each other, with the Pebas system spanning the period from 23 to 10 million years ago and draining to the north, and the slightly smaller Acre system spanning the period from 10 to 7 million years ago and draining to the east through the present course of the Amazon (Hoorn et al. 2010). Presumably the formation and elimination of an Amazonian lake is related to some of the phases of the Andean uplift, although the timeframe and details are uncertain (Leite and Rogers 2013, Hoorn et al. 2010). This model has been supported by a study of squirrel monkeys (Lynch Alfaro et al. 2015).

Refuge Model

One of the more influential models, the refuge hypothesis developed by Jurgen Haffer in 1969, argues that over the course of the Pleistocene and before, climatic cycles resulted in Amazonia becoming alternately wetter and drier, which caused the rainforests to fragment into "refugia" located in wetter pockets during the dry periods, and then to expand again during the wet periods. The matrix of habitat lying between these refugia is postulated to be tropical savanna and/or seasonally dry forest (Haffer 1969, Pennington et al. 2000), habitat unsuitable for either the habitation or dispersal of tropical rainforest organisms. This resulted in several cycles of divergence and secondary contact, leading to differentiation, for rainforest organisms located in those refugia (Haffer 1969, Haffer 2008). The current set of proposed refuges derives both from areas of high endemism (endemism refers to the presence of taxa found only in a given location), which have been identified by Cracraft (1985) as well as various physiographic features of the Amazon Basin (Haffer 1969).

Evidence in favor of the refuge hypothesis includes the distributions of several superspecies and the secondary contact zones between them (Haffer 1974, Haffer 2008), as well as within-species patterns of variation (e.g. Haffer 1974, Haffer and Fitzpatrick 1985, Quijada-Mascarenas et al. 2007), the localized geographical nature of several climatic factors and physiographic elements such as precipitation and the location of uplands (Haffer 1974), and findings of an increased rate of worldwide diversification of birds during periods of climatic change (Claramunt and Cracraft 2015). One study also discovered that most speciation events among Amazonian butterflies occurred within the last couple of million years, after the span of time during which physical barriers postulated by other models would have existed, but still within a time-span preventing the rejection of the refuge hypothesis (Garzon-Orduna et al. 2014). A similar process of fragmentation is hypothesized to have occurred in Amazonia for drier savanna habitat during the wet periods (Campagna et al. 2012), and differentiation of rainforest species west of the Andes has also been argued to have occurred as a result of recent climatic changes rather than primarily due to the Andean orogeny (Haffer 1967). The refuge hypothesis has also been postulated for the Congo Basin in Africa, where it appears to be supported for many lowland forest birds including members of forest floor, understory, and canopy guilds (Mayr and O'Hara 1986) but not for rainforest trees (Dauby et al. 2013), and the Atlantic Forest in Brazil, where patterns of antbird distributions support it in conjunction with other barriers (Raposo do Amaral et al. 2013).

The refuge hypothesis has been criticized on a number of grounds, including a lack of unequivocal palynological evidence across the entire Amazon Basin for the contraction or fragmentation of rainforests and for a more arid environment (Colinvaux et al. 2000), a lack of strong coincidence of the boundaries between species or subspecies with the predicted secondary contact zones between refugia (Beven et al. 1984), the potential for gallery forests between refugia to reduce the amount of differentiation which occurred (Meave and Kellman 1994, Haffer 2008), uncertainty about whether the type of vegetation in the matrix surrounding the refugia was sufficiently different to isolate many species (Bonaccorso et al. 2006, Collevatti et al. 2013), and the potential for a number of different vicariant events to explain the observed patterns of diversity equally plausibly (Cracraft and Prum 1988). The time scale for differentiation within many taxa pre-dates the processes inferred by the refuge hypothesis, with phylogenies of some parrots and toucans, for instance, showing diversification well before the Pleistocene (Eberhard and Bermingham 2005), and results from a multilocus study of two *Myrmeciza* antbirds suggesting that divergence times based on mtDNA, and especially using few loci, may be underestimates (Raposo do Amaral et al. 2013). However, advocates of this model point out that the predicted refugia need not have arisen only during the Pleistocene and may have been in existence during even earlier climatic cycles (Haffer 2008).

Delineating refuges using the areas of overlap of current distributions of endemic taxa (as in Cracraft 1985) also potentially leads to incorrect refuge boundaries or a failure to recognize some refuges altogether, since a study of Atlantic Forest refuges using Species Distribution Models found several areas of discord between refuges predicted by species-specific models and refuges predicted by an overall model including all species (Porto et al. 2013). Another study on the proposed refuges of the Atlantic Forest using similar methods found little evidence of them for mammals (Leite et al. 2015). Recent research into three plant chemical biomarkers (which are able to differentiate forests, grass-dominated habitats, and mangroves) from a drilling site in the Amazon Fan also shows no evidence of grassland or savanna intruding into Amazonia during the last glacial period, but instead shows evidence for continuous forest cover during the period (Maslin et al. 2012). It has also been proposed in response to the refuge model that areas of endemism correspond not to forest refugia, but rather to areas of increased disturbance during climatic shifts, and that these disturbances facilitated speciation in these areas (Bush 1994). In addition, it has been suggested for some North American birds that divergence occurred during rapid range expansion after the last glacial period rather than within refugia during the period, a hypothesis that might also apply to the South American avifauna (Mila et al. 2007).

A final problem confronting the refuge model concerns the difficulty in distinguishing it from the river barrier or the river-refuge models (below), the latter postulating that rivers are assumed to be secondary barriers to gene flow with refuges as the primary driver of differentiation. The assumption that rivers can be secondary barriers for populations which differentiated in refuges has been put forth by Haffer (2008) and others, and while it explains cases where taxa are river-delimited, it also raises two questions. First, why should the refuge model be favored over the river model in these cases, since vicariant events should not be multiplied unnecessarily? And second, if pre-existing hybrid or intergrade zones tend to migrate to areas of low gene flow (Moore and Price 1993), how are the original locations of the intergrade zones to be determined in order to support or fail to support the refuge hypothesis? Intergrade zone migration occurs when asymmetrical crossing of members of one parent population into the intergrade zone occurs. In these cases, the intergrade zone will move over time toward an area where gene flow from both parent populations is low, as has been documented in a number of species pairs, including birds (Buggs 2007).

Riverine Barrier Model

The riverine barriers hypothesis claims that large Amazonian rivers are sufficiently wide to prove a barrier to dispersal and result in isolation of populations on either bank. Some of the rivers in Amazonia can be several miles across in certain stretches, with many rivers or portions of rivers being nearly a mile across (Goulding et al. 2003). Such widths are enough to pose a substantial barrier to some species with behavioral aversions to crossing large open spaces, which can often show aversions even to crossing roads or other narrow gaps (Lees and Peres 2009). In one group of birds, the toucans (family Ramphastidae), an anatomical trait (the lack of a fused furcula) results in diminished capacity for sustained flight and is thought to be responsible for the role that rivers play as a barrier for this group (Short and Horne 2002).

Besides this, the rivers are generally surrounded on both sides by up to several miles of flooded forest (which takes the names várzea or igapó, depending on whether the river is a white water or black water river, respectively) (Goulding et al. 2003). This forest is generally flooded only at certain times of the year, but in some areas along the lower reaches of the Amazon it floods daily during high tides (Sick 1993). These flooded forests are unsuitable for many terra firme (non-flooded or upland) forest species, partially because the plant communities may differ from terra firme forests, but more importantly because there are a large number of bird species which are only found in flooded forests, have specialized for that habitat, and exclude more generalist species through competition. One estimate labels as much as 15 percent of Amazonian bird species as endemic to flooded forest, river island, and other floodplain habitats (Remsen and Parker 1983).

This hypothesis dates from the work of Alfred Russell Wallace, but it has more recently been postulated for species in a variety of taxonomic groups. For example, primates show substantial differentiation across several Amazonian rivers (Ayres and Clutton-Brock 1992, Ribas et al. 2015). Different groups of understory birds also show patterns consistent with this model, including but not limited to trumpeters (Ribas et al. 2011), toucans (Lutz et al. 2013), manakins (Capparella 1988, Cheviron et al. 2005), woodcreepers (Aleixo 2004), and antbirds (Hayes and Sewlal 2004, Fernandes et al. 2012). Molecular studies have found genetic differentiation across a number of Amazonian rivers for several passerine species (Capparella 1987). One study even found that extensive genetic differentiation exists across relatively small rivers in south Amazonia, but not across the headwaters of those rivers (Fernandes et al. 2015). However, researchers working with arboreal spiny rats have found equivocal results (e.g. Patton et al. 1994), and it was not supported for four understory birds in a study of the Magdalena River, the largest *trans*-Andean river (Sandoval et al. 2017).

Several issues exist with the riverine barriers hypothesis limiting its effectiveness (Haffer 2008). One of these issues is the reduced size of the rivers near their headwaters, allowing for dispersal and gene flow to the other bank. In addition, Amazonian rivers, like many other large rivers in floodplain situations (e.g. the Mississippi), show a propensity to change course dramatically and sometimes transfer large blocks of forest from one bank to the other as oxbows are created (Haffer 2008). Although this generally involves transferring sections of várzea forest, on occasion a change in river course can cut off a region of terra firme forest, as is hypothesized to have occurred along the lower courses of the Tapajos and Madeira Rivers (Willis 1969). Another issue is that strong-flying species which frequently disperse across open areas are not expected to be affected by rivers, a prediction borne out by data on parrots and certain flycatchers (Haffer and Fitzpatrick 1985). However, Sick (1993) describes several cases where species do not show the predicted behavioral responses to large rivers. One, a strong-flying parrot, was found to cross large rivers only rarely, even though it has the potential to do so. Another example involved scattered individuals of "photophobic" antbird species which nevertheless had crossed at least a kilometer of open river to reach small islands. In contrast, Willis suggests that the loss of several antbirds on Barro Colorado Island in Panama after its creation during the flooding of Lake Gatun was due to their behavioral aversion (presumably arising from fear of predation; Willis 1969) to fly across from the mainland in order to replenish the population (Willis 1974).

These problems limit the number and type of species this hypothesis can be applied to, although several very speciose taxa of suboscines including manakins, antbirds, antthrushes, woodcreepers, and others are all likely to be affected by riverine barriers and often show ranges delimited by rivers (where ranges are known). For woodcreepers, 50 taxa (62%) are delimited by rivers in at least a portion of their range, based on the ranges listed in Peters (1951) (Capparella 1987). In addition, headwater areas in at least some rivers may have different landscapes and habitats than are present farther downstream, preventing the movement of animals across the headwater region and leading one set of authors to expand the river barrier hypothesis to include other physical barriers such as patches of open country or small mountain ranges in the headwaters of rivers whose lower courses present barriers (Naka et al. 2012).

River-Refuge Model

A final model consists of the combination of the river barrier and refuge hypotheses into the “river-refuge hypothesis”. In this model, which can also be termed the river-forest contraction model, climatic shifts resulting in the contraction of the rainforests into only those areas surrounding the lower courses of the major Amazonian rivers enabled the rivers to act as a barrier to movement in conjunction with the unsuitable drier forests replacing the rainforests at the headwaters of the rivers (Haffer 2008). The model presumes that gene flow occurring at the headwaters of the rivers prevents them from being complete barriers under present conditions, but that in conjunction with past climate fluctuations they split up a large forest “refuge” into separate areas where speciation could take place. Patterns of hybridization more consistent with this hypothesis than the river barrier hypothesis were found for a number of species between the Xingu and Tapajos watersheds by Weir et al. (2015). This model has been criticized on the grounds that contraction of rainforests from north and south would likely be accompanied by fragmentation along the "conspicuous dry transverse belts that cross southwestern and central Amazonia from southeast to northwest" (Haffer 2008: 927), and the same problems that the refuge model suffers regarding a lack of strong evidence about the extent of fragmentation of Amazonian rainforests also apply here.

Models Not Tested In This Thesis

Several other models exist that will not be tested in this research. Of these, one of the most prominent is the environmental gradient model, proposed by John Endler (Endler 1982a). This states that strong ecological gradients which have driven parapatric speciation exist or have existed in Amazonia. Parapatric speciation is the speciation of populations that are not separated from one another by any barrier but which experience different selective pressures on opposite sides of a major step in the gradient and have reduced gene flow with each other due to low dispersal capabilities. The proponents of this hypothesis state that current ecological conditions can explain many of the distributional patterns present in Amazonia (and elsewhere) without a need for recourse to vicariance events or other historical hypotheses, and that indeed, many authors have focused on seeking historical explanations for variation without eliminating current ecological conditions as a potential explanation (Endler 1982b). The primary argument against this hypothesis is a lack of evidence, with no South American avian taxa demonstrated to support it and few examples of parapatric speciation more generally (Cracraft and Prum 1988, Haffer

2008). Outside Amazonia its application to African rainforests has been contradicted (Mayr and O'Hara 1986), but it has been applied to Australian skinks (Schneider et al. 1999) as well as to *Andropadus virens*, an African rainforest passerine (Smith et al. 2005).

Another paleogeography model that has not been tested in this research is the arch model. This model asserts that the effects of several geologic structural arches, or areas in which the basement or other early stratigraphic layers are exceptionally high, have divided Amazonia into multiple subbasins, with the uplift and subsidence of these arches through tectonic activity causing fluvial perturbations and changes in drainage and subbasins, which then result in isolation and differentiation of the biota (Rasanen et al. 1987). The original exposition of this model limited it to fish, but Leite and Rogers (2013) review several other studies documenting possible effects on amphibians and small mammals as well, although some of these studies were unable to rule out other vicariance events occurring during the same geologic timeframe, and no studies have investigated the potential importance of this model for birds. The model based upon these arches assumes that some surface expression of the arches served as a barrier to forest species, but this has been strongly challenged on the grounds that the arches are unlikely to have posed any sort of barrier for terrestrial vertebrates since even currently "young" arches appear only as slightly raised areas with no difference in habitat at present (Rossetti et al. 2005, Haffer 2008). Indeed, arches do not necessarily appear as a raised area on the surface, but can simply take the form of areas where Cenozoic formations lie nearly directly atop the particularly high basement, with little or no intervening layers and no increase in elevation over nearby regions with a lower basement (Caputo and Amaral 2016). Arches may have indirectly affected birds and other vertebrates through their role in redirecting the Amazon River from a western- and northern-flowing course to an eastern-flowing course, although the barrier would in this case be the river, not the arch. This subsidence and subsequent redirection would potentially have a greater effect on species isolated by the change in river catchment basins (Leite and Rogers 2013). A recent review by Caputo and Amaral (2016) clarifies certain details about the locations and movements of these arches (for instance that the subsidence of the Gurupá Arch in particular was responsible for the redirection of the Amazon River to its present path to the Atlantic in the Late Miocene), but does not provide any reason to reconsider the criticisms of the arch model described above.

A final model not tested in this thesis is the museum hypothesis. This hypothesis states that speciation occurred primarily in small localized pockets of habitat in mountainous areas, with the species produced in this way then spreading out of these locations over time and accumulating in adjacent areas as in a museum (Fjeldså et al. 1999). Speciation in these localized pockets continually produces species, which, as they are produced, leave these speciation centers and enter nearby areas, where they persist but do not speciate further. Thus adjacent areas serve as a "museum" for species produced elsewhere. This model may be applicable to Andean species, but any generalization to the Amazon Basin is not supported (Haffer 2008). Its exposition in Fjeldså et al. (1999) was confined to Andean cloudforest species, and the application of the concept outside of the Andes ignores the enormous differences in habitat type between the proposed speciation centers and the lowland Amazon Basin.

Models Outside Amazonia

Besides the Amazonian biogeographical models described above, other models have been proposed in areas beyond the confines of the Amazon Basin but within the range of *Glyphorynchus spirurus*. These include Central America (Panama), the Chocó region on the Pacific slope of northwestern South America, and the Atlantic Forest of Brazil.

The isthmus of Panama appears to have closed completely during the Pliocene, but to have closed briefly in the late middle Miocene prior to being breached in the late Miocene (Collins et al. 1996, Hosner et al. 2015). Prior to this time, dispersal of South American understory birds into Central America would have been unlikely. Repeated dispersal events after the closure of the isthmus appear responsible for patterns seen in quail (Hosner et al. 2015) and doves (Johnson and Weckstein 2011).

Many of the models proposed for the Chocó region mirror those of Amazonia. For instance, a marine transgression model stresses the importance of sea-level rise for fragmenting populations in the Chocó, while also recognizing the importance of the uplift of the Andes and of dispersal events across the northern edge of the Andes (Nores 2004). There is also a model proposing that recent climatic fluctuations resulted in forest refugia in this area (Haffer 1967). Other authors emphasize dispersal around the northern Andes (Cuervo et al. 2008) or are unable to differentiate between the competing hypotheses (Brumfield and Capparella 1996).

The Atlantic Forest of Brazil, which is currently disjunct from Amazonia but contains numerous lineages which are closely related to those found in Amazonia, has been hypothesized to have been connected to Amazonia via the expansion of forest across northeastern Brazil during wetter periods of the Pleistocene (Auler et al. 2004). Recent work with suboscine bird lineages supports the novel hypothesis that the Atlantic Forest was linked to the Amazon Basin via a southerly route through Bolivia during the Miocene, and via a northerly route during the Pleistocene, as opposed to only being linked through the northerly route during the Pleistocene (Batalha-Filho et al. 2013).

Methods of Addressing Biogeographical Models

Understanding that none of these models can be expected to account for all variation in Amazonian species, but that a strong model should explain a large proportion of the variation, at least for some types of ecologically similar organisms such as understory birds, there are two main methods used to address the biogeographical models described above. The first approach is to falsify the underlying geologic or climatic assumptions of each model. However, our knowledge is still too incomplete for this approach to be effective for most of the models. Certain models have been effectively rejected on geological grounds, such as the arch model (Rossetti et al. 2005) or Frailey et al. 's (1988) original version of the lake model (Haffer 2008). In other cases, the current state of geological knowledge cannot discriminate between plausible and implausible models (Haffer 2008).

The second approach is to compare observed species distributions or patterns of intraspecific variation to those predicted under a given biogeographical model. Because any model purporting to explain diversification in Amazonia must be borne out not only by geological evidence but also by the ability to explain the distributions of many species (Capparella 1991), this second approach more directly reaches the heart of whether a given model is plausible, even as it is less likely to produce clear, incontrovertible results due to both the muddying effects of individual species responses to the proposed vicariance events and of any changes to the distributions of individual species long after the presence of the proposed vicariance events. This method requires that the species used must be chosen with care. Species must be variable across their range, must be widespread enough to test the models, and must show adaptations making it likely that their distributions would be affected by the vicariance events proposed under each model but not subject to major changes after those vicariance events.

One group of organisms commonly used to test biogeographical hypotheses in Amazonia are relatively sedentary rainforest understory birds (Haffer and Fitzpatrick 1985, Capparella 1988). Sedentary organisms are more useful for biogeographical studies than more mobile species because there will be less gene flow between populations to obscure patterns of divergence, and because more of the mechanisms proposed by the different hypotheses may apply to them. Understory bird species in particular often have an aversion to crossing light gaps between patches of forest (Lees and Peres 2009), and this compounded with a sedentary nature means that they are exceptionally prone to both historical and current barriers to gene flow, if those barriers really existed. The most useful understory bird species are those with wide ranges, because this permits testing of models across the entirety of Amazonia and such birds are also not as likely to have undergone major changes in overall distribution in the extensive time period between the present and the proposed vicariance events.

This second approach has been used primarily in phylogeographic studies, in which phylogenies produced using genetic data are interpreted in terms of geography (e.g. Aleixo 2004, Fernandes et al. 2012, Leite and Rogers 2013). Very few studies have used phenotypic data, probably because molecular clock methods used to determine the age of a clade do not work with morphological data; however, in one case using species with genotypic and phenotypic data, phenotype was found to be a good proxy for genotype (Naka et al. 2012). Since phenotype can often change more rapidly than mtDNA (Patten 2010), studies mapping phenotypic characters may be more likely to show the full history of divergence within a species despite failing to provide the estimated times of divergence.

Introduction to Studies of Geographic Variation

Biogeography requires an understanding of geographic variation to answer basic questions. However, geographic variation in organisms is important in its own right. Patterns of geographic variation in both genetic and morphological characters illuminate the selection pressures affecting those characters as well as the evolutionary history of those characters. In addition, they allow us to discover the evolutionary history of the species exhibiting those characters (Zink and Remsen 1986). Besides being necessary to answer these questions, characterizations of the patterns of variation in an organism are also able to answer questions in other fields, especially systematics.

Accurate characterization of geographic variation is the first step in all taxonomic decisions (Zink and Remsen 1986, Remsen 2010). Zink and Remsen (1986) lay out a plan for a modern protocol for sampling and analysis of geographic variation, the last step of which concerns identifying diagnosable clusters of organisms, including those deserving the ranking of subspecies. Such emphasis on ensuring the validity of any patterns of clustered variation recovered and placing them within the context of a more general characterization of variation is important because all patterns of variation can be informative and useful for answering questions about the evolutionary history of a species. Which patterns will be most informative will depend on the question being asked. One example of such a question tests the existence of ring species, as in Patten and Pruett's use of both clinal variation and subspecies to document a ring species among several Southwestern populations of the Song Sparrow (*Melospiza melodia*) (Patten and Pruett 2009). Another type of question tests the effects of steep environmental gradients, which are predicted to result in strong clinal variation and to cause parapatric speciation (Endler 1982a). A third example is testing the predictions of certain vicariant biogeographical models, which predict diagnosable clusters to occur in certain regions separated by the proposed barrier (Capparella 1991). Each of these examples focuses on different aspects or combinations of aspects of geographic variation to address a question about a species' evolutionary history.

The Subspecies Concept

One of the primary tools used in characterizing geographic variation is the subspecies rank. The definition of a subspecies varies depending on the author, but one of the clearest expressions by a major proponent of the concept states that a subspecies is “a distinct population, or group of populations, that occupies a different breeding range from other populations of the same species; individuals are distinguishable from those other populations by one or more phenotypic traits at the 95% level of diagnosability” (Remsen 2010).

This definition is not universal, and although it shares much with other recent definitions, certain aspects such as individual diagnosability, the requirement for phenotypic diagnosability, and the use of the 95% level of diagnosability do not appear in every statement of what a subspecies is (Remsen 2010). Other definitions may use a 75% level of diagnosability (Amadon 1949), or omit such a level entirely. However, the Remsen (2010) formulation encapsulates a rigorous, statistically-based idea of the sort of variation encompassed by the term “subspecies”, and is both the most defensible and, when paired with other forms of geographic variation such as step clines (in which clinal variation exists on each side of a sharp change in character expression), the most biogeographically useful expression of the subspecies concept.

The subspecies concept is closely associated with the biological species concept (BSC), which claims as a species any cluster of populations which can interbreed but are reproductively isolated from all other such species. Indeed, Remsen (2010) claims that subspecies add a second layer of information about a species under the BSC, since while the species definition is concerned with processes related to the current biology of the populations (namely the ability to interbreed), subspecies allow the BSC to express information about the past evolutionary history of the species as well. Subspecies are thus similar to, if not quite equivalent to, the minimum diagnosable units (the evolutionary units of Cracraft 1983) labeled as species under the phylogenetic species concept (PSC) (Remsen 2010). The PSC considers a species to be the smallest population with a common ancestor which is distinguishable from other such groups by some derived heritable trait. Under this definition, any valid BSC subspecies will be labeled a species (although some BSC subspecies might include several phylogenetic species), meaning that there is no need for a separate category for subspecies.

Justification for the Use of the BSC

The subspecies concept as well as the manner in which it has historically been applied have drawn extensive controversy over the past half-century or more (e.g. Wilson and Brown 1953, Zink 2004). Recognizing this, it is necessary to justify not only the usefulness of the subspecies concept itself but also my choice of the BSC as the species concept under which to operate. Despite the growing influence of the PSC, ornithologists have generally found that the

BSC works well for birds and successfully delineates species boundaries in most cases (Mayr 1992).

Arguments against the BSC often focus on its inapplicability to many groups of organisms (especially asexual ones) and the inability of applying its primary criterion of reproductive isolation to allopatric populations. The latter argument emphasizes that the PSC is "multi-dimensional" in terms of time and space and ranks all populations based on their history, while the BSC is one-dimensional and can only be easily applied to sympatric populations, with allopatric populations requiring the use of secondary criteria as proxies for reproductive isolation (McKitrick and Zink 1988). However, as acknowledged by McKitrick and Zink (1988), the BSC does rank allopatric species, even if in these cases it must settle for focusing on whether the degree of difference in characters known to be important indicators of reproductive barriers is similar to that found in sympatric, reproductively isolated species. It is a matter of opinion as to whether a species concept should be allowed to work thus by “proxy”. As to the non-dimensionality in time, the use of subspecies allows for the ranking of distinct lineages within a species, while still preserving the biological information present in the rank of species under the BSC that would be lost under the PSC (which includes no reference to the current biology of the species) (Remsen 2010).

The other argument, that the BSC is not applicable to all types of organisms (Ehrlich 1961, Cracraft 1987, McKitrick and Zink 1988), such as asexual organisms, is again, a matter of opinion because scientists may differ about whether it is necessary to rank all organisms under the same species concept (Mishler and Donoghue 1982). This criticism is also not relevant to the use of the BSC for groups that it does differentiate well, such as birds. Among North American birds, the vast majority of populations (all but 46 from 607 species) were unambiguously ranked by the BSC (McKitrick and Zink 1988). Similarly, a survey of the flora of New Hampshire found less than 7% of taxa to present difficulties for the BSC, despite plants being considered one of the more difficult groups to classify under the BSC (Mayr 1992). However, Mayr's study was criticized for using species delimitations based in many cases on morphological characteristics and not solely on the existence of reproductive isolation (Whittemore 1993). To obviate the difficulties posed by more problematic taxa, some authors have recommended a species concept based primarily on the BSC but including aspects of other species concepts (Johnson et al. 1999), but this has not gained widespread acceptance and also faces problems with a few difficult taxa. An alternative view considers the BSC preferable for most organisms but believes other species concepts are useful in classifying those organisms for which the BSC encounters insurmountable difficulties (Mayr 1992).

Justification for the Use of Subspecies

The subspecies rank offers an additional level of information to users of the BSC, namely information about the evolutionary history of lineages within a species (Remsen 2010). However, not only has its usefulness often been obscured due to improper application, but debate has raged around it on other grounds as well. Those who favor the PSC argue against retaining the subspecies as a rank for various reasons, including that subspecies obscure diversity, produce incorrect phylogenies as compared to those produced via genetic methods, and injure conservation (Zink 2004). But even among BSC advocates, there are arguments against the use of subspecies, at least in its traditional usage.

For instance, it has been argued that there may not be concordance among the patterns of variation in the characters used in defining subspecies (Wilson and Brown 1953). This prevents objective designation of subspecies, since among several non-concordant but heritable characters, no one character can be favored over another. However, although subspecies cannot be used in those cases, such conflicts are relatively uncommon as concordance of characters within a species is the rule for the vast majority of bird species (Remsen 2010).

A similar argument is that unlike most other taxonomic ranks, many subspecies are only informative in terms of the specific characters used in their description (Barrowclough 1982). Barrowclough (1982) argues that membership in a ranked taxon predicts similarity to other group members of that taxon in characteristics beyond those by which the taxon is diagnosed, but that the same is rarely true of subspecies because of the small number of characteristics used in subspecies diagnosis and the high probability of non-concordance of a single character with other unstudied characters. He therefore recommends that studies of geographic variation in many characters should be undertaken before subspecies are described, and that these descriptions should use multiple characters (Barrowclough 1982). However, if conflicts among characters are rare, there is no reason that subspecies cannot be described on the basis of a few characters (or only one) and still possess predictive power. Indeed, studies of the Spotted Owl (*Strix occidentalis*) have found that the traditional subspecies, described using plumage characters that show enough overlap that one author suggested merging those subspecies (Oberholser 1915), reflect well those groupings produced by genetic methods which were used to address questions regarding the species' evolutionary history (Barrowclough et al. 1999).

Another frequent point is the lack of reciprocal monophyly at the subspecies level (Zink 2004). Reciprocal monophyly means that the members of a given population are more similar to each other than to members of another given population, and vice versa, which is used as a way to determine their evolutionary relatedness (i.e. if the members of population A are monophyletic, then they are assumed to be more closely related to each other than to any member of another monophyletic group, and to include all the descendants of a given common ancestor). However, a pair of populations labeled as phylogenetic species (which by definition are supposed to be monophyletic) may only be reciprocally monophyletic at certain genetic loci. There is no guarantee that because they are monophyletic at the loci tested, they are necessarily monophyletic at all or even most loci, and "only if all gene trees within a series of populations that share a common ancestor have topologies that do not conflict can a single population be labeled unambiguously monophyletic" (Remsen 2010: 68).

Thus even phylogenetic species may not be monophyletic if described using only a few genes. As an example of incongruence among gene trees in a well-studied group of organisms, see the work by Pollard et al. (2006) on *Drosophila*. Monophyly at the population level is hardly to be expected given potential differences in rates of character evolution for different characters and complex patterns of fragmentation and secondary contact among populations (Patten 2010). Indeed, Patten (2010) argues that since subspecies are a stage in the process of allopatric speciation and have not yet completely diverged from their sisters, the proper null expectation is that monophyly will not yet exist. Therefore, using its presence as a criterion to assess subspecies does not make sense if subspecies are assumed to be a step in the evolutionary history of a species (Remsen 2010). Subspecies can still be useful for assessing biogeographical hypotheses despite lacking monophyly across all possible characters or even at a single character, however, as long as the characters under study show variability that may have resulted from the events proposed in those biogeographical hypotheses. This is due to the focus being on past relationships among populations rather than on the current persistence of monophyletic populations.

Another argument is that subspecies are often labelled on the basis of phenotypic differences that do not hold up to the results from genetic studies (Zink 2004). However, just as not all gene trees for a given species are expected to yield identical results because they focus on different genetic characters, phenotypic characters are not expected to yield identical results to any given gene tree (Remsen 2010). This of course assumes that the phenotypic characters in question have a genetic basis, and that the genes regulating them have simply not yet been identified and studied. In addition, many studies showing discordance between genetic and phenotypic characters have only sampled a minuscule proportion of an organism's genes, and cannot claim that this discordance would extend to a much greater number of genes (Remsen 2010). Some studies, such as Barrowclough et al. (1999), have indeed found concordance between subspecies and groupings produced using mtDNA. In fact, some of the authors arguing against the use of subspecies based primarily on morphology focus almost exclusively on mtDNA and draw all their conclusions from a few genes from this source (Zink and Barrowclough 2008). In these cases, it is argued that nuclear DNA is a lagging indicator of divergence and therefore not as useful in detecting recent speciation (Zink and Barrowclough 2008).

However, in many cases mtDNA is a more lagging indicator than phenotypic characters if the latter are acted on by selection. Depending on the speed of divergence and what forms of natural selection may be acting on the population, a number of different scenarios might result in which populations may be distinct phenotypically but not at a neutral genetic locus, or even vice versa (Patten 2010). Morphological diagnosability of subspecies can thus be more useful at times than genetic diagnosability, since morphology is often more sensitive to selection (Remsen 2010). Microsatellite frequencies can also be used as a way of detecting recent divergence that would be missed by the use of mtDNA (Pruett and Winker 2010), although it is challenging to choose informative microsatellites (as with any genetic character but especially so in this case because sequences are so short) and there is a danger of back mutations with any genetic character because of the limited number of character states available. Finally, many of the studies showing a lack of genetic differentiation among subspecies have been done on Nearctic and Palearctic continental birds, and it has been shown that many more subspecies in the Southern Hemisphere and/or on islands are indeed genetically distinct as well as phenotypically distinct (Phillimore and Owens 2006). For these reasons, the theoretical arguments against the usefulness of subspecies are flawed and should not impede the continued use of subspecies where appropriate.

The Need for Improved Use of Subspecies

One of the most frequent arguments against using the rank of subspecies, mentioned as far back as the middle of the last century, is that subspecies names are injudiciously applied to all manner of populations with scant differentiation and diagnosability (Amadon 1949). This is true. However, it is not a weakness of the subspecies concept itself, but only a problem in application which can be solved through careful revisions (Patten and Unitt 2002, Remsen 2010). Very few studies which make use of subspecies begin by revising those subspecies classifications by the use of statistics, but this is a necessary step not only to amend our knowledge of the true patterns of variation in those species but also to ensure that valid conclusions are drawn from the analysis making use of those subspecies (Patten and Pruett 2009). If the subspecies in question are not valid, then blindly using them as units for biogeographical or other analyses may invalidate those analyses (Patten and Unitt 2002).

One reason so many subspecies names do not capture real patterns of variation is that they are often based on insufficient sampling. Large series of specimens from all areas of the range are necessary for a complete picture of geographic variation, but such series are difficult to collect for practical reasons. Another, less practical, reason is that subspecies were often described in an era before the wide application of statistics, or by scientists who were unaware of the proper use of statistics and often classified individuals based on qualitative differences in appearance (Remsen 2010). As early as the 1940's, a technique was in place to determine the percent of individuals in two populations which are diagnosable (Amadon 1949), and although this has been subsequently refined, many authors still focus on mean differences in populations, a method which is potentially misleading (Patten and Unitt 2002).

Mean differences are misleading because two populations may overlap extensively in values for a given character but still have significantly different means, especially as the sample size grows larger (Patten and Unitt 2002). If subspecies are important as a way to classify intraspecific patterns of variation, it follows that individuals must be diagnosable to one subspecies or another (or neither) for the subspecies to be useful. Focusing on mean differences, a researcher would potentially find spurious patterns (Type I errors) not reflected in the actual individuals used in calculating those means (Skalski et al. 2008).

There have been several approaches used to diagnose members of subspecies. A well-cited one developed by Amadon (1949) was a separation of 75% of individuals of one population from more than 99% of individuals from another population, using a normal distribution with Z scores. Essentially this was a way to compare the degree of overlap among populations to that of an expected distribution with complete overlap of populations, rather than simply comparing mean differences (Patten 2010). This tactic has been improved to take into account non-normal distributions by replacing the Z-score with a similar D-statistic (Patten and Unitt 2002). In addition, Patten and Unitt (2002) recommended raising the cutoff for diagnosability from 75% to 95%, in order to increase the rigor of classifications, which has been reiterated by Remsen (2010). These methods, while excellent for cases with only one or a couple characters, require amendment when dealing with many characters at once. One recommendation is that the scores from each character be combined in a Principal Components Analysis (PCA) (Patten and Unitt 2002); canonical discriminant and discriminant function analyses have also been used (Marantz and Patten 2010). Other multivariate techniques have been proposed, such as MANOVA, which is claimed to have high likelihoods of Type I errors if clinal variation exists, and cluster analysis, which exists in a number of forms but may lack objective criteria by which to assess results (Skalski et al. 2008). Some spatial statistics such as kriging are also promising, but must be used in a univariate context or with principal components derived from a PCA (Skalski et al. 2008). However, unlike techniques such as MANOVA, the spatial statistics by their nature show the actual portions of the species range where differences are located. Non-spatial statistics will only tell whether or not differences exist, not where they are, which is critical for testing biogeographic hypotheses.

The subspecies concept is one way to express certain patterns of variation which may occur within a biological species, and not all species will include subspecies. There are some species which show no differentiation across their entire range, while many others show clinal variation in which values for a given character vary smoothly across a particular area with no objectively definable break points. Others may show a step pattern similar to a cline but with large areas of certain values and small clines in between these. This variety has led to some authors opposing the use of subspecies because in intermediate cases defining subspecies can be based on individual subjective judgment and even “art” (Fitzpatrick 2010), but eliminating subspecies altogether rather than limiting their use to unambiguous cases may lead to a loss of valuable information, namely which geographically well-circumscribed populations within a species have undergone a great enough degree of divergence to be diagnosable as different from all other populations, potentially even as incipient species. Therefore, the most appropriate response to the various criticisms of subspecies is to acknowledge the place of subspecies as one form of variation that should be implemented whenever statistically justified, rather than as a primary, *a priori* goal of a characterization of variation (Zink and Remsen 1986).

The Wedge-billed Woodcreeper As a Study Organism

The choice of *Glyphorynchus spirurus* (Vieillot) 1819, or the Wedge-billed Woodcreeper, as my study organism enables me to address all three goals of this research, namely to characterize variation in key morphological characters, to address the major Amazonian biogeography models, and to revise the subspecies taxonomy of the species.

This species, a member of the Dendrocolaptidae (woodcreepers, sometimes considered a subfamily of the Furnariidae), inhabits primarily lowland tropical rainforest throughout Amazonia, parts of northwestern South America, the Atlantic Forests of Brazil, and much of Central America (Marantz 2003) north to southern Veracruz and eastern Oaxaca, mainly on the Caribbean slope, in Mexico (Howell and Webb 1995). It ranges up to 1500 m elevation in the Ecuadorian Andes (Mila et al. 2009). Within Amazonia, it can be found in both terra firme and várzea forest, as well as slightly human-disturbed forest habitats (Marantz 2003). The Wedge-billed Woodcreeper is among the most commonly encountered birds in terra firme forest habitats based on captures in mist nets (Remsen and Parker 1983), but it has far lower estimated densities in várzea forest (Marantz 2003). Although interspecific aggression is known to be important in community assembly of other woodcreepers in these habitats (Robinson and Terborgh 1995, Beja et al. 2009), no competitor is known for this species. Its unique bill shape and appearance more similar to a xenops than to other woodcreepers (Marantz 2003) may lessen competition with other woodcreepers but expose it to other potential competitors such as *Xenops minutus*.

The abundance and wide range of this species make it a good choice with which to address biogeographical hypotheses. Equally important, it is extremely sedentary, with an estimated dispersal distance of 0.1 km or less (Bates 2002). In comparison, more mobile species such as parrots may traverse many kilometers in one day (Haffer and Fitzpatrick 1985). Its sedentary nature and reliance on the forest understory make it likely to have been subject to any geographic barriers to gene flow which may have existed during the period of its existence. In addition, the species is placed in a monotypic genus that is one of the most basal branches of the Dendrocolaptidae and appears to have diverged from the common ancestor of other woodcreepers sometime between 24 and 17 million years ago (Derryberry et al. 2011). This time range lies within the early Miocene, meaning that vicariance events in any of the biogeographic hypotheses described above could have affected the evolution of variation within this species.

There are either thirteen or fourteen currently recognized subspecies (listed below in Table 1), depending on the source, with Marantz (2003) merging *sublestus* with *pectoralis*. This signals a large amount of morphological variation in the species, another necessity for biogeographical studies and a ripe opportunity for characterizations of morphological variation. In addition, there is speculation that the Wedge-billed Woodcreeper actually includes multiple cryptic species, due to the existence of three distinct song types across its range (Marantz 2003). Song is one of the principal traits used in mate choice in many passerines, meaning that differences in song often signal reproductive isolation and potential speciation (Price 2008: 213). Two of these song types are a relatively similar long, fast series of slurred whistles, and are found in Central America and in northern and western Amazonia, while the third song type, found in southeastern Amazonia and the Atlantic Forests, is a pair of clear whistles. It is unknown whether these song types show geographic concordance with variation in other characters within the species (Marantz 2003). However, the potential existence of cryptic species could affect conclusions drawn in studies sampling the entire range of the Wedge-billed Woodcreeper, and should be addressed by investigating whether variation in morphology and song type are concordant.

Table 1

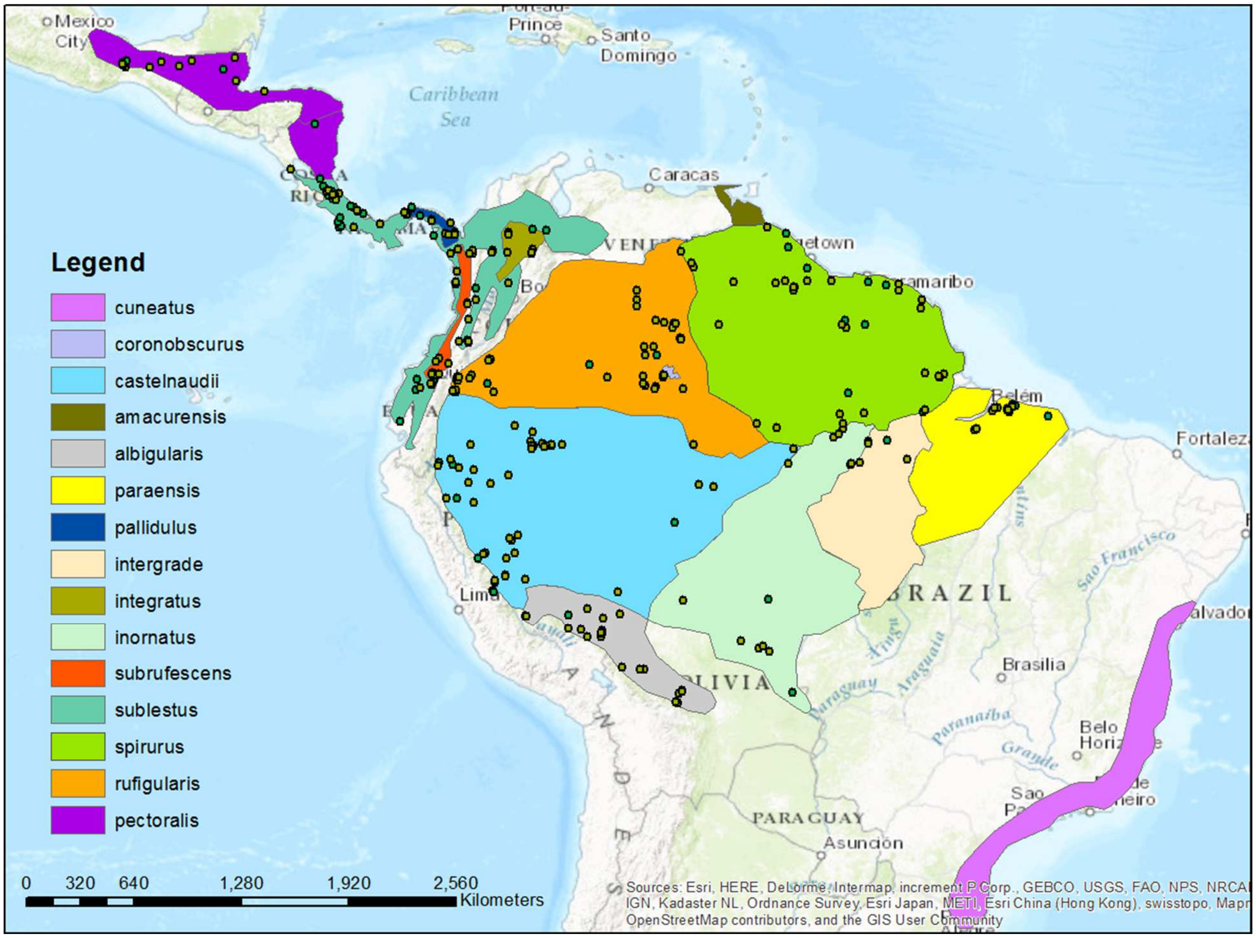
Current Subspecies of Glyphorynchus spirurus

Subspecies	Date described	Approximate range
spirurus (nominate)	1819	NE Amazonia: N of Amazon, E of Rio Negro
cuneatus	1820	Coastal E Brazil (N Bahia south to N Espirito Santo)
castelnaudii	1855	W Amazonia, S of Amazon and Napo, S to Junin, Peru, and W of Rio Madeira
pectoralis	1860	Northern Central America from Mexico to Costa Rica
albigularis	1923	SE Peru (Puno) and N Bolivia, S to La Paz, Cochabamba
sublestus	1929	Southern Central America from Costa Rica S into Colombia
inornatus	1934	S Amazonian Brazil: S of Amazon, W of Tapajos, E of Madeira, S to SW Mato Grosso, also in NE Bolivia (Santa Cruz)
rufigularis	1934	NW Amazonia, W of Rio Negro and N of Amazon and Napo
integratus	1946	N Colombia and W Venezuela
subrufescens	1948	Pacific coast of SE Panama, W Colombia, and W Ecuador: Chocó region
amacurensis	1952	NE Venezuela (Sucre, Delta Amacuro)
coronobscurus	1955	Cerro de Neblina, Venezuela
pallidulus	1970	E Panama and adjacent NW Colombia
paraensis	1974	SE Amazonian Brazil: E of Rio Xingu

Note. All information is from Marantz (2003), with the exception of *sublestus*, which is found only in Peters (1951) because Marantz (2003) subsumed it into *pectoralis*.

The species is also due for a full revision of its subspecies using modern statistical methods (Fernandes et al. 2013). Many of its subspecies were described in the 19th and early 20th centuries (see Table 1) and were therefore not defined using contemporary standards. In some cases, even early authors believed the range of variation in some subspecies to lie mostly or entirely within the range of variation in other adjacent subspecies, casting doubt on the validity of those subspecies (Hellmayr 1925). In addition, characterization of the intergrades between this species' subspecies is needed, as there are only two currently described intergrade regions, which is likely an underestimate (Peters 1951, Marantz 2003).

Other work on the subspecies of the Wedge-billed Woodcreeper has also sometimes generated as much uncertainty as it eliminated, with two examples being the lack of a revision of the subspecies ranges upon description of several new subspecies, and a lack of justification given for the elimination of *sublestus* by Marantz (2003). The description of *pallidulus, subrufescens*, and *integratus* placed three subspecies within the former range of the previously described *sublestus*, but in no case were the boundaries of *sublestus* clearly revised, so its currently inferred range exists in several nearly or possibly completely disjunct patches in Central America and northern South America (Figure 1). To compound matters, when Marantz (2003) subsumed *sublestus* into *pectoralis*, he failed to explain his reasoning for doing so. These errors must be remedied in order to remove subjectivity from the subspecies taxonomy of this species.



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, Mapm OpenStreetMap contributors, and the GIS User Community

Figure 1. Current subspecies ranges of the Wedge-billed Woodcreeper. Ranges were prepared from Marantz (2003) and the original descriptions. Locations for which specimens exist that were used in this study for a subspecies revision are marked by green points.

In order to properly evaluate the subspecies listed above, it is necessary to also analyze the characters by which they were originally defined (Patten and Unitt 2002). Although several genetic studies have been done on the species (though not over its full range), their findings may not reflect the variation present in its morphological characteristics and it is important to consider the bird’s phenotypic characters as well as genetic (Marks et al. 2002, Mila et al. 2009, Fernandes et al. 2013). Previous studies have never covered more than about 80% of the species' range (with the areas in which extensive sampling has occurred being far lower, closer to 30%), and no study has sampled more than 8 of the 14 subspecies.

Previous Work on the Wedge-billed Woodcreeper

Recent genetic work on the Wedge-billed Woodcreeper has not found concordant patterns with the current subspecies groupings, which has led one set of authors to specifically call for rigorous work to be done using morphological characters in order to determine whether concordance does or does not exist (Fernandes et al. 2013). In an early study, Marks et al. (2002) sampled 3 mtDNA fragments from 72 individuals at 30 localities scattered across the range of the species. However, despite this extensive sampling design, locations in northern and central Amazonia and northwestern South America were poorly represented by existing specimens. This study found that there was some support for one published biogeographic hypothesis regarding the connections among South American areas of endemism, and that there was some discordance between their mtDNA results and subspecies based on morphological data, specifically concerning populations in southwestern Amazonia (subspecies *inornatus* and *albigularis*) (Marks et al. 2002).

A study by Mila et al. (2009) investigated the patterns of variation in the Wedge-billed Woodcreeper on either side of the Ecuadorian Andes. They used an mtDNA sequence and 136 nuclear AFLPs, as well as limited morphological data, and found significant structuring of populations, with western and eastern Andean populations forming different clusters. Morphological data showed some differences with elevation, leading the authors to suggest different selective pressures at different elevations due to habitat differences, specifically differences in tree density and in the amount of moss on tree trunks (Mila et al. 2009).

Fernandes et al. (2013) provided the most in-depth genetic study of the Wedge-billed Woodcreeper to date. They sampled 134 individuals from 63 localities throughout the majority of the South American range of the species, but with particularly high sampling in the Madeira-Tapajos interfluve and spotty sampling in some other parts of South America. They used sequences from 2 mtDNA and 3 nuclear genes. Their results generally support the role of rivers as vicariance barriers, although some large rivers did not delimit groupings. In addition, they found widespread cryptic diversity and discordance with the current subspecies taxonomy, although not in the same places as Marks et al. (2002), leading them to call for morphological analyses (Fernandes et al. 2013).

In a later study, Fernandes et al. (2015) used *Glyphorynchus spirurus* and two other species to test whether rivers were delimiting clusters of variation in the Madeira watershed. This study only used one mtDNA sequence and had limited geographical sampling, although it did choose sites on either side of all major rivers in the watershed. It found that even small rivers appear to serve as boundaries for this species in this area, with genetically differentiated populations on opposite sides (Fernandes et al. 2015).

Finally, a study by Weir et al. (2015) investigated SNPs (4631 loci) in 12 individuals of the species from the Tapajos-Xingu interfluve and watersheds, and found evidence for mixture of populations near the headwaters of these rivers. However, their sample size was quite low, with only 12 individuals. All the studies summarized above show the need for improved characterization of morphological variation in this species, comparisons of morphological data with genetic data and revision of the current subspecies groupings using morphological data, and broader and/or denser geographic sampling in order to more effectively answer biogeographical questions.

Hypotheses and Predictions

There are a number of biogeographical hypotheses and systematics hypotheses tested in this research. Each of the six biogeography models is a separate hypothesis about the origin of variation in the species, and each of the fourteen current subspecies groupings and rankings is a separate hypothesis. The first objective, being a characterization of variation, does not have any associated hypotheses besides a null hypothesis that there is no variation in the characters studied.

Testing the subspecies hypotheses is straightforward and takes the form of determining how many specimens from the range of each subspecies are mis-assigned in a discriminant function analysis. The alternative hypothesis (the existence of the subspecies as a diagnosable entity) is only accepted when a population can be diagnosed using the 95% rule described previously.

Testing the biogeographical hypotheses is more complicated due to the uncertainties inherent both in the predictions found in the literature for each model and in my data set itself. The latter set of uncertainties concerns exact locations of specimens as well as what character values exist in the areas without specimen coverage. These two sources of uncertainty do not permit me to use measures such as the centroid distance, percent overlap of predicted and observed polygons, or location of observed suture zones to definitively address the biogeographical hypotheses. Therefore, I used a method comparing expected and observed rates of significant clustering within and outside of polygons where clustering is predicted under each model. A nonsignificant result obtained with this measure signifies that the clustering pattern is not different from what is expected by chance, and thus that support is lacking for that model and therefore the null hypothesis remains in effect. A significant result, however, does not automatically signify support for the model in question. A significant result could be produced as a result of strong influences by points whose pattern contradicts that expected under the model. Or, significant results may signify that there is very strong support for one or a few polygons but not for the entire set of polygons. The prediction polygons for each model are discussed below in Chapter II (Methods).

A final hypothesis concerns my use of specimen locations with imprecise location data. The addition of these might inadvertently skew the results obtained, so to test for this possible effect I have run all my analyses on three ever-smaller data sets with ever-increasing stringency in location data. The hypothesis is that removing records with doubtful location data will affect the results because of the decreased sample size. I predict that this hypothesis will not be supported. Due to the large size of the data set even after the removal of doubtful records or records that are missing data in any of the variables (552 males and 373 females), I predict that removal of such data will not affect the results.

CHAPTER II: METHODS

In order to address the three objectives, I used a combination of mapping and statistical methods in ArcMap (ArcGIS 10, ESRI, Redlands, CA) and the SAS statistical software package (SAS 9.4, The SAS Institute, Cary, NC). The first objective, characterizing variation in the species, was accomplished by generating contour maps in ArcMap for all specimen characters in my original dataset. The second objective, determining which biogeographical models were best supported by the data, was addressed using cluster analyses in ArcMap after reducing the number of variables involved with a canonical discriminant analysis in SAS. The third objective, addressing the validity of the current subspecies designations in the Wedge-billed Woodcreeper, involved the use of discriminant function analyses in SAS and the measurement of a number of plumage characters from museum specimens at the American Museum of Natural History.

In order to address the biogeographical hypotheses, prediction polygons were manually drawn for all six models. The prediction for the Andean uplift model (Figure 2) consists of two polygons of expected clustering, one comprising most of the *trans*-Andean (western side) areas of Colombia, Ecuador, and the Darién region of Panama, and the other comprising nearly all of the bird's *cis*-Andean (eastern side) range. Certain areas in the Magdalena valley and in *cis*-Andean Colombia and Venezuela are predicted to show no clustering due to more recent gene flow here between *cis*- and *trans*-Andean populations, as this portion of the Andes was the last to arise. These polygons represent clustering (or uniform character expression) expected under a situation where the only important vicariance event in the species' history is hypothesized to be the Andean uplift. This is unlikely to have been the case, but any other combination of this model with others would have unpredictable patterns. Central America is omitted because at the time of the Andean uplift it was not attached to South America and therefore populations there are expected to have been affected by additional events.

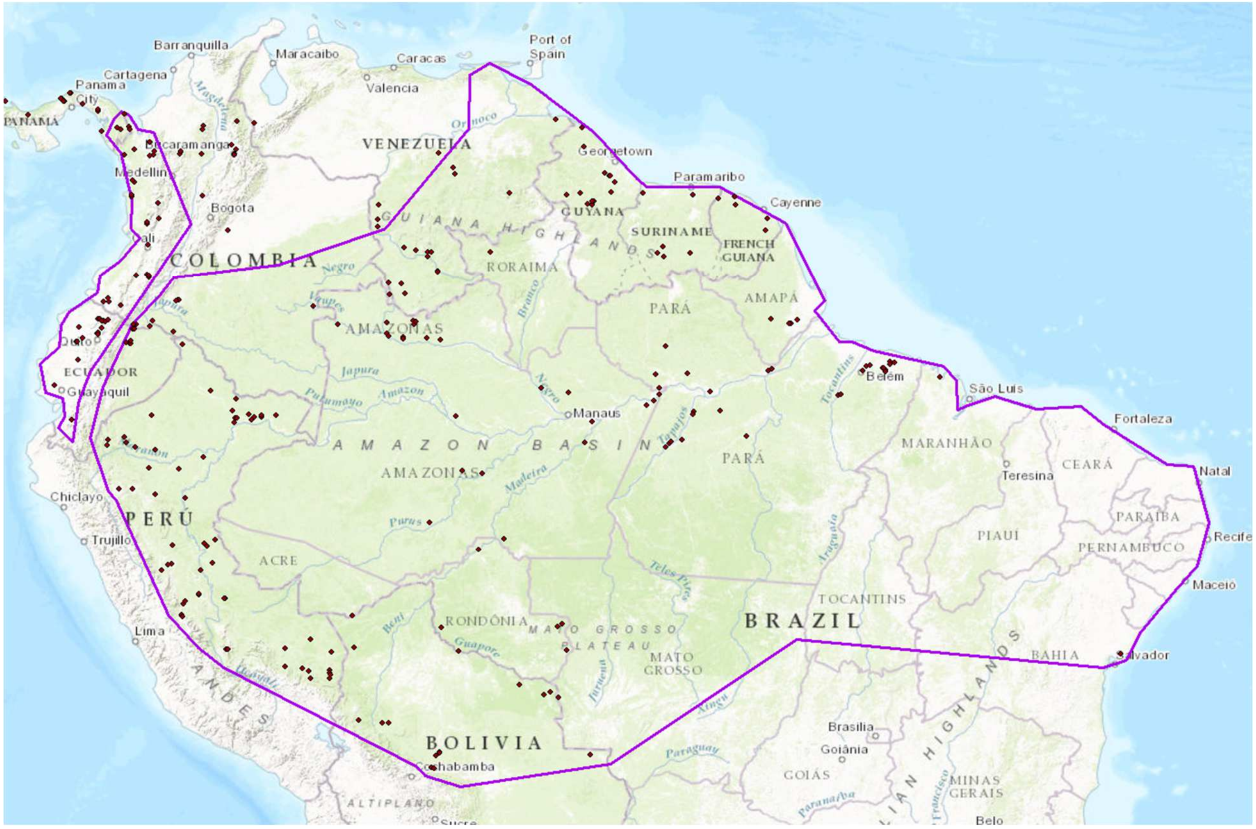


Figure 2. Prediction map for the Andean uplift model. The purple polygons correspond to areas of predicted clustering. Points mark locations with specimen data.

It is particularly hard to extract predictions from the marine incursion model because different authors give widely disparate locations and extents of proposed marine incursions. Therefore, I have created three sets of polygons ranging from spatially conservative to spatially liberal in interpreting this model (Figure 3). In this and all further instances, polygons were created by juxtaposing figures (or combinations of figures, or written descriptions where necessary) from the appropriate articles on the computer screen adjacent to ArcMap, and using river courses, national and department boundaries, and other geographical features as guides to delineate polygons that matched those in the original literature. Slight uncertainties or departures from the original boundaries were permitted (except where rivers served as boundaries) because clustering would be expected to remain present for a short distance as the birds expanded out of the original area of differentiation.

Under the most conservative predictions, based primarily on Nores (1999), clustering is confined to the highest areas of Amazonia which are the Guianan and Brazilian Shields. A more liberal interpretation, based primarily on Hoorn et al. (1995) and Hoorn et al. (2010), places extensive incursions and associated habitats from the Caribbean, and perhaps the Pacific, throughout western Amazonia but not as far south as envisioned under the more conservative predictions, meaning that the areas of clustering are located in the same general region as the conservative prediction but are much larger. The region of either incursion or lacustrine habitat in central Amazonia is also lessened, although a large incursion in the Belém area is predicted. The most liberal interpretation of clustering, based mainly on Hoorn et al. (2010), is similar to the second set of predictions but predicts smaller incursions in all areas resulting in more territory added to each clustered area.

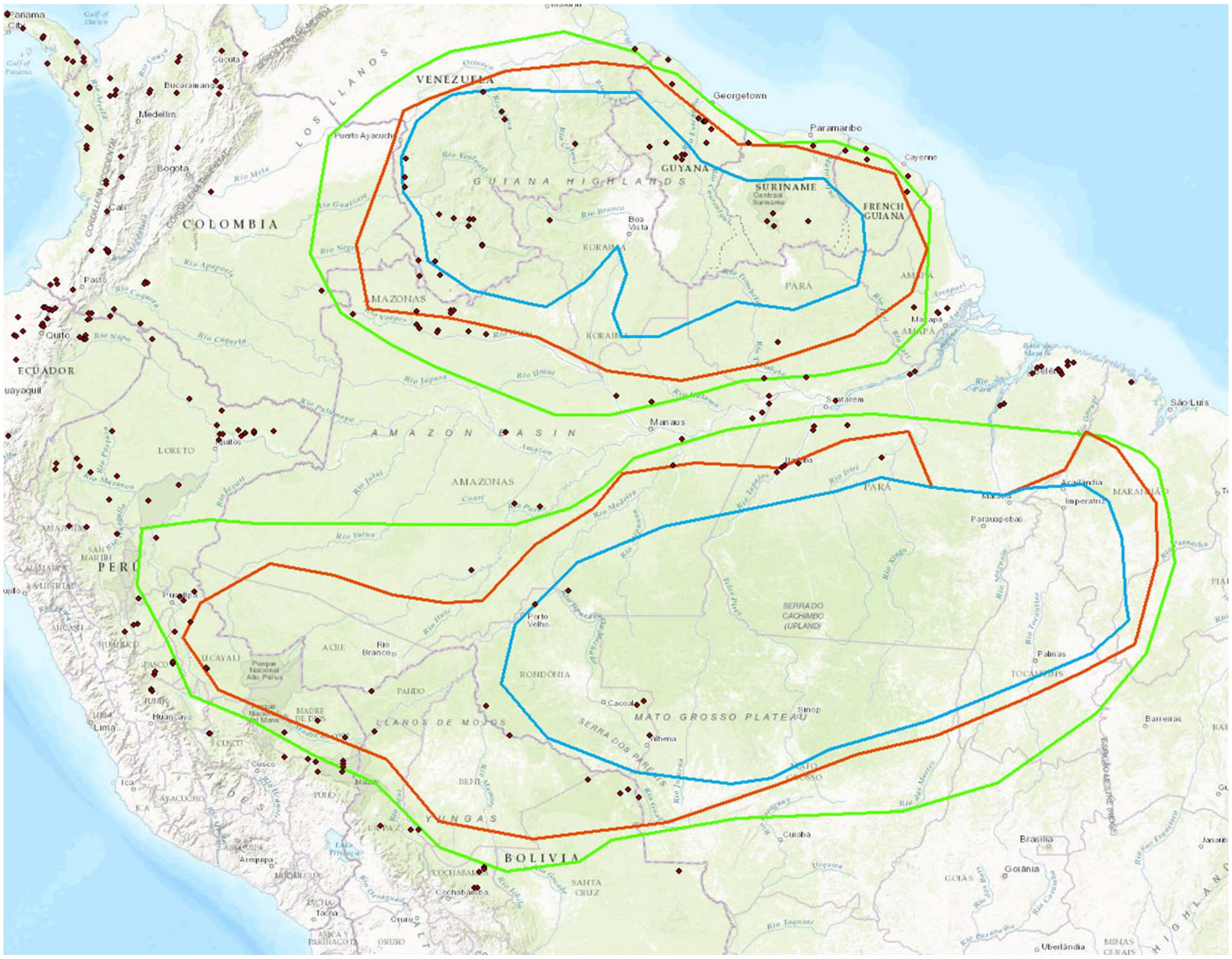


Figure 3. Prediction map for the marine incursion model. The blue polygons correspond to areas of predicted clustering under the most conservative interpretation (Nores 1999), red to a moderate interpretation (Hoorn et al. 1995, Hoorn et al. 2010), and green to a more liberal interpretation (Hoorn et al. 2010). Points mark locations with specimen data.

The predictions for the lake model (Figure 4) consist of more and less conservative areas of clustering. The more conservative predictions are based closely on Hoorn et al. (2010) and predict that the Pebas and subsequent Acre systems would separate three areas of clustering in the Guianan Shield, Brazilian Shield, and the fringe of the Andes, with the placement of the thicker portion of the Andean cluster following Hoorn et al. (2010). The less conservative clustering predictions are based on a looser interpretation of Hoorn et al. (2010) that assumes the same general patterns but assumes that the areas separated by the lake systems would have been larger than in the conservative prediction.

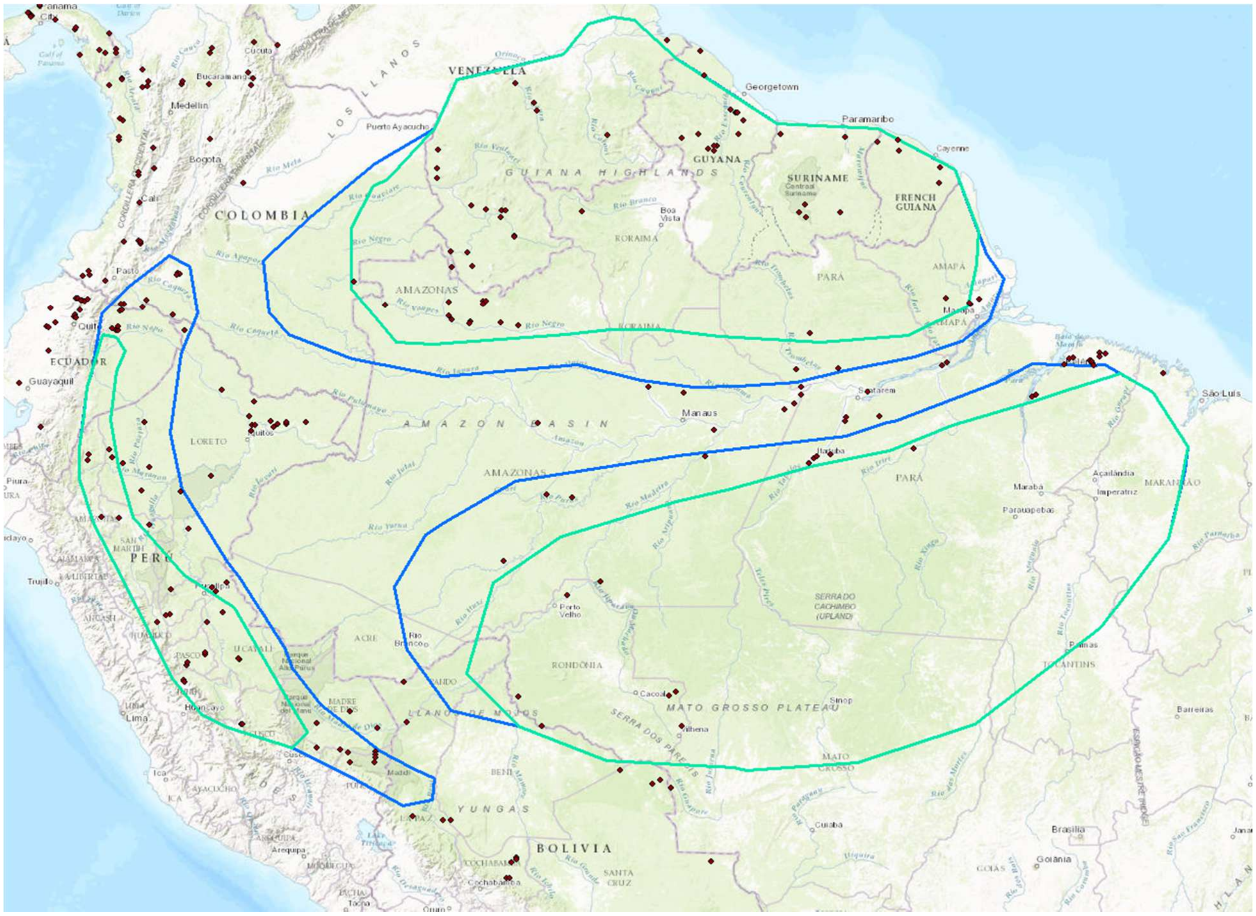


Figure 4. Prediction map for the lake model based on Hoorn et al. (2010). The turquoise polygons correspond to areas of predicted clustering under a more conservative interpretation, while the dark blue polygons correspond to clustering under a more liberal interpretation. Points mark locations with specimen data.

The river barrier model predictions (Figures 5 and 6) are again divided into two more and less conservative sets. The more conservative interpretation (Figure 5) places clustering only comparatively far down the major rivers and omits several rivers which might not prove a sufficient barrier (due to the large number of meanders, the short length of the river with forest even at the headwaters, or small width). This model is based mainly on Haffer (2008), especially with regard to the outer limit of each polygon. The less conservative interpretation (Figure 6) is similar overall but with the extent of the cluster polygons being somewhat expanded, to represent rivers posing a barrier along more of their lengths. Many more rivers are considered barriers under this interpretation, although some minor ones are still excluded. The rivers included consist of all those listed in Capparella (1991) except the Trombetas, which is relatively short and entirely within rainforest habitat, and has not been named as a barrier in more recent literature (although it may be a barrier between two subspecies of *Percnostola rufifrons*, an antbird; see Peters 1951). Several rivers which have been proposed as barriers in more recent literature are also included. Studies such as Bates et al. (2004) have shown that differentiation occurs across some south Amazonian tributaries even where they are 100-300 m wide, and the exact width needed to prevent gene flow is not known. However, Bates et al. (2004), Hayes and Sewlal (2004), and others point out that the ability of a river to pose an important barrier is likely to vary from species to species, and will also depend on the habitat in the headwaters and the number of meanders. This prevents making any strong argument for which rivers to consider as barriers based on a single metric such as river width.

Figure 5. Prediction map for the more conservative version of the river barrier model. Figure based on Haffer (2008). Red polygons correspond to areas of predicted clustering. Points mark locations with specimen data.

Figure 6. Prediction map for the less conservative version of the river barrier model. Purple polygons correspond to areas of predicted clustering, which mainly follow Capparella (1991), in addition to certain rivers based on Bates et al. (2004), Fernandes et al. (2013), Fernandes et al. (2014), Boubli et al. (2015), and Fernandes et al. (2015). Points mark locations with specimen data.

The predictions for the river refuge model are similar to those for the river models and can be thought of as an exceptionally conservative form of those predictions. They consist of eleven polygons (Figure 7) enclosing only the innermost portions of the rivers, where the extent of the polygons follows Haffer (2008).

Figure 7. Prediction map for the river refuge model based on Haffer (2008). Orange polygons correspond to areas of predicted clustering. Points mark locations with specimen data.

For the refuge model predictions (Figure 8) I have developed more and less conservative polygons with the more conservative polygons following the refuges from Haffer (2008) very closely, but with a slight added fringe to represent the early stage of expansion out of that refuge, and the less conservative polygons having a much greater extent and including a greater area of unimpeded expansion.

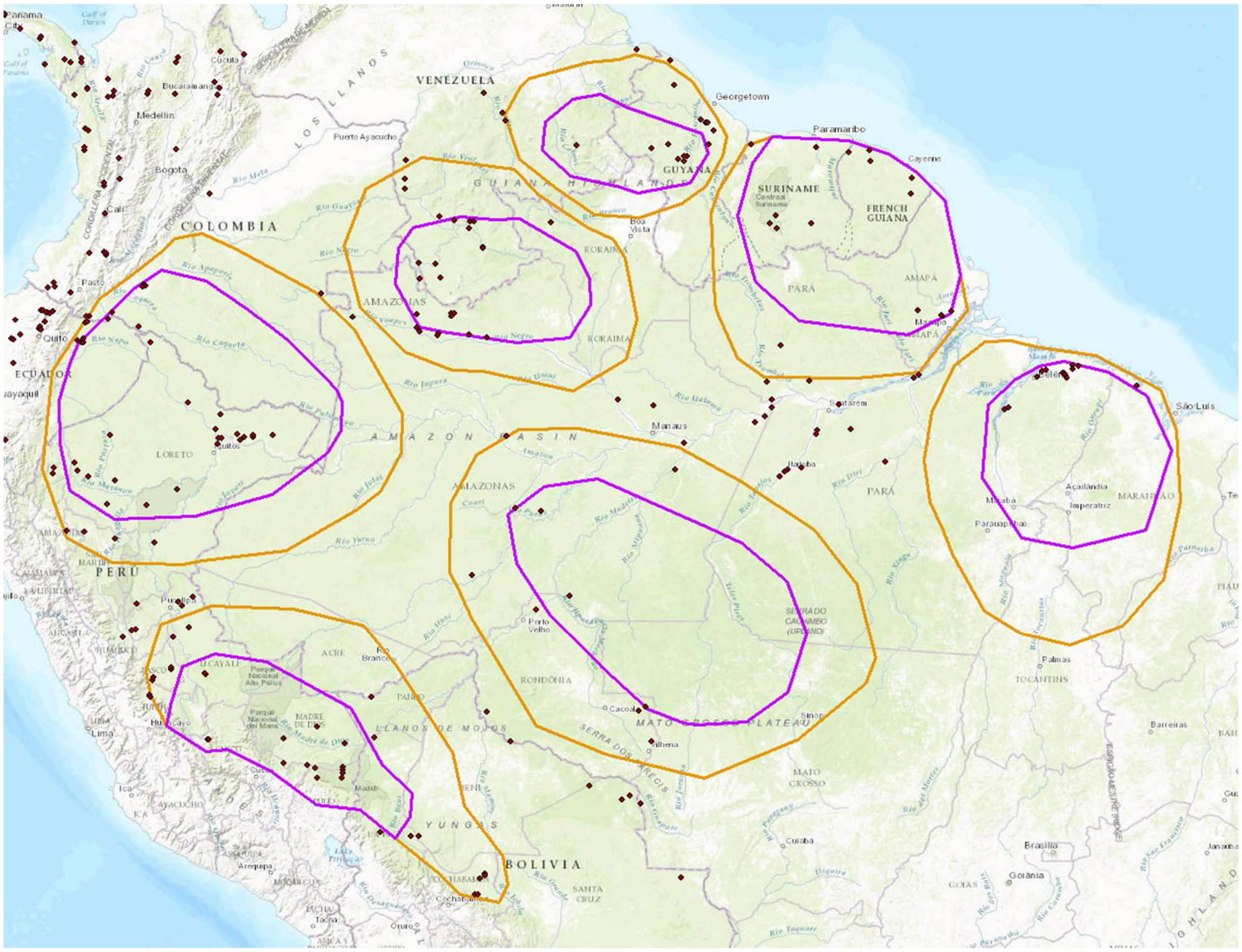


Figure 8. Prediction map for the refuge hypothesis. Purple polygons correspond to areas of predicted clustering under a more conservative interpretation, while orange polygons correspond to clustering under a less conservative interpretation. Points mark locations with specimen data.

The primary dataset for this project was collected by Angelo Capparella and consists of specimens at the following museum collections: the American Museum of Natural History (AMNH), the Field Museum of Natural History (FMNH), the Yale Peabody Museum (YPM), the Academy of Natural Sciences in Philadelphia (ANSP), the Louisiana State University Museum of Natural Science (LSUMNS), the Carnegie Museum of Natural History (CMNH), the National Museum of Natural History (USNM), and the University of Michigan (UM). Data collected from each specimen included specimen number, subspecies, date, collector, and location of collection, sex, skull pneumatization (used to determine age), mass, and anything else on the specimen label, as well as the following measurements (Table 2).

Table 2

Measurements in the Primary Data Set

Name	Character	Details
Plum1	Width of latero-distal portion of margin of center throat feather, at posterior margin of eye	In mm
Plum2	Color of throat feathers	Score based on reference series; white to rufescent, whole or half scores only, 0.5-5.5. Reference series: 1- 148482, 2- 822252, 3- 256123, 4- 282200, 5- 116439
Plum3	Widest width of central light mark on a breast feather in center of breast	In mm
Plum4	Crown color	Score based on reference series; buffy to dark brown, whole or half scores only, 0.5-3.5. Reference series: 1- 239335, 2- 525300, 3- 117907
Plum5	Amount of streaking on lower breast/upper belly	Score based on reference series; white streaks to no streaks, whole or half scores only, 0.5-3.5. Reference series: 1- 282203, 2- 820148, 3- 525346
Culmen	Exposed culmen	From margin of feathers to tip (mm)
MaxillaW	Width of maxilla	At anterior edge of nares (mm)
MaxillaD	Depth of maxilla	At anterior edge of nares (mm)
MandibleW	Width of mandible	At gonys (mm)
MandibleD	Depth of mandible	At gonys (mm)
Wing	Wing length	Bend in wing to tip of longest primary (mm)
Tail	Tail length	From skin between central rectrices to inflection point of barbs at distal end of feather (mm)
Tarsus	Tarsus length	Proximal notch of tarsometatarsus to outer lateral edge of last scute covering distal end of tarsometatarsus (mm)

Note. All reference series are from the AMNH.

These key characters were chosen because they encompass the range of morphological variation in the species. They show substantial geographic variation, unlike many other characters present in this species, they are easily taken and replicable, and they include both typical mensural characters such as tarsus length as well as characters addressing the variation known to occur in this species, such as throat color. Many of the latter include those characters used in the subspecies descriptions for this species. The measurements and characters used were chosen after careful examination of a large series of specimens covering all subspecies in order to determine what characters appeared to show substantial variation (AP Capparella, pers. comm.). Table 3 shows the correspondence between this data set and the characters used in subspecies descriptions.

Table 3

Comparison of Characters Used in Subspecies Descriptions for the Wedge-billed Woodcreeper and Those Found in This Data Set

Character used in subspecies descriptions	Presence in the primary data set	Presence in the secondary data set
Bill size	Yes	
Throat color	Yes	
Color/size of breast streaking	Yes	
Color of underparts		Yes
Forehead color		Yes
Crown color	Yes	
Back color*		
Eyebrow and cheek color		Yes
Rump color*		
Color of outer remex margin		Yes
Color of band across inner webs of remiges*		
Color of margins of pectoral feathers		Yes
Overall color*		
Overall size	Yes	

Note. The table also shows which characters were measured for inclusion in the secondary data set for this study (described more fully below in Table 4). All characters which were not included in either data set were found to have no discernible variation or, in the sole case of "overall color", were presumed to correlate closely with characters already present in the data set. The omitted characters have asterisks beside them.

Several initial steps were taken to prepare the dataset generated by Capparella for use in this project. All data were transferred from paper to Excel, and coordinates in the WGS 1984 geographic coordinate system were added for each specimen for which the specimen label provided sufficient detail to determine the location of collection. The majority of collection locations were taken from the gazetteer series "Ornithological Gazetteers of the Neotropics" published by the Museum of Comparative Zoology at Harvard (Paynter et al. 1985-1993). In many cases, the locations listed in this series still have a small amount of geographic uncertainty associated with them. This is due to the gazetteer series providing base camp locations for collecting expeditions, while specimens were often collected a few kilometers away from the base camp (Wiley 2010). All locations in Central America as well as some South American locations not listed in the gazetteers were found through searching online. Searches were made in Google Maps for each location, and when these failed to produce results the location was searched in Google in order to determine what villages, rivers, or other features lay nearby. These latter were then searched in Google Maps.

A certainty designation of 3, 2, or 1 was given to all locations to describe the level of geographic uncertainty associated with the use of its coordinates. A designation of 3 was the highest and referred to sites confidently located within a circle with a radius of 25 miles around the coordinates listed, and on the same side of any nearby large rivers as the coordinates listed. This radius would encompass an area several times the daily collecting radius from a base camp, which generally was no more than 6 km (Wiley 2010). This is important because often the location of collection listed is actually the location of the base camp. Certainty designations of 2 are those confidently located within a radius of 75 miles (a distance chosen for its relationship to the radius of the ranges of the subspecies and because it encompasses a moderate amount of area) from the listed coordinates, although not necessarily on the same side of any large rivers. Such distances, though large, are still insignificant relative to the much greater distances necessary to cross Amazonia or even to move across the putative range of a single subspecies, with all subspecies but *coronobscurus* (for which only one specimen exists in this data set) having ranges with a radius of at least 100 miles. Designations of 1 refer to locations that could not be located with even moderate confidence. The most uncertain of these locations, namely those corresponding simply to an entire country, were removed from the dataset, while those corresponding to a particular province or department were kept.

The next step was to check for violations of the assumptions of the statistical tests used. The Shapiro-Wilk test was used to detect departures from normality. Several variables were transformed to fit the assumption of normality using log base 10, square root, and reciprocal transformations, while others could not be successfully transformed. Visual inspection of normal probability plots showed most of the departures from normality to be trivial and probably due to the large size of the data set. Such departures were therefore ignoredexcept in the single most egregious case– Plum1 (see Table 2 for the identity of all plumage characters). This character had such a heavily skewed distribution that it was left out of the analysis because of the danger that it would bias the results.

Homogeneity of variances and for covariance of the mean and the variance was examined via inspecting plots of the residuals. The extremely large data set makes it likely that the central limit theorem is applicable; thus departures from normality are unlikely to be a problem.

Several other potential sources of error existed which were examined prior to beginning the analyses. First, differences between males and females in some of the variables were tested using two sample t-tests (SAS PROC TTEST) for each character. A number of variables showed a significant difference between males and females, so the sexes were analyzed separately. Second, foxing, or the tendency of certain reddish-brown plumage colors to become more reddish-brown under certain preservation conditions, was evaluated by regressing specimen age against plumage score (Plum 2 and Plum 4) (Patten and Unitt 2002). Foxing has been found in a variety of birds (e.g. Gabrielson and Lincoln 1951, Maley and Winker 2007) and even in black melanin-based pigments (Doucet and Hill 2009), and like other changes to pigment colors in birds, it appears to occur through three processes: soiling with dust or oils; damage to the feathers; or breakdown of the pigments themselves from ultraviolet light and humidity (Doucet and Hill 2009). All of these processes can be slowed or halted through careful curation of specimens, meaning that preservation history is likely more important than age.

After checking these sources of error, PROC DISCRIM in SAS was used to run a canonical discriminant analysis and a discriminant function analysis. The canonical discriminant analysis was used as a dimension reduction technique to reduce the number of variables in the data set and to determine which variables were correlated. The crossvalidate option was used to subset the data set into training and trial data sets for the discriminant function analysis. These analyses were performed on males and females separately and on high certainty, high and medium certainty, and all birds within each sex, making for 6 separate analyses. The output data sets from these analyses were exported to Excel and ultimately into ArcMap.

In ArcMap, separate sets of analyses were run on the original data set and on the output data sets from the 6 SAS analyses. The original data set was used to fulfill the first objective of the study, namely characterizing variation. This was accomplished by interpolating values from the point locations in the original data set to generate a raster spanning the entire range of the species, and then using the contour tool to draw contours based on that raster. This was done separately for all 13 characters in the original data set. Three interpolation tools in ArcMap were tested: Inverse Distance Weighting, Kriging, and Local Polynomial Interpolation. Of these, Kriging provided the best balance between sensitivity to sharp differences in character value and lack of unsupported sharp breaks in character value, so it was used for all analyses.

The second objective, addressing the biogeography models, was tested in ArcMap using cluster analysis with the Optimized Hot Spot Analysis tool. This tool is related to the Getis-Ord Gi* tool and simplifies some of the decisions surrounding the parameters of that latter tool by optimizing some of the parameters based on the data set in question. It automatically corrects for multiple tests and its output includes locations where significant clustering of hot and cold values (high and low character values, respectively) occurs at p values of 0.1, 0.05, and 0.01. Cluster analyses were run for the output data sets containing values of the first two canonical variables for males and females, and for all three certainty levels. Therefore, 12 separate cluster analyses were run.

The results from the cluster analyses were compared to the predicted patterns under each biogeography model by using a goodness-of-fit test (SAS PROC FREQ) on count data generated from ArcMap. Prediction polygons were created in ArcMap prior to any analyses and showed the predicted locations of significant clustering under each model. For some models, more and less spatially conservative sets of polygons were created to account for the lack of certainty in the precise boundaries of predicted clustering (e.g. Figures 3, 4, and 8). The polygons were drawn manually in ArcMap using figures and verbal descriptions found in the relevant biogeographical literature. The numbers of points with significant and non-significant levels of clustering were counted for each polygon as well as the area outside all polygons (all within the overall study area), along with whether there were significant hot or significant cold spots within a polygon. These count data were obtained using the Select by Location tool in ArcMap. The counts were then analyzed in SAS using a χ^2 test in SAS PROC FREQ to determine whether there were significant departures from predicted proportions of significant or nonsignificant points. Due to the small number of points located within many polygons, the χ^2 test's validity may be affected in some cases. Therefore, all polygons were pooled by creating tables listing significant and nonsignificant points within any polygon and outside of all polygons, and an additional set of χ^2 tests for canonical variables one and two for all individuals for each sex were run to compare the results to those obtained when polygons were not pooled.

The third objective, revising the subspecies taxonomy of the Wedge-billed Woodcreeper, was done in SAS and ArcMap using the results from the cross-validation linear discriminant function analysis in SAS. The percentages of specimens of a given subspecies that were mis-assigned to other subspecies permitted testing of the hypothesis that each subspecies represented a diagnosable grouping at a 95% level of diagnosability (i.e., if a subspecies is diagnosable at that level, then it will have 5% or fewer of its specimens mis-assigned). The scores for each specimen on the discriminant function were then mapped in ArcMap and sharp breaks in score values were found using interpolation and contour tools as in objective 1. The boundaries for all subspecies were then redrawn using the locations of sharp breaks and new subspecies designations were given to all individuals within the new subspecies polygons. The discriminant function analysis was then re-run using the new subspecies designations to determine whether the subspecies themselves might be valid even if the described ranges are faulty.

In addition, I measured a small group of specimens at the American Museum of Natural History for a number of characters which were not in my primary data set but were mentioned as diagnostic in the original subspecies descriptions. These specimens consisted of 9 to 21 from each subspecies, with subspecies having fewer than 5 specimens excluded due to small sample size. Subspecies that were excluded were: *pectoralis, pallidulus, integratus, amacurensis, coronobscurus*, and *cuneatus*. The measurements and the number of specimens from each subspecies are listed below in Table 4. These measurements were then analyzed in SAS using a nonparametric discriminant function analysis. A nonparametric method was necessary because some variables had so few character states and so little variation that normality was not attainable, and the sample size was small enough for non-normality to affect the results of parametric methods. The nonparametric method used was nearest neighbor distance, using 20 nearest neighbors, because it requires the input of fewer *a priori* predictions than the alternative (the kernel method).

Table 4

Characters Measured in the Secondary Data Set from the AMNH, and Specimen Numbers for Each Subspecies in the Data Set

Character	Notes	Reference Series
Color of breast streaking	Streaking white to very buffy, on a scale of 0.5 to 3.5 with units of 0.5.	1- 820148; 2- 278032; 3- 177394
Color of underparts	Underparts pale brown-olive to reddish-brown, on a scale of 0.5 to 3.5 with units of 0.5.	1- 146194; 2- 274163; 3- 525329
Streaking of posterior underparts	Streaking absent to abundant, on a scale of 1 to 3 with units of 1.	1- 278032; 2- 820148; 3- 247591
Forehead color	Two character states- pale grayish, contrasting (1) vs. brownish, not contrasting (2).	1- 525288; 2- 274150
Supercilium color	white (1) or buffy (2)	1- 147722; 2- 278033
Color of outer remex margin	pale brown (1) or dark ruddy brown (2)	1- 176859; 2- 432938
Color of margins of pectoral feathers	Color pale gray-brown to very dark ruddy-brown, on a scale of 1 to 3 with units of 1.	1- 146193; 2- 274163; 3- 109688

Subspecies	Number of specimens
albigularis	9
castelnaudii	20
inornatus	11
paraensis	21
rufigularis	20
spirurus	20
sublestus	17
subrufescens	20

Note. All reference series are from the AMNH.

CHAPTER III: RESULTS

Objective 1: Characterizing Variation

Contour maps were generated in ArcMap for all the original, untransformed variables in the data set, fulfilling the first objective of characterizing morphological variation in the Wedge-billed Woodcreeper. These maps are in Appendix A, although a few examples are presented here. The contours used depended on the range of variation in the character under study.

Many of the contour maps exhibited similar patterns, especially the bill measurements. One example of such concordance has Culmen Length, Maxilla Width, Maxilla Depth, and Mandible Depth all showing areas of low character values of varying extents in the Guianan Shield, and Mandible Depth, Mandible Width, and Maxilla Depth all showing low character values in northwestern Amazonia and parts of nearby *trans*-Andean Colombia. Mandible and Maxilla Widths were both high across most of south Amazonia and the northern parts of Central America, while Culmen Length showed a similar pattern but of lesser geographic extent—high culmen values are only found in the southern parts of Mexico and in areas of southeastern and southwestern Amazonia. These patterns can be seen in Figures 9 and 10, as well as in Figures A-1 through A-5 in the Appendix.

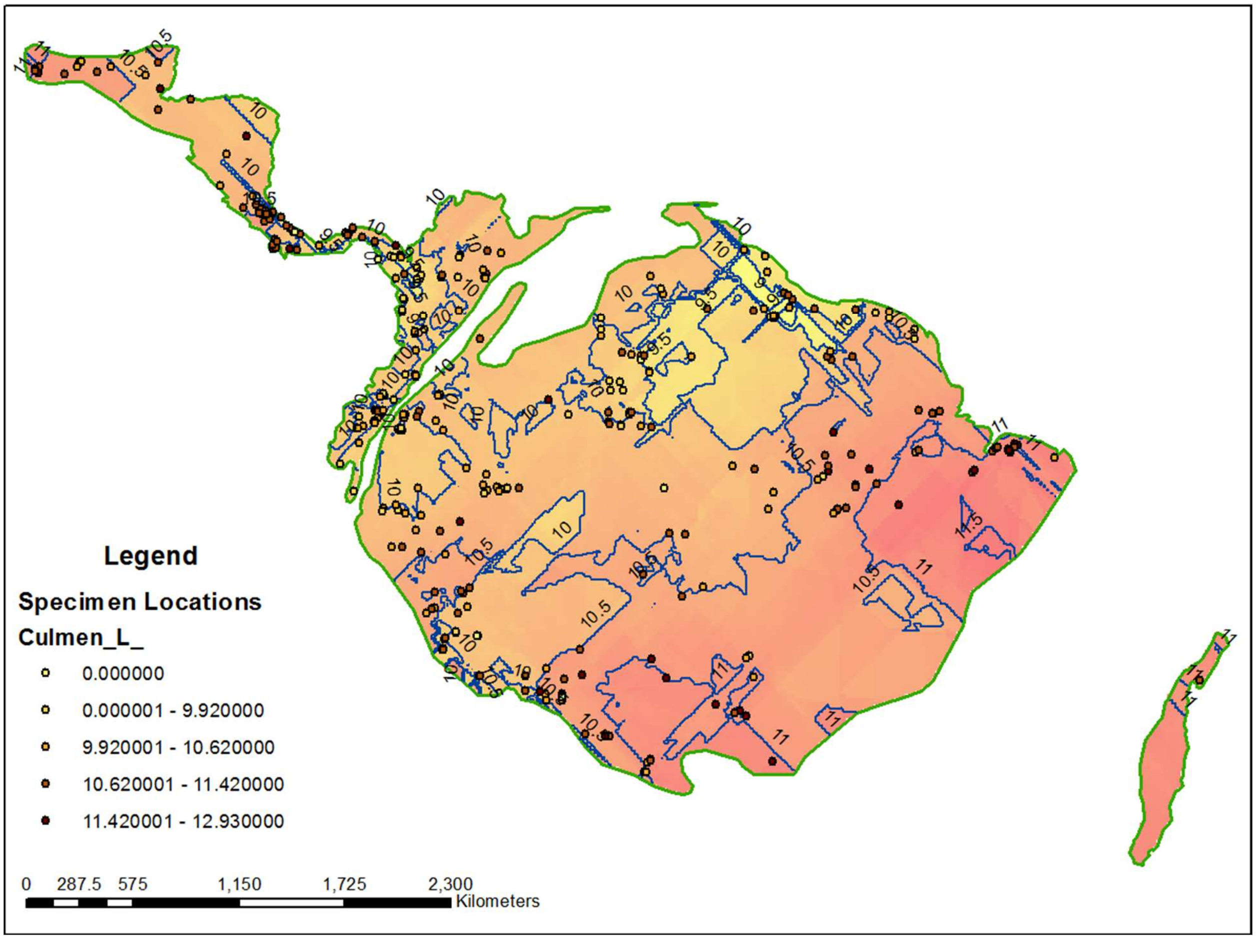


Figure 9. Contour map of culmen length. Darker colors signify higher values. This map shows smooth clines across the range, with areas of high character values in southeastern and southwestern Amazonia and in southern Mexico, and areas of low character expression in the Guianan Shield.

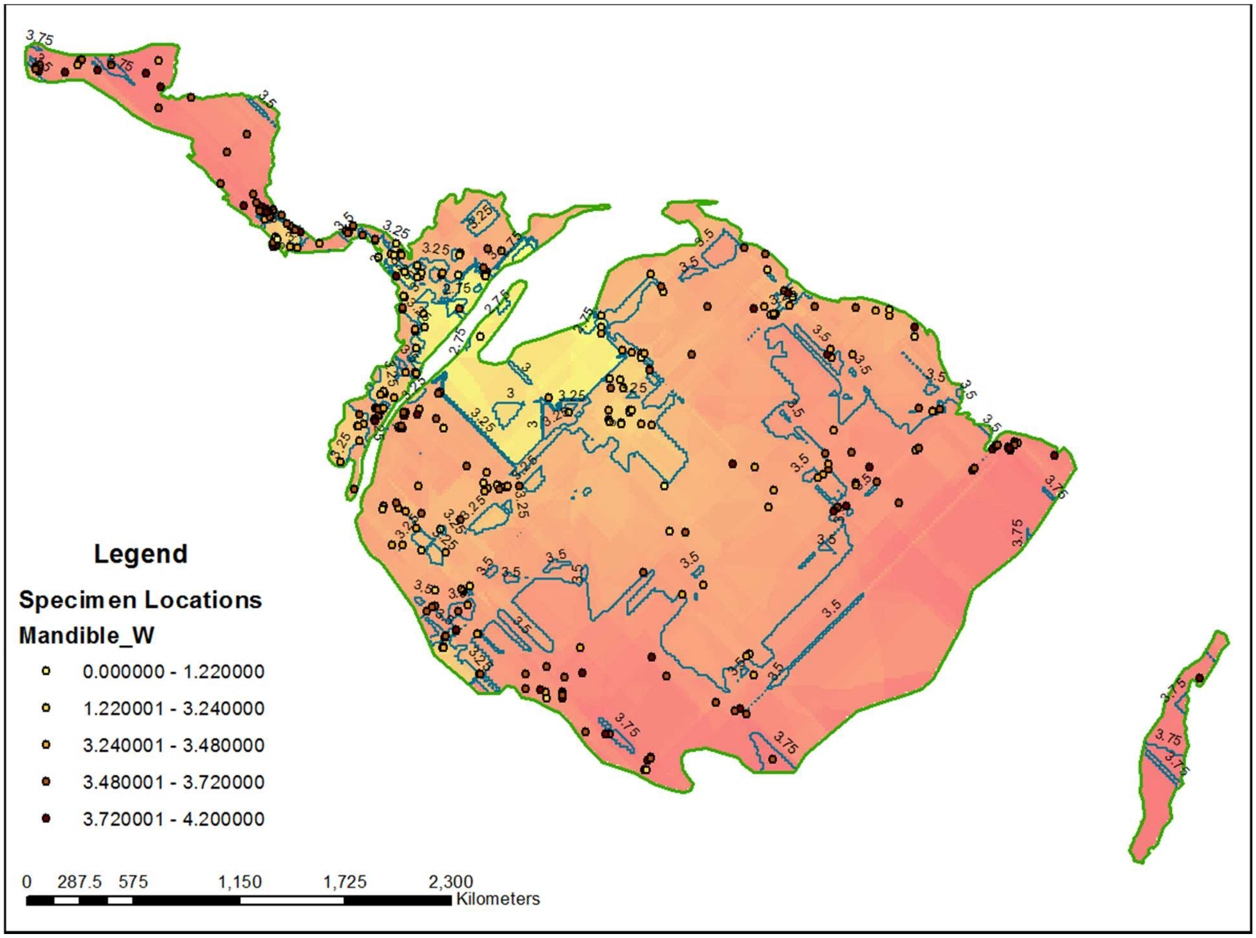


Figure 10. Contour map for mandible width. Darker colors signify higher values. This map shows smooth clines across the range as well as an area of very low mandible widths in the northwestern Amazon Basin and nearby areas across the Andes. The highest values are south of the Amazon, like the pattern from Figure 9.

Three other measurements did not show concordance with these trends in bill measurements. Tarsus Length (Figure 11) showed a smooth, shallow cline (generally no steeper than 0.5 mm per 500 km) over most of the range but had a step in the cline of 1.5 mm per 100 km in part of northwestern Colombia. A drop in central Amazonia corresponds to an area without specimen records and should be treated with caution. Tail length showed no clear pattern across the range, with minimal variation (Figure A-7). Finally, Wing Length (Figure A-8) was high throughout most of the range with a shallow cline (no steeper than 5 mm per 1000 km) but had steps (10 mm per 500 km or steeper) in northwestern Amazonia, parts of south Amazonia, and in Costa Rica.

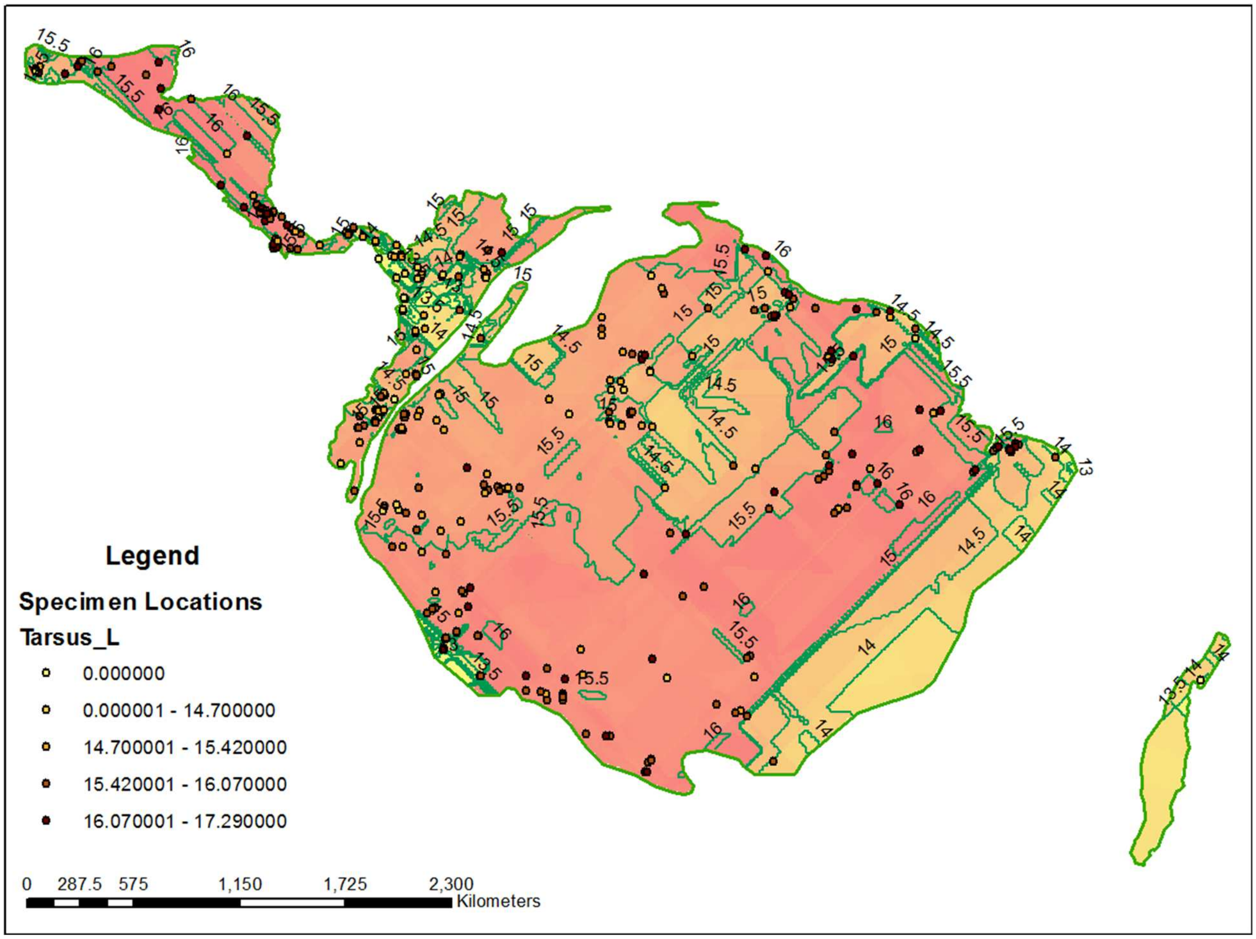


Figure 11. Contour map of tarsus length. Darker colors signify higher values. This map shows a smooth cline over nearly the entire range, with a noticeable drop in northwestern Colombia and eastern Panama. It also exemplifies, in the southeastern part of Amazonia, the strange patterns sometimes produced by interpolation in cases where no data points exist in the area to be interpolated.

The plumage characters showed limited concordance with each other, but some showed strong concordance with some of the other variables. Plum1 showed a step (0.5 mm in 100 km) in the Guianan Shield, like certain bill measurements (Culmen Length, Mandible Length, Maxilla Width, and Maxilla Length), but otherwise did not show a strong pattern (0.5 mm in 1,000 km) (Figure A-9). Plum5 also showed high values in the Guianan Shield, as well as in Central America and Ecuador. In all areas, however, Plum5 showed smooth clines (Figure A-13). Plum4 had a similar pattern of clines between several peaks and dips, but there were approximately 10 peaks or dips scattered evenly throughout the range (Figure A-12). None of these peaks or dips had a steeper step than the others. Plum2 (Figure 12) and Plum3 (Figure A-11) were in some respects similar, showing smooth clines throughout and featuring low values south of the Amazon (except for Amazonian Peru) and most prominently in southwestern Amazonia (Bolivia), but Plum2 had high values in northwestern Amazonia and the Chocó and low values in northern Colombia, while Plum3 had medium values in northwestern Amazonia and high values throughout the *trans*-Andean region.

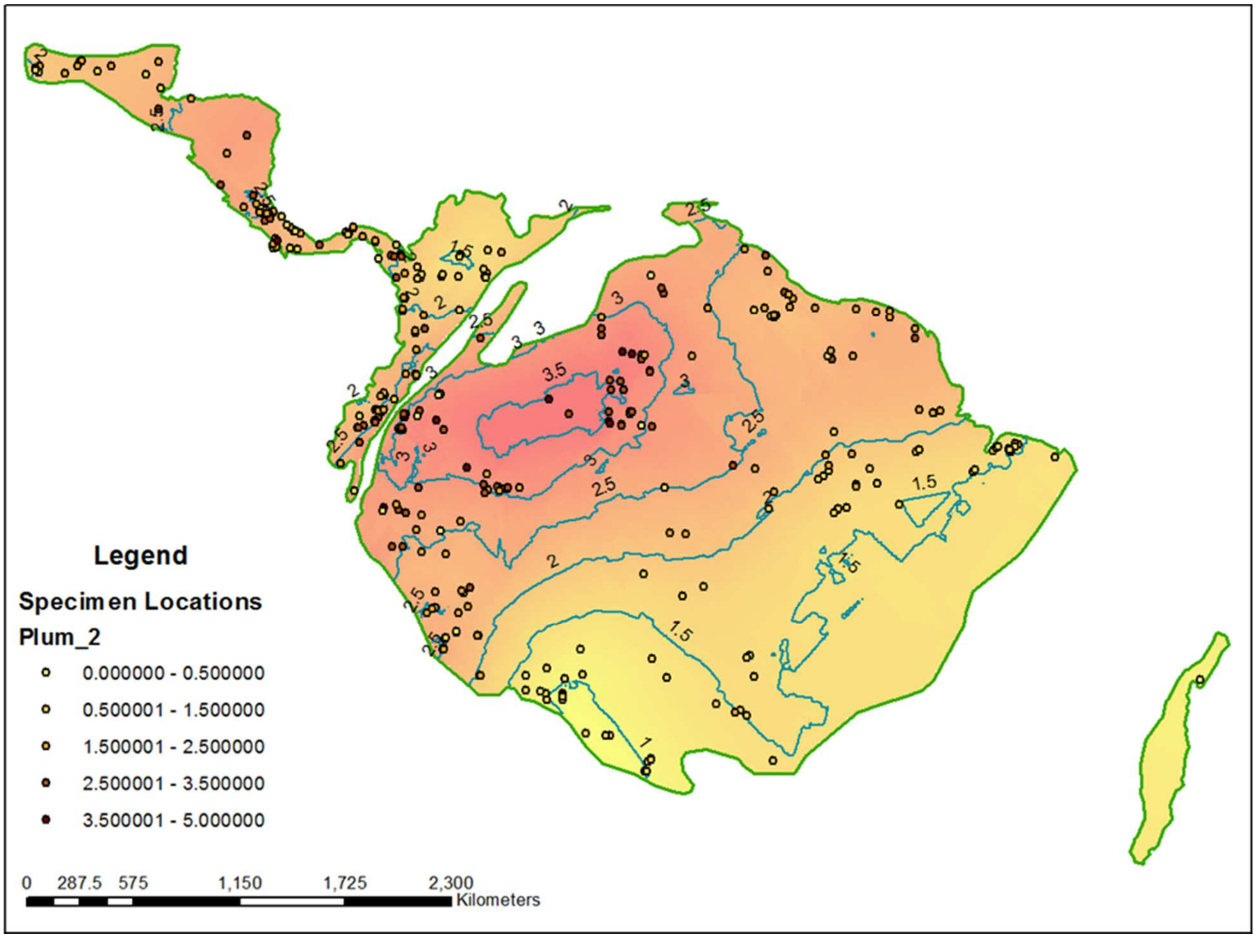


Figure 12. Contour map for plum2 (throat color). Darker values signify more orange throats. This map shows the smooth clines found in multiple plumage characters as well as a strong north-south gradient in throat color in Amazonia.

A number of the contour maps showed smooth clines with few contours, but others exhibited a more complex pattern with numerous contour lines crossing at right angles and filling up much of the range. In these cases such patterns can be found in areas lacking specimen records (e.g. Figure 11). This pattern results from the method of interpolation, which is sensitive to abrupt changes in areas with data, but which also extrapolates into areas without data based on whatever patterns exist nearby, despite the lack of support for such extrapolation.

Objective 2: Testing Biogeographical Models

Tests of Assumptions Prior to Testing Biogeographical Models

In preparation for the canonical discriminant analysis, the following variables were transformed to meet assumptions of normality: Tail Length (log 10), Culmen Length (reciprocal), Mandible Depth (square root), and Wing Length (reciprocal). In addition, effects of sex and foxing were investigated. The following variables showed significant effects of sex: Culmen Length, Mandible Depth, Maxilla Depth, Tarsus, Tail Length, Wing Length, and Plum3. Of these, only Tail Length and Wing Length showed extensive differences in character value, with Figures A-26 and A-27 showing box plots of the distributions of these characters and the disparity between the sexes. Females showed significantly smaller wing and tail lengths than males. This relationship, while not described in Marantz (2003), corroborates the findings of Zimmer (1934), who found females to be on average smaller in these characters and culmen length, with a sample size of 40 males and 20 females taken from the range of *rufigularis,* and Ridgway (1911), who found males to be larger in length, wing length, tail length, tarsus length, culmen length, and middle toe length, with a sample size of 19 males and 17 females from across the range.

Foxing was tested for throat color and crown color because both these characters may contain reddish-brown pigments, but did not appear to explain much variation in this species for either variable. The regression line for crown color and specimen age showed an F value of 1.55 (1; 1148 df) and a non-significant p of 0.2135. The regression line for throat color and specimen age did show a significant p value (F of 9.95 (df 1; 1135), p of 0.0016). However, the associated r-squared value was 0.0087, meaning that an extremely small proportion of the variation in throat color is explained by specimen age despite the significant p value. In addition, examining the graph of the regression line (Figure A-28) makes it clear that the data do not show the predicted pattern were foxing occurring. Under the predicted pattern, the oldest specimens should show noticeably reddish colors, but they do not. In addition, even the very small proportion of variation that is explained by specimen age could merely be a result of differential collecting in different parts of the species' range. Much of the collecting in the first half of the 20th century (when the highest numbers of orange-throated individuals were collected) occurred within the range of *rufigularis*, an orange-throated subspecies, and fewer specimens have been collected from this area since then. Likewise, collecting in the range of *albigularis*, a white-throated subspecies, was rare early in the 20th century but has increased greatly during recent decades. Therefore, we can conclude that foxing does not have an important effect on this data set.

Canonical Discriminant Analyses

For canonical discriminant analyses, the results were similar between sexes and across all levels of geographic uncertainty. The sample size for the males was somewhat larger overall and for most subspecies (see Tables 5 and 6), but for both sexes there were several hundred specimens used in the most inclusive analysis. The high- and medium-certainty-only analyses included 513 male specimens and 344 female specimens, and the high-certainty-only analyses used only 433 and 284 specimens for males and females respectively. The large overall sample sizes and the large sample sizes for individual subspecies presented in Tables 5 and 6 give reason for confidence in the results.

Table 5

Sample Sizes for Each Subspecies for the Canonical Discriminant Analysis and Linear Discriminant Function for All Male Specimens

Subspecies	Number of specimens
albigularis	41
amacurensis	2
castelnaudii	124
coronobscurus	1
inornatus	32
integratus	21
south Amazonian intergrade zone	5
Central American intergrade zone	2
pallidulus	12
paraensis	41
pectoralis	13
rufigularis	89
spirurus	61
sublestus	21
subrufescens	52
Total	517

Table 6

Sample Sizes for Each Subspecies for the Canonical Discriminant Analysis and Linear Discriminant Function for All Female Specimens

Subspecies	Number of specimens
albigularis	19
castelnaudii	66
inornatus	17
integratus	12
south Amazonian intergrade zone	4
Central American intergrade zone	6
pallidulus	16
paraensis	26
pectoralis	7
rufigularis	73
spirurus	44
sublestus	25
subrufescens	35
Total	350

Due to the similarity of the results, I will now only describe the results from the most inclusive analyses, except where results from more restricted data sets differ. For the males, although the first seven canonical variables showed significant p values and together accounted for 98% of the variability in the data, only the first two canonical variables had eigenvalues above the benchmark of 1 (or even close to it) and together account for nearly 74% of the variability in the data (Table 7). These canonical variables are heavily influenced by positive contributions from Plum2 in the case of Canonical Variable 1 (Can1) and Plum5, and logTail, and Plum3 (in that order) in the case of Canonical Variable 2 (Can2) (Table 8). This means that high values of Can1 are very closely associated with high values of throat color, while high values of Can2 are closely associated with high values for breast streaking, the width of light marks on the breast feathers, and tail length. The other variables are much less important, affecting mainly the various less important canonical variables, all of which together explain only a quarter of the variation in the data.

Table 7

The First Two Canonical Variables and Their Eigenvalues for All Males

	Canonical Correlation	Eigenvalue	Difference	Proportion	Cumulative	Likelihood Ratio	F	Num df	Den df	p
1	0.835416	2.31	1.256	0.506	0.506	0.051	10.36	168	4529	<.0001
2	0.716409	1.054	0.614	0.231	0.737	0.168	6.87	143	4185.6	<.0001

Note. Eigenvalues above 1 are considered substantial. "Proportion" refers to the proportion of variation explained by this canonical variable, while "cumulative" refers to the variation explained by this and all higher canonical variables. High eigenvalues and significant p-values suggest that a canonical variable captures an important amount of the variation in the data.

Table 8

Standardized Canonical Coefficients for All Males

Variable	Label	Can1	Can2
Mandible Width	MandibleW	-0.30435	0.293038
Mandible Depth	rootManD	0.000318	-0.26841
Maxilla Width	MaxillaW	-0.14529	-0.08903
Plum2	Plum2	1.308057	-0.21271
Plum4	Plum4	-0.05071	0.111566
Plum5	Plum5	0.170643	0.762687
Culmen Length	recCulmen	0.338385	0.120254
Maxilla Depth	MaxillaD	0.048505	-0.05835
Tarsus	Tarsus	-0.00521	-0.0183
Tail Length	logTail	0.057917	0.558512
Wing Length	recWing	0.012213	0.000394
Plum3	Plum3	0.336816	0.555248

Note. Higher coefficients signify a greater contribution from the associated variable to the overall canonical variable score.

The females showed a very similar pattern to the males in terms of which canonical variables were important and how much of the variation they explained (Table 9), with the first two canonical variables together explaining about 78% of the variation and being the only variables with eigenvalues over 1, while the first six were nominally significant. The contributions of each variable to these two canonical variables was also very similar to the pattern found in the males, with Plum2 dominating the first canonical variable and Plum5, Plum3, and logTail making up the major contributors to the second canonical variable (Table

10). However, the contributions of Plum3 and logTail to Can2 were slightly more modest than for the males.

Table 9

The First Two Canonical Variables and Their Eigenvalues for All Females

	Canonical Correlation	Eigenvalue	Difference	Proportion	Cumulative	Likelihood Ratio	F	Num df	Den df	p
1	0.847853	2.5569	1.4995	0.5501	0.5501	0.0548632	7.88	144	2809.1	<.0001
2	0.716899	1.0574	0.5651	0.2275	0.7776	0.1951418	4.94	121	2585	<.0001

Table 10

Standardized Canonical Coefficients for All Females

Variable	Label	Can1	Can2
Mandible Width	MandibleW	-0.11455	-0.10727
Mandible Depth	rootManD	-0.09679	-0.2404
Maxilla Width	MaxillaW	-0.1182	0.180591
Plum2	Plum2	1.358279	0.334519
Plum4	Plum4	-0.10146	0.152827
Plum5	Plum5	0.08343	0.762101
Culmen Length	recCulmen	0.525957	0.00897
Maxilla Depth	MaxillaD	0.103815	0.015339
Tarsus	Tarsus	-0.09402	0.152048
Tail Length	logTail	0.018341	0.475585
Wing Length	recWing	0.141495	-0.26777
Plum3	Plum3	0.105375	0.424115

In almost all cases, the patterns found in the most inclusive analysis held true for the less inclusive analyses as well, with the single exception that for the high-certainty-only females, the second canonical variable was heavily influenced positively by Plum2 (coefficient 0.68), making that character the second most important (after Plum5) in determining the value of Can2. In all other cases, the number of eigenvalues above 1, the approximate percentage of variation accounted for by the first two canonical variables, and the direction and approximate size of all the largest contributing variables to each canonical variable all remained the same compared to the most inclusive analysis.

Cluster Analyses

The first two canonical variables were then mapped in ArcMap and used for cluster analyses using the Optimized Hot Spot Analysis tool. This was done for males and females separately and for all three certainty levels for each sex, resulting in twelve cluster maps, all of which can be found in Appendix A. Due to the similarity of the spatial patterns across the different certainty levels, only the most inclusive analysis will be discussed here. The spatial pattern for Can1 for males (Figure 13) showed significant clustering of high values (meaning that there is clustering of orange throats, since Plum2 is the main contributor to Can1) throughout most of northern and northwestern Amazonia as well as the Chocó region. Significant clustering of low values occurred in southeastern Amazonia (the Belém area) as well as southwestern Amazonia and in the Magdalena River valley in Colombia. Males and females (Figures 13 and 14) showed the same pattern with two exceptions—there was no significant clustering for females in the Magdalena River valley, and the extent to which significant clustering of high values in northern Amazonia extended eastward into the Guianan Shield was dramatically reduced.

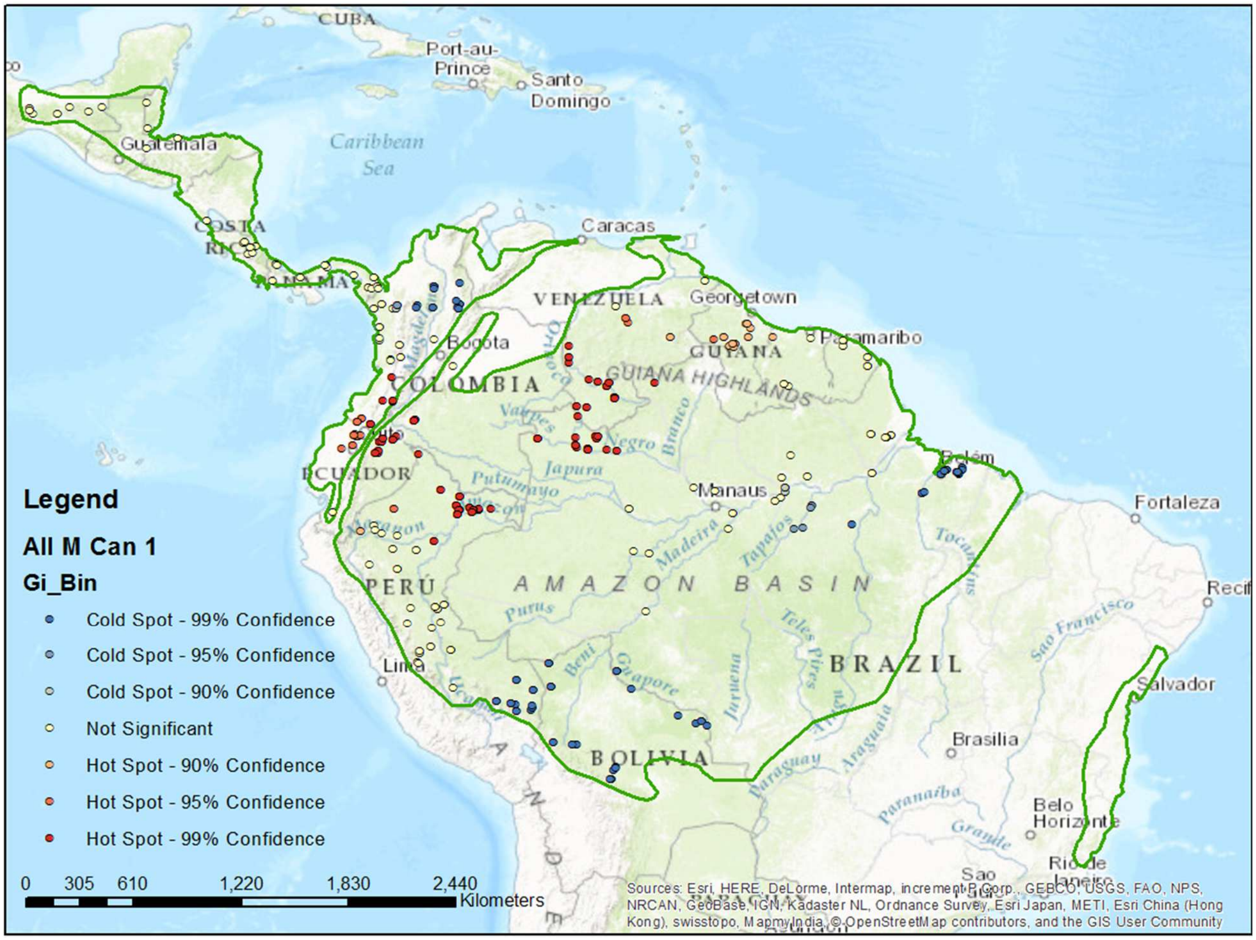


Figure 13. All males canonical variable 1 cluster results. The areas with dark red points show areas with clustering of high values of Can1, while dark blue points show areas with clustering of low values of Can1. The map shows that high values of Can1 are clustered in the Chocó and in northern and northwestern Amazonia, while low values are clustered in northern Colombia, southwestern Amazonia, and southeastern Amazonia. The remainder of the range has a mixture of high and low values (yellow points).

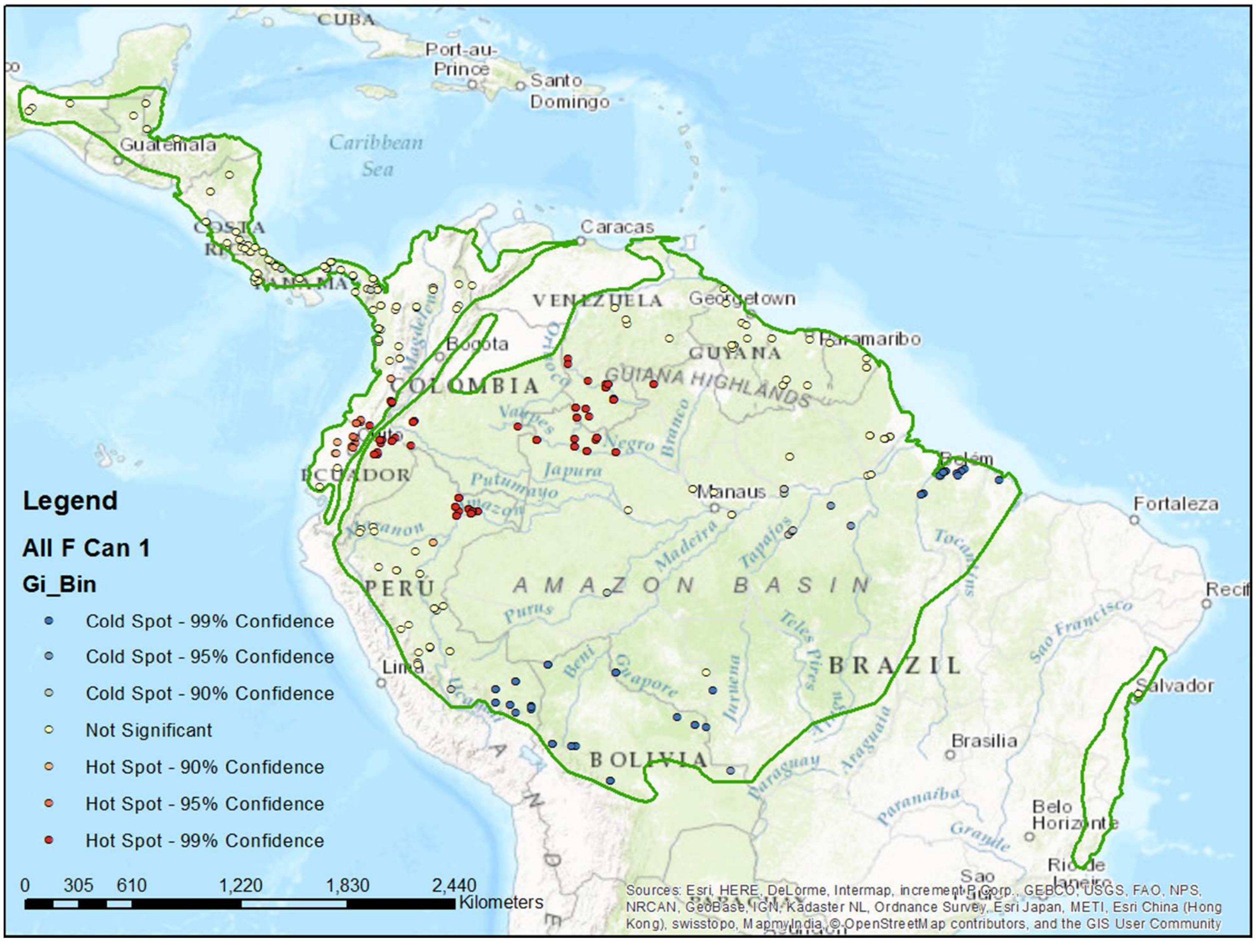


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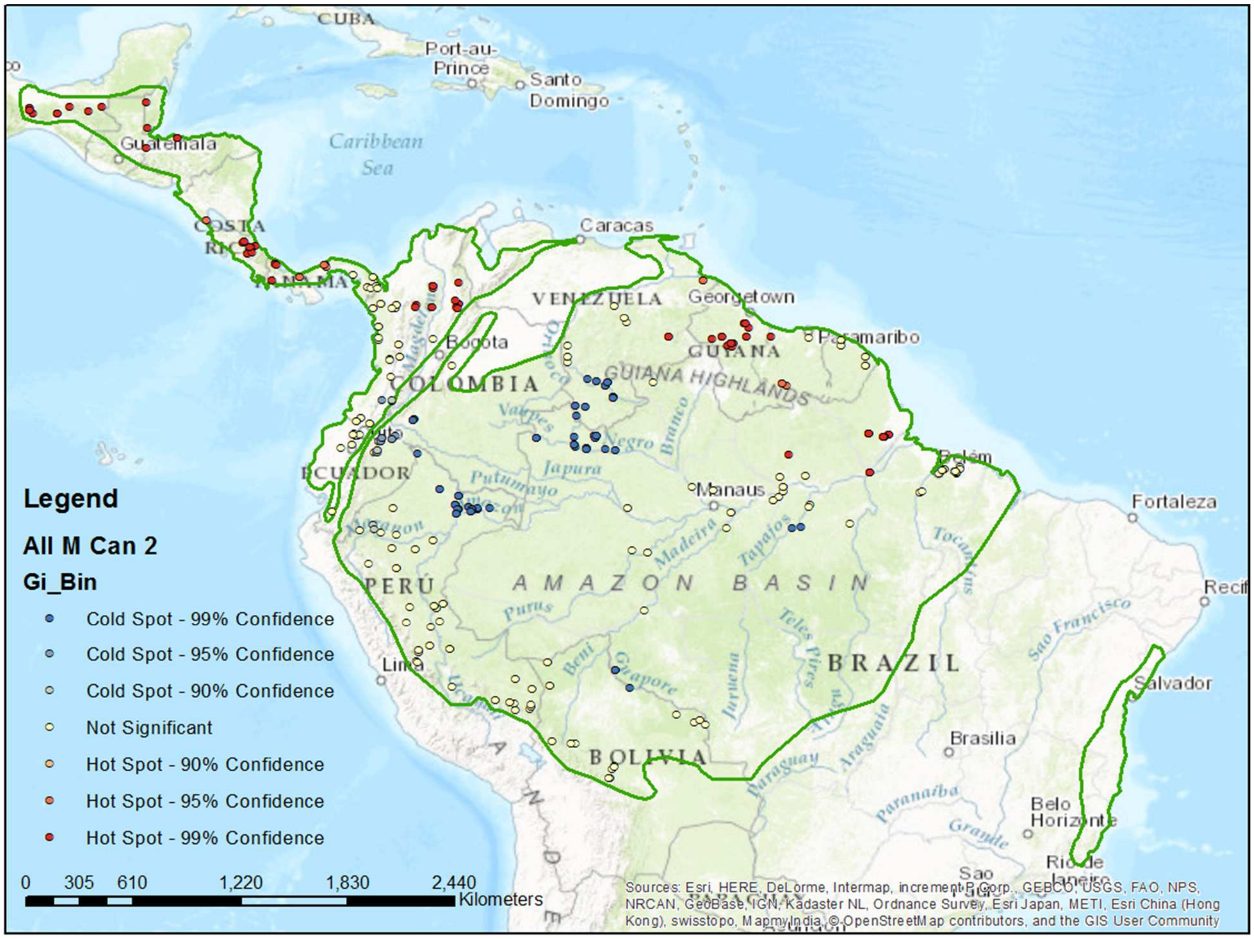
Figure 14. All females canonical variable 1 cluster results. This map shows clustering of high values (red points) in northwestern Amazonia and in limited parts of the Chocó, while low values cluster in southeastern Amazonia and southwestern Amazonia.

The second canonical variable for males (Figure 15) showed a different pattern but not one which was discordant with that for Can1. Significant high clustering was found in the Guianan Shield area as well as in the Magdalena River valley and in most of Central America. Significant low clustering was found in the northern and northwestern portions of Amazonia as well as in scattered locations on the fringes of the Brazilian Shield. The pattern for females (Figure 16) was almost identical but with three differences. First, there was no clustering in the

Magdalena River valley; second, there was more extensive significant low clustering in southwestern Amazonia; and third, there was some limited significant low clustering in the northern Chocó.



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure 15. All males canonical variable 2 cluster results. This map shows clustering of high values (red points) in the Guianan Shield and in northern Colombia as well as in most of Central America. Clustering of low values is found in a few places in south Amazonia but is more widespread in northwestern Amazonia.

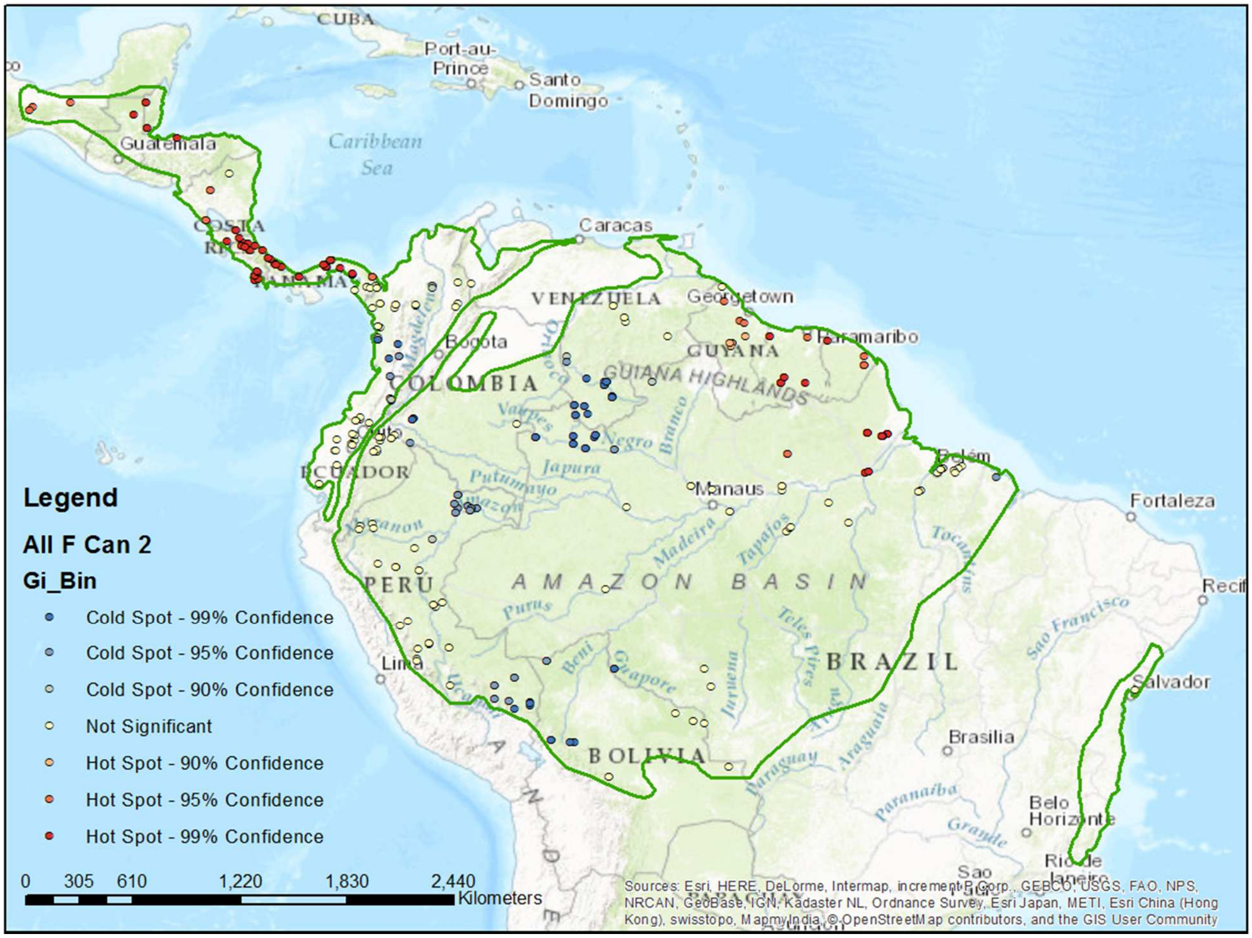


Figure 16. All females canonical variable 2 cluster results. This map shows clustering of high values in Central America and the Guianan Shield, and low values in northwestern Amazonia and parts of southwestern Amazonia.

The other two certainty levels were in most respects similar to the most inclusive certainty level, but with a few notable differences. For males, no differences in certainty levels exist. For females, the high- and medium-only and the high-only levels both showed slightly increased low clustering in the Chocó for Can2, and extensive significant low clustering in Panama, Costa Rica, and the Magdalena Valley for Can1 for high only.

χ^2 Analyses on Counts of Clustered Points Falling Within Each Prediction Polygon

After running the cluster analyses, the counts of clustered points falling within each prediction polygon were analyzed in order to determine whether clustering was more or less abundant within a given polygon than would be expected by chance. The count results were analyzed in SAS using χ^2 tests of goodness-of-fit, and produced very similar results across all certainty levels and for both sexes. Within a sex, the certainty levels produced the same patterns in almost every case, so only the most inclusive certainty level is shown in Table 11. The results from the unpooled and pooled analyses were also quite similar. Overall, for the unpooled data, only a few models (namely all three versions of the marine incursion model) could be rejected as unsupported due to a lack of a significant χ^2 result, and no model could be rejected in every case due to All Males Can2 showing significant departures from the expected proportions for every model (Table 11). In general, several regions which fall within prediction polygons for multiple models proved to be important contributors to the overall significant results in many cases. These include all parts of the Guianan Shield, the area in western Amazonia around the Napo River, and the Belém area in southeastern Amazonia (Table 11).

Table 11

χ^2 Results for All Males and Females for the Unpooled Data, Showing Test Statistics and the Prediction Polygons Which Contributed the Most to the Overall χ^2 Test Statistic

Dataset	Model	Sig chi	df	chisq	p	most important contributors
All M Can 1	Marine Incursion- conservative	n	2	2.4173	0.2986	
	Marine Incursion- medium	y	2	7.1724	0.0277	Brazil
	Marine Incursion- not conservative	n	2	2.7331	0.255	
	Lake- conservative	y	3	48.0939	<.0001	Peru
	Lake- not conservative	y	3	46.4555	<.0001	inter polygon region
	Andean Uplift	y	2	15.7338	0.0004	*trans*-Andes
	River- conservative	y	10	213.6443	<.0001	Guiana and Putumayo-Napo
	River- not conservative	y	15	260.5074	<.0001	Guiana, Putumayo-Napo, Branco-Negro
	River Refuge	y	9	138.7797	<.0001	Guiana, w Amazon
	Refuge- conservative	y	7	227.1615	<.0001	Guiana
	Refuge- not conservative	y	7	260.5836	<.0001	Guiana
All M Can 2	Marine Incursion- conservative	y	2	43.0113	<.0001	Guiana
	Marine Incursion- medium	y	2	78.7635	<.0001	Guiana
	Marine Incursion- not conservative	y	2	103.8588	<.0001	Guiana, Brazil
	Lake- conservative	y	3	117.5197	<.0001	Guiana
	Lake- not conservative	y	3	111.1867	<.0001	Guiana
	Andean Uplift	y	2	83.2936	<.0001	*trans*-Andes
	River- conservative	y	10	158.4029	<.0001	Putumayo-Napo, Belém
	River- not conservative	y	15	279.4733	<.0001	Putumayo-Napo, Branco-Negro, Belém
	River Refuge	y	9	138.5996	<.0001	W Amazon, Belém
	Refuge- conservative	y	7	235.1219	<.0001	Negro, Napo, Belém
	Refuge- not conservative	y	7	264.555	<.0001	Belém, Negro, Peru

(Table Continues)

Dataset	Model	Sig chi	df	chisq	p	most important contributors
All F Can 1	Marine Incursion- conservative	n	2	0.7849	0.6754	
	Marine Incursion- medium	n	2	0.859	0.6508	
	Marine Incursion- not conservative	n	2	5.5931	0.061	
	Lake- conservative	y	3	38.9594	<.0001	Peru
	Lake- not conservative	y	3	29.8238	<.0001	inter polygon region
	Andean Uplift	y	2	36.2923	<.0001	*trans*-Andes
	River- conservative	y	10	146.7496	<.0001	Guiana
	River- not conservative	y	15	194.5384	<.0001	Guiana
	River Refuge	y	10	91.3789	<.0001	Guiana
	Refuge- conservative	y	6	163.4335	<.0001	Guiana
	Refuge- not conservative	y	7	167.6721	<.0001	Guiana
All F Can 2	Marine Incursion- conservative	n	2	4.2199	0.1212	
	Marine Incursion- medium	y	2	8.9799	0.0112	Guiana
	Marine Incursion- not conservative	y	2	29.9134	<.0001	Guiana
	Lake- conservative	y	3	51.6041	<.0001	Peru, Guiana
	Lake- not conservative	y	3	65.0561	<.0001	Peru, Guiana
	Andean Uplift	y	2	42.736	<.0001	*trans*-Andes
	River- conservative	y	10	105.1187	<.0001	Belém
	River- not conservative	y	15	154.2857	<.0001	Belém
	River Refuge	y	10	99.5316	<.0001	W Amazon, Belém
	Refuge- conservative	y	6	154.2738	<.0001	Belém
	Refuge- not conservative	y	7	132.1043	<.0001	Belém

Note. Several areas were overwhelmingly common as important contributors to the χ^2 results.

In order to interpret the many significant results, attention must be paid to the direction of the patterns in the cluster maps themselves, because in some cases these patterns directly contradict what would be expected under a given model. Thus, looking at Figures 9-12 in conjunction with Table 11, it becomes evident that the conservative lake model can be rejected for Males Can1 and both Females Can1 and 2, because the significant χ^2 results derive in large part from the Peru polygon, and here the cluster results have a preponderance of nonsignificant points in place of the significant clustering that would be predicted under the lake model. The other models have similar conflicts with the patterns in the cluster maps, which are summarized below in Table 12.

Table 12

Comparison of Support for Biogeographical Models from χ^2 and Cluster Results

Model	Support from χ^2	Support from cluster maps?	Problem area
Marine-conservative	M Can 2	no	both hot and cold in Guiana
Marine- medium	M Can 1, M Can 2, F Can 2	no	both hot and cold in Guiana
Marine- liberal	M Can 2, F Can 2	no	both hot and cold in Guiana
Lake- conservative	all	no	both hot and cold in Guiana, many nonsignificant in Peru
Lake- liberal	all	no	both hot and cold in Guiana, not enough nonsignificant in inter polygon region
Andean	all	no	many nonsignificant in *trans*-Andes
River-conservative	all	partial	support in Putumayo-Napo interfluve but not in Guiana or in Belém
River- liberal	all	partial	support in Putumayo-Napo interfluve and Branco-Negro interfluve but not in Guiana or in Belém
River Refuge	all	partial	support in W. Amazon but not in Guiana or Belém
Refuge-conservative	all	partial	support in Negro and Napo areas, not in Belém or Guiana
Refuge- liberal	all	partial	support in Negro and equivocal support in Guiana, no support in Belém or Peru

Note. Problem areas listed are only those which were found to have particularly high effects on the overall χ^2 results and also show conflict with the models (based on cluster map results), not merely those which appear from the cluster maps to conflict with the models.

Table 12 therefore shows that under no circumstance is there complete support for any of the models, and that in many cases there is an outright lack of support for a given model. In the cases where partial support for a model exists, this support is based on only a fraction of the predicted areas of clustering, and is contradicted in other predicted areas of clustering.

The pooled cluster count data were also analyzed for all males and females, with overall similar results to those obtained when each polygon was listed separately in the χ^2 analysis. Differences included rejection of the conservative form of the river model in all cases, rejection of the river-refuge model for Can2 for both males and females, and rejection of the conservative lake model for Can2 in females. However, the pooled data do not allow determination of which particular areas were important in producing a significant χ^2 result, and are thus geographically "blind" and not particularly informative. The results produced by pooling polygons to eliminate bias from polygons that contain very few points were very similar to the results produced without pooling any polygons. This suggests that the presence of polygons with very few points in the original, unpooled analyses did not bias those results.

Objective 3: Testing the Validity of the Subspecies of *Glyphorynchus spirurus*

Discriminant Function Analyses On the Original Data Set

The third objective, analysis of the current subspecies in the Wedge-billed Woodcreeper, was performed primarily using discriminant function analyses on males and females separately. The discriminant functions themselves can be found in Appendix B. Discriminant functions with crossvalidation produced fairly high error rates for both all males and all females (Table 13 and Table 14). Although not presented, the results for the more stringent certainty levels were extremely similar in all cases.

Table 13

Error Rates for Each Subspecies and Overall Error Rate, for All Males

Subspecies	Error Rate
albigularis	0.2439
amacurensis	0
castelnaudii	0.7177
coronobscurus	1
inornatus	0.4688
integratus	0.4286
Amazonian intergrade	0.8
Central American intergrade	1
pallidulus	1
paraensis	0.2927
pectoralis	0.3077
rufigularis	0.3258
spirurus	0.4590
sublestus	0.6190
subrufescens	0.4231
Total	0.5391

Note. None of the error rates for subspecies with large numbers of specimens (see Table 5) is near the 0.05 level needed for diagnosability at 95%.

Table 14

Error Rates for Each Subspecies and Overall Error Rate for All Females

Subspecies	Error Rate
albigularis	0.4211
castelnaudii	0.7121
inornatus	0.4118
integratus	0.6667
Amazonian intergrade	0.75
Central American intergrade	0.5
pallidulus	0.75
paraensis	0.3462
pectoralis	0.4286
rufigularis	0.2329
spirurus	0.5682
sublestus	0.76
subrufescens	0.8
Total	0.5652

Note. None of the error rates for subspecies with large numbers of specimens (see Table 6) is near the 0.05 level needed for diagnosability at 95%.

While the overall error rates were high for both males and females, the crossvalidation summaries (Tables 15 and 16) for males and females show that some current subspecies are much more diagnosable than others. Of the subspecies with large sample sizes, *albigularis*, *paraensis*, *pectoralis*, and *rufigularis* were diagnosable at over 60% accuracy for males, while *paraensis* and *rufigularis* were diagnosable at over 60% accuracy for females. In addition, most subspecies were easily diagnosed from all but a few other subspecies. In no case was any subspecies diagnosable at a level near the 95% benchmark which has been argued should be the new standard, and only *albigularis* (males) and *rufigularis* (females) could be diagnosed at a level of 75% from all other subspecies.

Table 15

Crossvalidation Summary for All Males

Subspecies	Rate of reclassification	Number reclassified	Total number
albigularis	75.61	31	41
amacurensis	100	2	2
castelnaudii	28.23	35	124
coronobscurus	0	0	1
inornatus	53.13	17	32
integratus	57.14	12	21
Amazonian intergrade	20	1	5
Central American intergrade	0	0	2
pallidulus	0	0	12
paraensis	70.73	29	41
pectoralis	69.23	9	13
rufigularis	67.42	60	89
spirurus	54.1	33	61
sublestus	38.1	8	21
subrufescens	57.69	30	52

Note. The second column corresponds to the percent of putative members of a subspecies reclassified into the same subspecies. The third column corresponds to the number of specimens reclassified into the same subspecies. If subspecies are diagnosable at a given level, the second column of the table should show percentages at or above that level for all diagnosable subspecies.

Table 16

Crossvalidation Summary for All Females

Subspecies	Rate of reclassification	Number reclassified	Total number
albigularis	57.89	11	19
castelnaudii	28.79	19	66
inornatus	58.82	10	17
integratus	33.33	4	12
Amazonian intergrade	25	1	4
Central American intergrade	50	3	6
pallidulus	25	4	16
paraensis	65.38	17	26
pectoralis	57.14	4	7
rufigularis	76.71	56	73
spirurus	43.18	19	44
sublestus	24	6	25
subrufescens	20	7	35

Note. The second column corresponds to the percent of putative members of a subspecies reclassified into the same subspecies. The third column corresponds to the number of specimens reclassified into the same subspecies. If subspecies are diagnosable at a given level, the second column of the table should show percentages at or above that level for all diagnosable subspecies.

Contour Maps Based on Discriminant Function Scores

These discriminant function results were used to generate contour maps in GIS for both males and females (Figures 17 and 18) in order to find potential areas where subspecies boundaries could be redrawn. The contour maps show that in most areas, change in discriminant function scores is rather slow and clinal. Sharp change occurs only in a few areas where several contour lines lie close together. Four such areas were found in both males and females, with slight differences in the boundaries between the sexes. The red polygons in Figures 17 and 18 correspond to revised potential subspecies boundaries based on sharp contour slopes in one or both sexes. The boundaries are shown in Figures 19 and 20 as well, where they can be seen next to the whole range of the species and superimposed on the current subspecies ranges, respectively. The specimens within these boundaries were then re-examined in SAS.

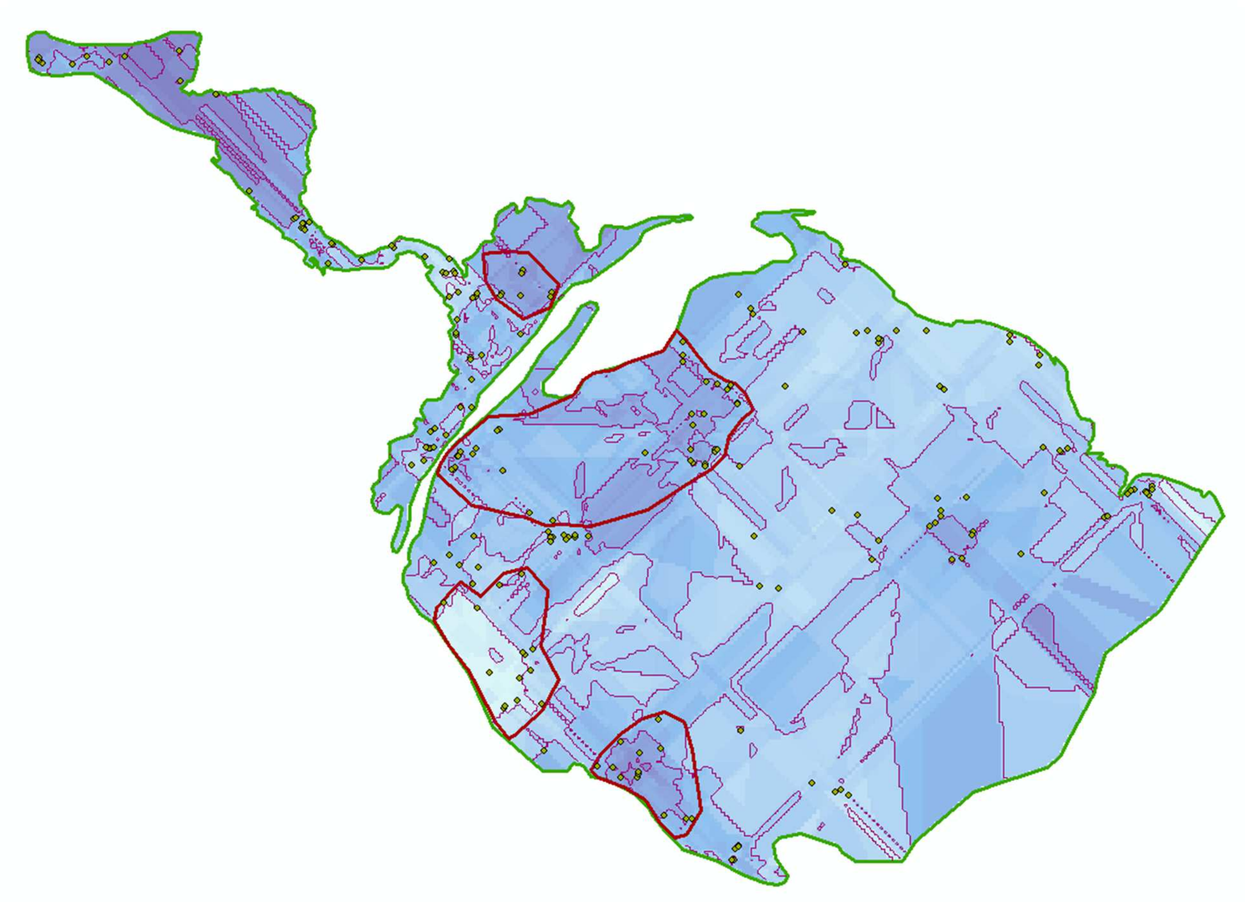


Figure 17. Discriminant function score contour for all males. Darker blues correspond to higher discriminant function scores, and contours mark every 0.1 difference in scores. The red polygons refer to revised potential subspecies boundaries.

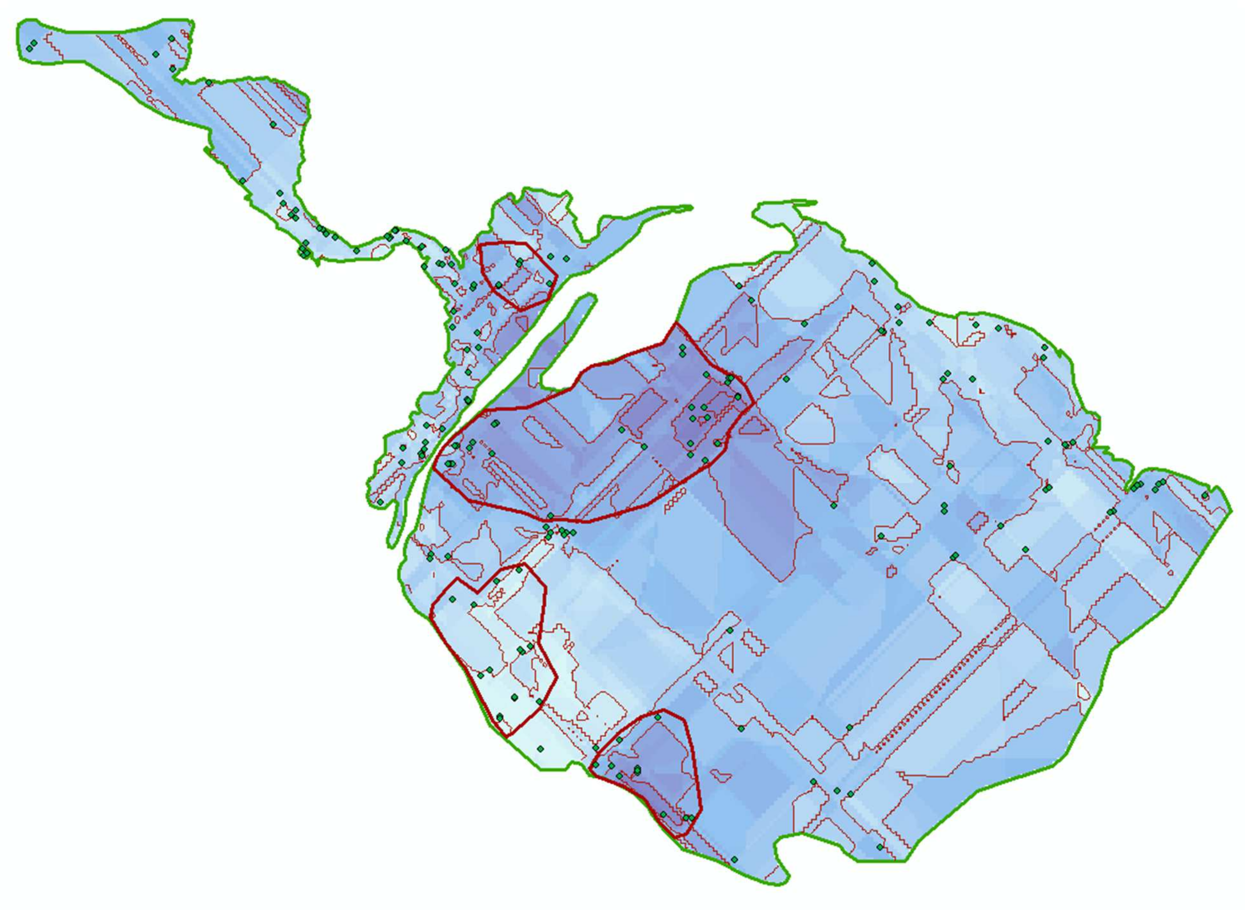


Figure 18. Discriminant function score contour for all females. Darker blues correspond to higher discriminant function scores, and contours mark every 0.1 difference in scores. The red polygons refer to revised potential subspecies boundaries.

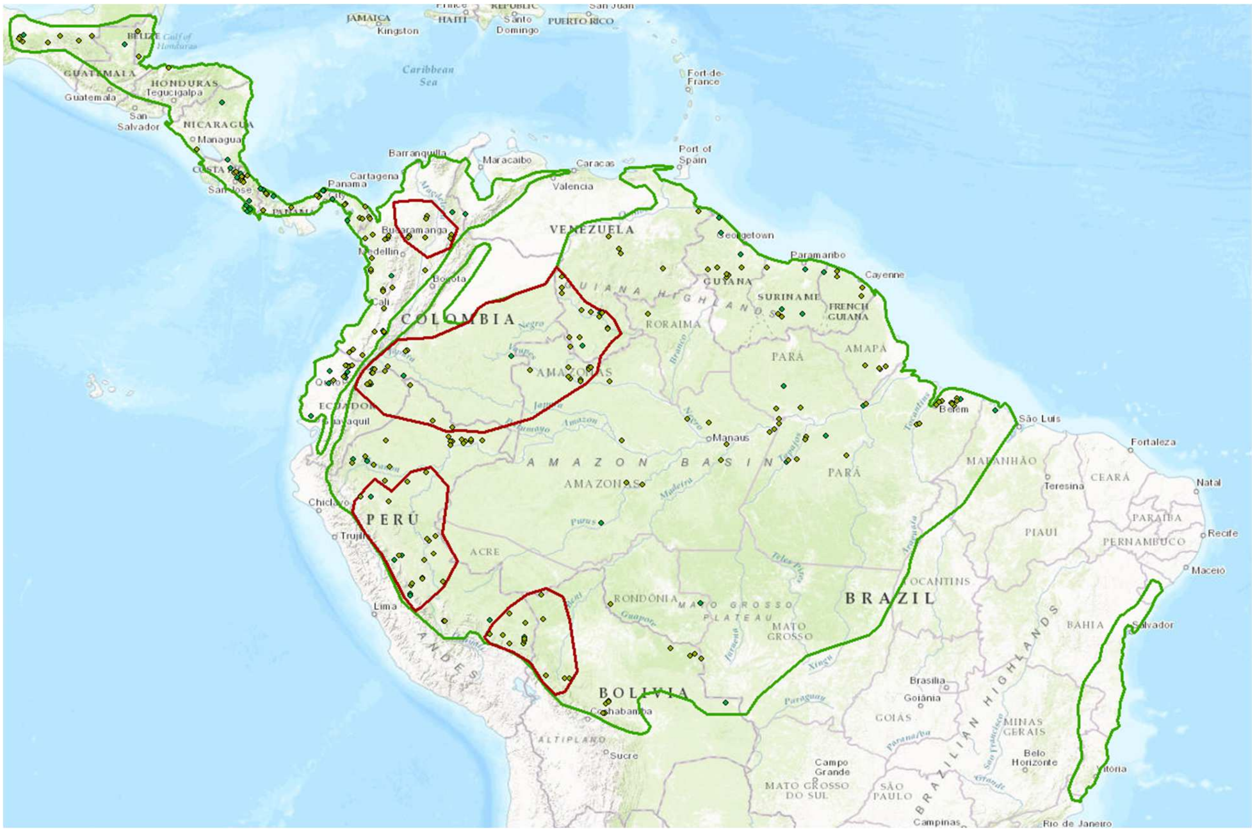


Figure 19. Potential revised subspecies boundaries, relative to the species' range. The range in this map (the green polygon) was developed from the descriptions in Marantz (2003), Cornell's Neotropical Birds Online website's account for the Wedge-billed Woodcreeper, and records on the eBird website for the species. eBird records were used only in making additions to the range, not in subtracting areas, and they were only used where more than one record existed in an area (thereby excluding a few scattered observations in the cerrado between the Amazon Basin and the Atlantic Forest).

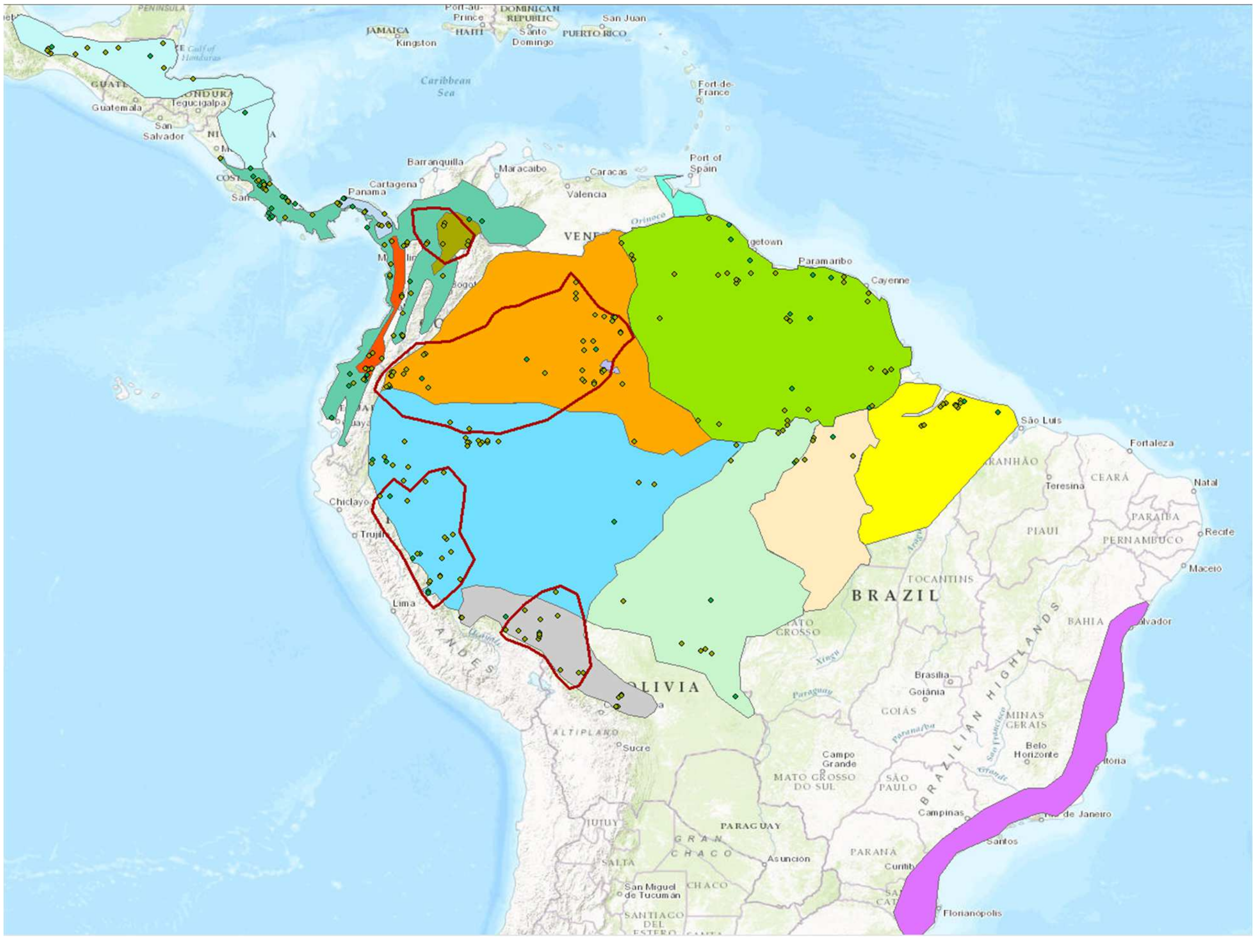


Figure 20. Potential revised subspecies boundaries, relative to the current subspecies boundaries. For the identity of current subspecies, refer to Figure 1.

Diagnosability Using Additional Characters From the Original Subspecies Descriptions But Not Present in the Original Data Set

In addition to the re-analysis of the specimens in the potential new subspecies boundaries, I also tested whether certain subspecies are diagnosable using other characters, with a series of specimens from the AMNH. The resubstitution summary for a nonparametric discriminant function analysis on these specimens is found in Table 17. I found that several subspecies were diagnosable at a high level using just these characters. In particular, *albigularis* had 100%

diagnosability (albeit with a sample size of 9), and *inornatus* and *subrufescens* both had very high diagnosabilities as well, although not above the 95% level.

Table 17

Resubstitution Summary for Subspecies Tested Using a Series from the AMNH

Subspecies	Rate of reclassification	Number reclassified	Total number
albigularis	100	9	9
castelnaudii	20	4	20
inornatus	90.91	10	11
paraensis	66.67	14	21
rufigularis	35	7	20
spirurus	45	9	20
sublestus	47.06	8	17
subrufescens	85	17	20

Note. The second column corresponds to the percentage of putative members of a subspecies reclassified into the same subspecies. The third column corresponds to the number of specimens reclassified into the same subspecies.

Testing Diagnosability of Select Subspecies with a Discriminant Function Analysis Using Revised Subspecies Boundaries

The discriminant function analysis performed on the specimens in the revised subspecies boundaries is summarized below in Table 18 (females) and Table 19 (males). Although even these revised boundaries did not permit diagnosability of any subspecies at greater than 95%, there were several groups for which very high diagnosability was reached, and nearly all groups had diagnosability over the traditional cutoff of 75%. For the females, three subspecies showed diagnosability levels higher than 80%, and for the males, all four showed diagnosability levels higher than 80% with two being higher than 90%, and rufigularis reaching 94%. Therefore, diagnosable units do exist in this species, though not necessarily at the new level argued to name them as subspecies.

Table 18

Crossvalidation Summary for Revised Subspecies, All Females

From Ssp	albigularis	castelnaudii	integratus	rufigularis	Total
albigularis	16	0	2	0	18
	88.89	0	11.11	0	100
castelnaudii	1	21	2	1	25
	4	84	8	4	100
integratus	1	1	5	0	7
	14.29	14.29	71.43	0	100
rufigularis	0	6	2	45	53
	0	11.32	3.77	84.91	100
Total	18	28	11	46	103
	17.48	27.18	10.68	44.66	100

Note. The second row of cells in every subspecies row corresponds to the percent of putative members of a subspecies reclassified into the subspecies listed in the column heading. The first row of cells corresponds to the number of specimens reclassified into each subspecies in the columns.

Table 19

Crossvalidation Summary for Revised Subspecies, All Males

From Ssp	albigularis	castelnaudii	integratus	rufigularis	Total
albigularis	32	1	2	0	35
	91.43	2.86	5.71	0	100
castelnaudii	0	36	4	3	43
	0	83.72	9.3	6.98	100
integratus	2	0	16	0	18
	11.11	0	88.89	0	100
rufigularis	0	6	0	94	100
	0	6	0	94	100
Total	34	43	22	97	196
	17.35	21.94	11.22	49.49	100

Note. The second row of cells in every subspecies row corresponds to the percent of putative members of a subspecies reclassified into the subspecies listed in the column heading. The first row of cells corresponds to the number of specimens reclassified into each subspecies in the columns.

CHAPTER IV: CONCLUSIONS

The objectives of this study were to characterize geographic variation in a number of key morphological characters in the Wedge-billed Woodcreeper, to determine whether the patterns of geographic variation in morphological characters were predicted under six of the most-studied biogeographical models for the origin of bird diversity in Amazonia, and to test the validity of the current subspecies groupings and rankings in the Wedge-billed Woodcreeper.

Objective 1

The objective of characterizing geographic variation in the characters used was achieved. There appears to be a good deal of smooth clinal variation in most of the characters, with abrupt change between character states being extremely rare in this data set. However, the degree of "smoothness" of the clines characterized varies depending on the character and has yet to be rigorously designated using spatial techniques (e.g. Euclidean distance to contours). Many of the characters showed concordant patterns, and there do not appear to be any instances of discordance between characters, corroborating the impressions of other workers on geographic variation in birds (Remsen 2010). This high degree of concordance, seen particularly in the bill measurements, also validates our choice to use a dimension-reduction technique in place of testing the biogeographical and subspecies hypotheses on each character in turn (Marantz and Patten 2010).

The high or low ends of clines in the characters studied were frequently located in areas known or believed to have had a unique geographic history, such as the Guianan Shield, the Chocó, or the southwestern fringe of Amazonia along the Andes. This suggests that the species, and more specifically these characters, are carrying useful biogeographic information. Now that the variation in these traits has been characterized, it can be used to draw further conclusions about the species' history (e.g. whether any selective pressures may have resulted in adaptive changes to these characters over parts of the range), as per Zink and Remsen (1986).

The characterization of variation in this species also brought up a potential problem with my conclusions, by emphasizing the tentative character of my conclusions in many parts of the bird's range where specimen data are scarce or not as easily available due to world-wide distribution of specimens. These regions with sparse sampling include Nicaragua, the Atlantic Forest of Brazil (where I had only one specimen), the majority of Amazonian Colombia, the area around the Jurua and Purus rivers in southwest Amazonia, portions of the northeast Amazon Basin in southern Roraima, and large areas of south Amazonia.

Most of these regions are poorly sampled for all birds, not just *Glyphorynchus spirurus*, and specimens are lacking in museums due to challenges of accessibility (e.g. the Jurua and Purus rivers) sometimes combined with unstable political environments (e.g. Amazonian Colombia). In some cases, museums are adding to their collections of *Glyphorynchus spirurus* but only in the form of skeletal specimens or tissue samples, which are preparation types that had traditionally been ignored. This is evident from the preponderance of such types of specimens in recent entries on VertNet (an online database listing the holdings of many collections) as well as from communication with staff at the AMNH. In other cases, collection is being accomplished in these areas (most notably south-central Amazonia), but the specimens are being deposited, understandably, in South American museums such as the National Institute of Amazonian Research in Manaus, Brazil (Fernandes et al. 2015).

The lack of specimen data in these areas makes difficult any analyses that require points in those regions or even sampling across the entire range. In addition, the characterizations I have made of the variation in each morphological character should not be taken too seriously in parts of the range without sampling, especially at the fringes of the range. For instance, despite the superiority of kriging to other forms of interpolation, a number of contour maps (e.g. tarsus length, tail length) still showed extensive contouring in south-central Amazonia and other areas with no sampling. Such results may be spurious and due to unmerited continuation of trends from the closest data to these areas. The contour maps do seem to show substantially more of such odd results at areas without sampling at the edges of the range compared to similar areas within the range, implying that the results for the latter areas are probably more robust .

Objective 2

The second objective addressed the ability of the various biogeography models to predict the observed data. I found no overwhelming support for any model, either in the chi-square results or in the examination of the patterns in the cluster results subsequent to performing the chi-square tests. Because I analyzed sexes and each canonical variable separately, a model would need to have non-significant results in all four analyses to be fully rejected solely based on the χ^2 tests. However, I was able to reject several models or versions of models due to the clustering patterns important for the significant χ^2 value not being in the right direction to support the model. I also found no support for all predicted areas of clustering even for those models showing support for a subset of their predicted areas of clustering (see Table 12). Therefore, I can conclude that based on this data set, none of the proposed models appear to predict the morphological variation in this species, suggesting that they may also not accurately explain the evolutionary history of the species.

The models which were completely rejected are the marine incursion model, the lake model, and the Andean uplift model (in the sense of it being the sole explainer of variation in the species). The marine incursion model was rejected because in all interpretive levels, clustering of both high and low values occurred in the well-sampled Guianan Shield area, where predictions expect clustering of either high or low values, but not both. The lake model was rejected for the same reason, as well as for a lack of clustering in the Peruvian polygon (the primary area of differentiation from the marine incursion model) and a disproportionate lack of non-significant points in the areas between prediction polygons. Even drastic alteration of these models (for instance, fragmentation of the Peruvian polygon into northern and southern portions due to increased size of the lake systems) would not lead to support for them. According to our current geologic understanding, the entire Guianan Shield would have been free from marine incursions or lacustrine environments (Hoorn et al. 2010, Caputo et al. 2016), and indeed the Guianan Shield has a geographical pattern of clustering inconsistent with these models and was among the largest contributors to the χ^2 results for all interpretations of the models. Finally, the Andean uplift model was also rejected due to the presence of too many non-significant points in the *trans*-Andean region. This implies that vicariance events or other processes have shaped the *trans*-Andean region after the rise of the Andes to form the complex mix of high and low canonical variable values seen today. The Andean uplift model in its many less extreme forms was not tested in this study because of the impossibility of creating polygons to show the expected patterns, and may still apply to these characters. These less extreme forms state that the

Andean uplift did result in isolation and divergence between *cis*- and *trans*-Andean populations, but that subsequent vicariance events on either side of the Andes further obscured the pattern.

There were a few geographic areas where clustering patterns fit with the predicted patterns under several models, but none of these models predicted clustering patterns across the entirety of Amazonia or even across all areas which were important contributors to the significant χ^2 results. Thus, the clustering pattern in the Branco-Negro interfluve and the Putumayo-Napo interfluve support predictions of the river, refuge, and river-refuge models, while the patterns in the Belém, Guiana, and Peruvian areas contradict predictions of these models. Therefore, the only way these models could apply to this data set would be to reduce their predicted extent from the entirety of Amazonia to portions in the northern and western parts of Amazonia. Doing this, however, essentially repudiates these models unless there is a plausible reason why only these areas would have been affected or another process operated to obscure the operation of that model outside of these areas.

There are no good reasons to presume that rivers should be barriers only in northern and western Amazonia, especially considering the size of the southern rivers and the fact that their headwaters often lie outside of the rainforest (Goulding et al. 2003), and that recent genetic work on the Wedge-billed Woodcreeper has found support for the river barrier hypothesis for major and minor rivers in south-central Amazonia (Fernandes et al. 2013). Another alternative would be that the rivers are, or were, barriers, but that this pattern has been obscured in a number of areas (e.g. Belém) for unknown reasons. This argument is plausible and cannot be ruled out because, despite this being an unusually large data set compared to other studies, my sampling is still so low in many of the Amazonian interfluves that I cannot be sure that I have captured the true character values in many of these areas. However, another argument concerns the similarity in character values in nearby interfluves with high clustering. Although this is not impossible under the river hypothesis, it is nevertheless assumed that some divergence in character values will result between adjacent or nearby interfluves. We do not find such a result either in the clustering results or the contour maps for the individual characters.

Similar arguments against the plausibility of the river refuge model even in a reduced state can also be raised, along with the argument that there is no evidence for a general contraction of rainforest only into northern and western Amazonia. Concerning the refuge model, the latter argument also applies, because only two refuges are shown to have support from these results, the Napo refuge associated with the Napo River and the Imeri refuge near the Rio Negro. An alternative also exists that only in northwestern Amazonia did rainforest fragment, but while this would explain the observed results, it has no support from the literature and is highly implausible based on Amazonian precipitation patterns (Haffer 2008).

Based on this study, none of the models are supported in their proposed interpretations, and any dramatically reduced versions are implausible on various grounds. In addition, no patterns in the clustering results appear to be easily explainable by a combination of two or more models. I conclude that the morphological variation in this species is not due primarily to the events presumed to have occurred under any of the models.

This has a number of implications. Firstly, it may suggest that there are current ecological factors selecting for different character states in different parts of the range. This is a form of the ecological gradient model (Endler 1982b). This species has been found to exhibit variation across an elevational gradient in Ecuador (Mila et al. 2009), and it is plausible that this process could be occurring on other characters throughout the whole range. The wide range of characters used in this study includes some connected to foraging, movement, or other activities which might be affected by ecological factors (e.g. bill measurements, tail length, tarsus length, wing length). However, these had only minor contributions to the first two canonical variables, with the exception of tail length.

The more important contributors were three plumage characters. While the amount of streaking on the underparts (usually invisible due to this scansorial bird's position on the tree) and the width of the light marks on the breast do not appear to have any relation to selection pressures or ecological gradients, it seems at least plausible that the increased orange throat color in certain areas may be an example of Gloger's Rule, which states that organisms in wetter or more humid areas will have darker coloration than those in drier areas (Zink and Remsen 1986). In birds this may be a defense against feather-degrading bacteria, which more easily degrade unmelanized feathers (Burtt and Ichida 2004, Gunderson et al. 2008). The highest areas of rainfall in Amazonia are now concentrated in a broad area in the northwestern part of the Amazon Basin as well as in a narrow elevational band on the fringe of the Andes (Haffer 1969, Goulding et al. 2003). There is also extremely high rainfall in the Chocó. Although there does not appear to be a trend toward very orange throats along the edge of the Andes, the other two listed regions are those in which *Glyphorynchus spirurus* shows the greatest degree of orange coloration in the throat.

Another important implication of these results is that despite the timescale for the existence of *Glyphorynchus spirurus* as a separate lineage overlapping with all the potential biogeographical models, the current morphological variation in this species may be much more recent and may even be a result of current ecological processes. Or, if it is ancient, so many processes have affected it that no pattern supporting a single process is now discernible (which we denote as the palimpsest model). The palimpsest model derives its name from manuscripts in which older texts have been partially erased and new texts written over them, but without completely obscuring the existence of the older writing. In either case, the usefulness of morphological data from this species for biogeographical questions appears to be limited. Presumably genetic data sets may be more effective in determining which models may have affected the evolution of this species, although any genetic data set used must include characters with a slow enough rate of divergence that effects of the more ancient biogeographical models can be seen, as well as more-quickly-evolving characters with which to test the more recent models. Using multiple genetic characters with well-known rates of evolution may be superior to morphological characters in this case because rates of evolution of most morphological characters are not well-known. It is therefore unclear to what extent any particular morphological character in use might have undergone drift after the events proposed in the six biogeographical models I tested.

A similar implication concerns the mismatch between previous genetic data sets and this morphological data set. Despite using numerous characters and the most complete sampling design to date for a morphological study on the Wedge-billed Woodcreeper, this study was unable to recover the groupings suggested by several previous genetic studies. For instance, river-delimited groupings were not recovered, contra Fernandes et al. (2013) and Fernandes et al. (2015), and character values on either side of the Andes in Ecuador appeared similar, contra Mila et al. (2009). This means that morphology in this species may not be a useful proxy for genetic data for biogeographical questions, although it may be useful in other ways.

Finally, the lack of any strong results in favor of any biogeographical model calls into question the generalization of morphological results from this species to other forest understory birds. Some other forest understory birds have been found to show genetic and morphological population structure congruent with certain biogeographical models (such as the river barrier model, e.g. Fernandes et al. 2015), implying that the lack of results from this study may derive more from the origination age of variation in the characters used or perhaps from the history of the species itself, and not from the inapplicability of these models to other species.

Objective 3

The third objective, to accomplish a revision of the subspecies in the Wedge-billed Woodcreeper, was accomplished using discriminant function analyses. This study found minimal support for the current subspecies groupings and rankings, in accord with recent genetic studies that discovered mismatches between genetic structure and current subspecies taxonomy (Marks et al. 2002, Mila et al. 2009, Fernandes et al. 2013). However, unlike these genetic studies, which found that cryptic diversity was widespread in this species and that a number of phylogenetic species might exist within *Glyphorynchus spirurus*, this study finds that the morphological variation in the species is mainly smoothly clinal and does not admit of more than a very small number of areas of transition between distinct character expressions (i.e. step clines). Depending on the level of diagnosability and the sample size required for the elevation of such groupings to subspecies rank, there are between 0 and 6 valid subspecies within *Glyphorynchus spirurus*.

Using the primary data set, between 0 and 4 subspecies can be diagnosed depending on the level of diagnosability chosen. Based on the most stringent level of diagnosability, that of 95% (Patten and Unitt 2002, Remsen 2010), no subspecies are valid. Using a somewhat less stringent level of diagnosability, that of 90%, would result in two valid subspecies (*rufigularis* and *albigularis*), but with somewhat reduced ranges. These two subspecies are diagnosable at 90% using the primary data set and adjusted ranges, but for males only. The least stringent level of diagnosability, that of 75%, recovers *albigularis* (diagnosable for males) and *rufigularis* (diagnosable for females) without any adjustment to their ranges. Using the revised ranges and the 75% level, the primary data set allows for the diagnosis of *albigularis*, *castelnaudii*, and *rufigularis* for females, and all three of these plus *integratus* for males.

Using the secondary data set derived from a subset of the specimens at the AMNH, between 1 and 3 subspecies can be diagnosed, depending on the diagnosability level. The character set used to diagnose these subspecies includes a number of characters but is dominated by breast streaking color, supercilium color, and color of the margins of the breast feathers, characters not measured in the large primary data set. Using the 95% level with the secondary data set, only the subspecies *albigularis* is valid. However, only 9 specimens were available for use with this data set, meaning that the validity of *albigularis* may be questionable given the small sample size. This sample size is in fact smaller by two than that (11) used to originally describe this subspecies (Chapman 1923). At a level of 90%, *inornatus*, found in southern Amazonia, is also valid based on the secondary data set, but with a sample size of only 11, versus 12 in the original description (Zimmer 1934). At a level of 75%, the secondary data set allows diagnosis of *subrufescens* as well as *albigularis* and *inornatus*. However, the sample sizes in the secondary data set are low, except for *subrufescens* with 20 specimens, and this data set is not accompanied by a characterization across the whole range of the variation in the characters used, meaning that it should be used with caution.

Therefore, if the conclusions from the two data sets are combined and the revised ranges are used, a level of 95% results in 1 valid subspecies, a level of 90% results in 3 valid subspecies, and a level of 75% results in 6 valid subspecies.

Due to the cutoff for diagnosability for subspecies being partly a matter of taste, anywhere from 0 to 6 subspecies can be supported. In all four cases in which new subspecies ranges have been drawn (*rufigularis, integratus, albigularis,* and *castelnaudii*), the type specimens for each subspecies appear to lie within the new range, meaning that no nomenclatural changes are needed. Given that subspecies are increasingly thought of as similar to phylogenetic species and thus constitute distinct lineages (Remsen 2010), I chose *a priori* to use a more stringent diagnosability cutoff of 95% in this study. This would leave only *albigularis* as a valid subspecies. Despite the small sample size in the secondary data set, its conclusions should be used because they show the same trend that is present in the other data set, which is that *albigularis* is diagnosable at a very high level and certainly represents a distinct evolutionary entity. This is apparent even when using the original subspecies range and diagnosing it from all other specimens in the species' range. In order to better reflect the pattern found using the characters in the primary dataset, the range of *albigularis* should be reduced to that shown in Figure 19. All other subspecies names should be discarded from use under a diagnosability level of 95%.

The use of different diagnosability levels would, however, lead to different conclusions about the validity of certain subspecies, such that a discussion appears to be warranted among avian systematists of the diagnosability level that best balances the need for rigor and the need to recognize entities with unique evolutionary histories. Subspecies revisions are not common in the recent avian literature, but among those few there is still a diversity of opinion about what diagnosability level to use. Besides the several studies described in the Introduction, only two advocated or used a level of 95%: Donegan and Avendano (2015) and Zink (2015). Four used the traditional level of 75%: Cicero and Johnson (2006), Bot and Jansen (2013), Patten (2015), and Lloyd (2016). In particular, Patten (2015) does not mention a 95% rule at all but does mention a cutoff of 75%, implying that he may now espouse that level instead of the 95% rule he originally promoted. Four studies neglected to use any cutoff of diagnosability: Dietzen et al. (2015), Kearns et al. (2015), Kirwan et al. (2014), and Luttrell et al. (2015).

Even though the other groupings described as being diagnosable above 75% are not ranked here as subspecies, they do appear to be distinct diagnosable entities and convey information about which areas of the range have undergone divergence. Therefore, although based on my *a priori* choice of a diagnosability level I cannot rank them as subspecies here, they call into question the assumption that a very high level of diagnosability is necessarily best. Others might consider these groupings subspecies based on different levels of diagnosability. In addition, I found that even where I could not diagnose a subspecies from all other subspecies, I could often diagnose it at a very high level from the vast majority of the other subspecies, meaning that most subspecies are dissimilar from each other (probably because they are on different ends of various clines in character values). Specimens from a number of sections of the range appear to be fully diagnosable from specimens in other extremes of the range, but not from nearby or intervening populations, exemplifying clinal variation.

It is also important to note that certain subspecies rankings could not be adequately tested in this study due to extremely small sample sizes. These include *coronobscurus*, *amacurensis*, and *cuneatus*, inhabiting a tiny mountainous area of Venezuela, the Orinoco delta, and the Atlantic Forest, respectively. Two of these subspecies have tiny ranges within or adjacent to other populations which have been shown not to be diagnosable, and might therefore be expected, based on the patterns of character variation, to also not be diagnosable and to have been the result of over-eager subspecies describers. The third, *cuneatus*, is sufficiently isolated that it can be expected to have potentially undergone divergence sufficient to diagnose it, but until more specimens are located testing this is not possible.

These morphological results do not appear to show concordance with the patterns in song vaguely described in Marantz (2003), which have been hypothesized to represent multiple cryptic species. Variation in song is frequently used for delineating species boundaries in suboscine passerines (including woodcreepers) due to the innate nature of songs in this group (Isler et al. 1998, Marantz 2003, Remsen 2005, Seddon 2005). Learned song, found in oscine passerines, may lead to a decreased chance of differences in song type causing reproductive isolation relative to species that do not learn their songs, making this character useful for determining species limits (Seddon and Tobias 2007). However, uncertainty over the true degree of song learning found in suboscines has led some authors to argue for a more nuanced role of vocal characters in delimiting suboscine species (Raposo and Hofling 2003, Kroodsma et al. 2013), particularly given the discovery that at least some suboscines show song learning

(Kroodsma et al. 2013). The available evidence does not support song learning in woodcreepers, but many woodcreepers do show significant geographic variation in song, meaning that song type remains an important character for inferring reproductive isolation in this group (Marantz 2003). In light of this, our finding that song type and morphological variation do not appear concordant implies that if the different song types represent different biological species, the morphological characters in our data set have not been important in the speciation process.

However, this conclusion is rendered less robust due to the uncertainty surrounding the geographic delimitation of the song types in *Glyphorynchus spirurus*. The terms used in their description indicate that one song type exists in Central America and northwestern South America, that a second, similar to the first, exists in northern and western Amazonia, and that a third, radically different from the other two in basic pattern, exists in the southeastern portion of the range (Marantz 2003). These designations exclude all mention of intergrade zones between song types and also do not make clear the precise boundaries of northern, western, and southeastern Amazonia.

None of the characters are concordant with a boundary placed somewhere in southern Amazonia, although this may be a result of poor sampling in much of this area. In addition, no characters support a sharp break between all *trans*-Andean birds and those in northwestern Amazonia. If the boundary between the two Amazonian song types fell in north-central Peru and continued along the Amazon, however, there would be concordance between part of the length of this boundary and the discriminant function scores. Despite this, even here none of the individual characters are concordant with a break in song at this location. There is clinal variation throughout southern, central, and western Amazonia, as well as to the west of the Andes, rather than a sharp break as would be expected if morphological variation and song variation were in concordance. Therefore, the variation in song as currently understood does not appear to be concordant with morphology. In addition, a cursory examination of the song recordings in the Cornell Lab of Ornithology's Macaulay Library shows song types which from a subjective perspective appear intermediate in parts of south-central Amazonia (Mato Grosso, Brazil) and in southwestern Amazonia (Tambopata, Peru), with an apparently intermediate recording as far north as Iquitos (northern Peru). Songs clearly fitting the description of the southeastern Amazonian type only begin to appear as one moves eastward into the state of Pará. The potential existence of such a wide geographic zone of intermediate songs calls into question the notion that these song types represent cryptic species (Isler et al. 2005).

Notes On Uncertainty

One of the great potential sources for error in this study came from geographic uncertainty. As with any study in which spatial relationships are tested, having accurate locations of the point and polygon data being used is extremely important. For this reason, I graded each specimen location with a certainty level and tested progressively more inclusive certainty levels in all my analyses for objectives 2 and 3 in order to determine whether uncertainty in specimen locations would affect my conclusions. I found that certainty levels were all extremely similar in all analyses, and that changing the certainty level did not change the pattern of my results in any case. This may in large part be due to the extremely large sample size used in this study, which was still apparently more than sufficient to produce results even after being reduced by a hundred points or so.

Another area of uncertainty which I accounted for consisted of uncertainty in where the boundaries of predicted clustering should be under each model. To combat this, I used multiple sets of polygons for most models and analyzed them separately. This also did not appear to have an effect on the results, especially in the interpretation of significant chi-square results.

Uncertainty also exists regarding the boundaries of intergrade zones between potential subspecies as well as the nature of variation within these intergrade zones. This uncertainty has the potential to affect which subspecies are recovered as valid because inadvertently sampling specimens from an intergrade zone and including them within the sample for a subspecies being tested will skew the results toward decreased diagnosability of that subspecies. This becomes an issue in cases where two subspecies have well-defined boundaries with an intergrade zone in between, but the existence or location of those well-defined boundaries is not known. I accounted for this source of uncertainty by re-drawing the boundaries used to assign specimens to a subspecies based on the locations of sharp breaks in a contour map of the discriminant function scores, and then running a second discriminant function analysis with these revised boundaries so as to exclude intergrade zones from the analysis.

However, it is possible that uncertainty in the form of a lack of knowledge about the nature of variation in areas with poor sampling may have had an effect on my ability to draw conclusions. I was unable to characterize variation confidently in certain parts of the range, such as much of south Amazonia, and I also had decreased counts of points to use in cluster analyses from those areas, which affected my ability to draw conclusions about how predicted and observed clustering in these areas compare. Also, the lack of sampling in parts of south Amazonia, in the core of the range of *inornatus*, means that it is possible that many of the specimens labeled as this subspecies might actually come from intergrade zones with nearby subspecies. The existence or size of such intergrade zones, however, is conjectural. Sampling for all other subspecies included a predominance of specimens in the core of the range of each subspecies.

Despite these sampling difficulties, I nevertheless managed to fulfill all three of my objectives. I characterized variation in several morphological characters, found little support for any of the six biogeographical models tested, and determined that only one current subspecies is diagnosable at a level of 95%.

Future Directions

Based on the findings of this study, several recommendations can be made to researchers seeking to address in other organisms or in the Wedge-billed Woodcreeper any of the three major objectives described here. First, characterizations of morphological variation should be made not only on their own accounts, but also as a critical first step in any biogeographical or systematic analysis. Prior knowledge of morphological variation in the Wedge-billed Woodcreeper was limited to that encapsulated in the subspecies rankings for this species. However, this study found that variation in the characters studied did not match those subspecies, and that the subspecies boundaries, many of which followed river courses, did not correspond to actual boundaries in the clinal variation found in this species. Had we accepted the existing subspecies at face value and used them to perform a biogeographic or other analysis on this species without first characterizing the variation present, we may have found spurious support for one or more of the biogeographic models. Therefore, we urge anyone performing a biogeographic analysis to preface it with a study of variation in the chosen organism(s), and we recommend that researchers in other fields take into account possible geographic variation in the characters they plan to use.

Although practical difficulties often exist in obtaining a series of specimens across the entire range of a species, making the best effort possible in that regard is paramount as a first step toward an accurate characterization of variation. This study had a much greater sample size and geographic distribution than any other study, genetic or morphological, of the Wedge-billed Woodcreeper, and yet uncertainties in the patterns of variation found in certain poorly-sampled portions of the range still exist. Workers in the field must recognize that such uncertainties will likely be present when working with any species, even the very common (e.g. American Robin, Zink and Remsen 1986). With regard to future directions for characterizing variation in *Glyphorynchus spirurus*, there are two important recommendations. First, specimens from the remaining gap areas from this analysis should be obtained to complete the picture of variation in the species, either by visiting the appropriate South American collections or by sending collecting expeditions to the under-studied areas. In addition, continued collecting from all areas of the range should be undertaken whenever feasible in order to ensure that variation over time can be documented in this species, since some species have been found to show variation over short periods of time (Zink 1983). Second, variation in song type should be characterized and compared to morphological and genetic data sets.

A number of recommendations for future tests of biogeographical models can also be made. Firstly, the species and characters chosen for such tests should be chosen with care in order to afford specific tests of one or a few biogeographic processes. When a species or character is ancient enough to be used in tests of all the biogeographical models, it is important to include the palimpsest model (the inability to distinguish between the effects of multiple biogeographic processes) as a testable possibility. We recommend developing predictions of what the expected patterns in genetic or morphological variation might be under certain combinations of models in order to better test the palimpsest model. Another recommendation is to determine which morphological characters might be most effective in testing more ancient models vs. more recent models, much like the way certain genetic characters are known to be more effective for testing models of a particular age due to their rate of mutation. In addition, tests of biogeographical models using the Wedge-billed Woodcreeper might benefit from using additional genetic characters or song. The patterns of morphological variation in this species appear too complex to distinguish any of the models. Finally, tests of some of the less-studied biogeographical models may be warranted, particularly for this species. The ecological gradient model could be applicable to *Glyphorynchus spirurus*, with precipitation as the ecological factor. The arch model should also be tested, due to its having been ignored for birds.

Finally, a few recommendations can be made for future work in subspecies revisions. The most important is that the field of systematics should carefully consider what level of diagnosability is most appropriate for defining subspecies. These results make clear that not only can the diagnosable clusters for some species change depending on whether 75%, 90%, or 95% diagnosability is chosen, but that the clusters which drop out as the diagnosability level is increased appear to represent distinct entities in this case, meaning that the role of subspecies in recognizing well-defined clusters of variation within a species is not necessarily served by the use of a very high diagnosability level. This has implications beyond systematics, due to the importance of diagnosable entities in focusing conservation efforts (Garnett and Christidis 2017).

Of these three levels, we recommend either returning to the 75% rule and avoiding the use of very high diagnosability levels, or including additional percentages (e.g. 85%, 95%) to explore the utility of the subspecies rank for its different users (e.g., systematists, conservation biologists).

A very high diagnosability level also requires excellent knowledge of the locations of sharp breaks in character expression, because even well-defined entities will not be diagnosable if individuals from intergrade zones are included in the "range" of the subspecies being tested. Therefore, we recommend that a characterization of variation identify these prior to performing a final test of the diagnosability of subspecies, as was done in this study. A final direction for future work is to obtain more specimens of the range-restricted subspecies of the Wedge-billed Woodcreeper which were not adequately tested by this research and test the validity of these using the same techniques used herein.

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APPENDIX A: MAPS

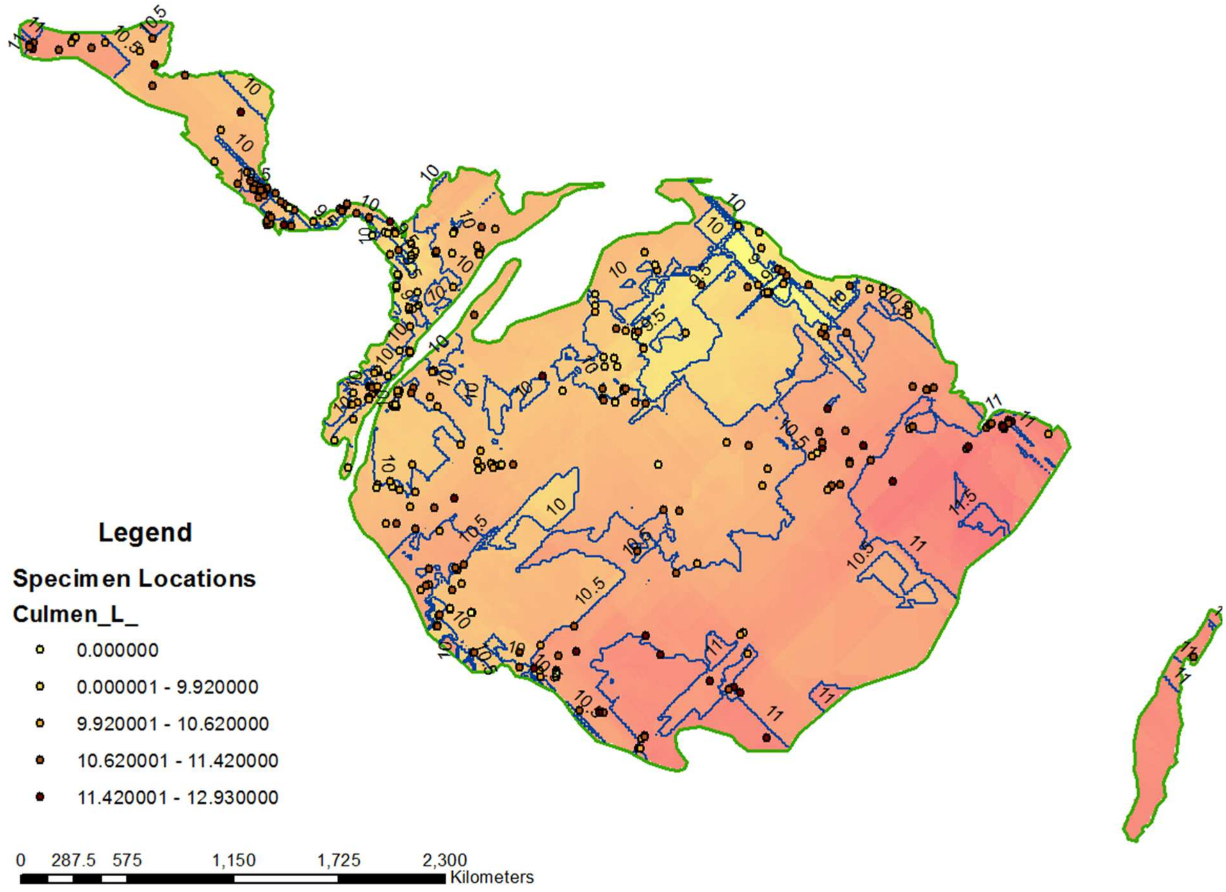


Figure A-1. Contour map for culmen length. Darker colors signify higher values.

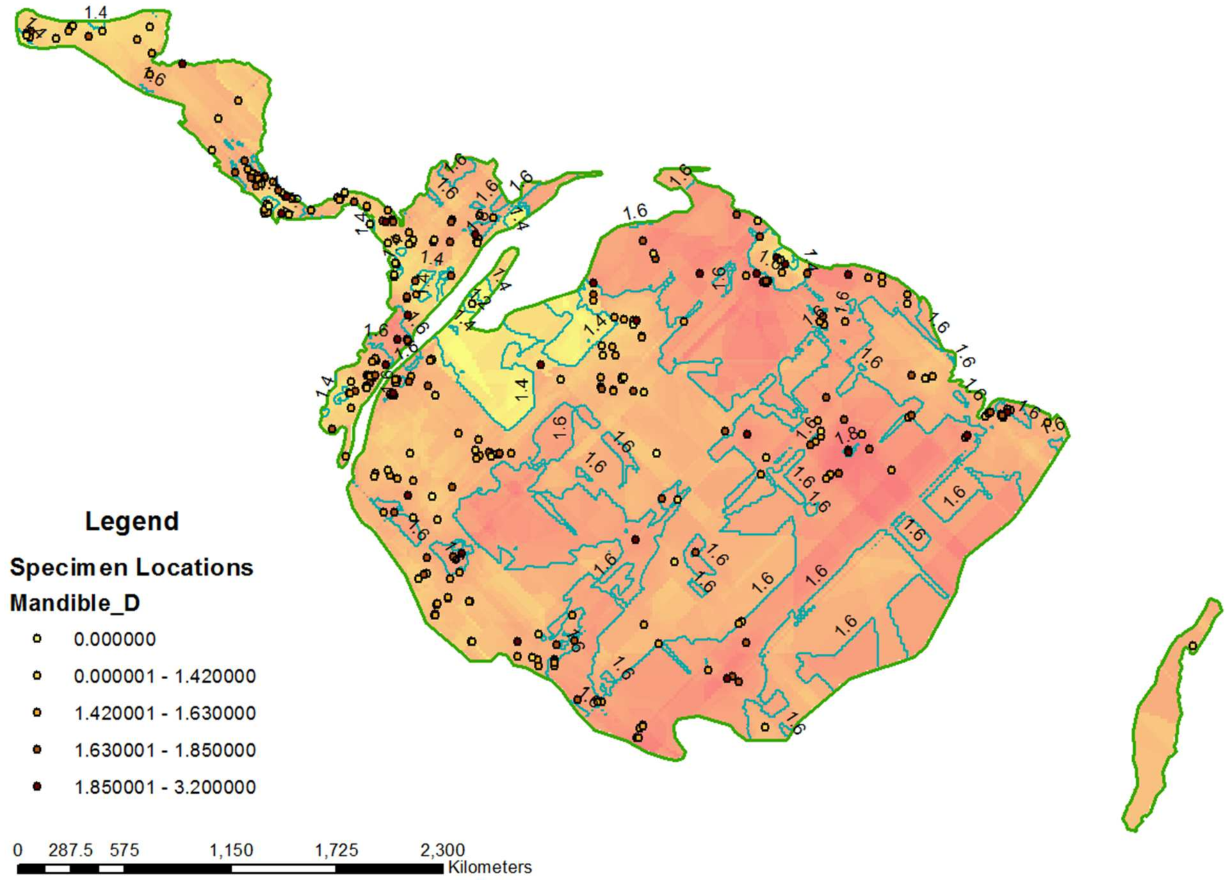


Figure A-2. Contour map for mandible depth.

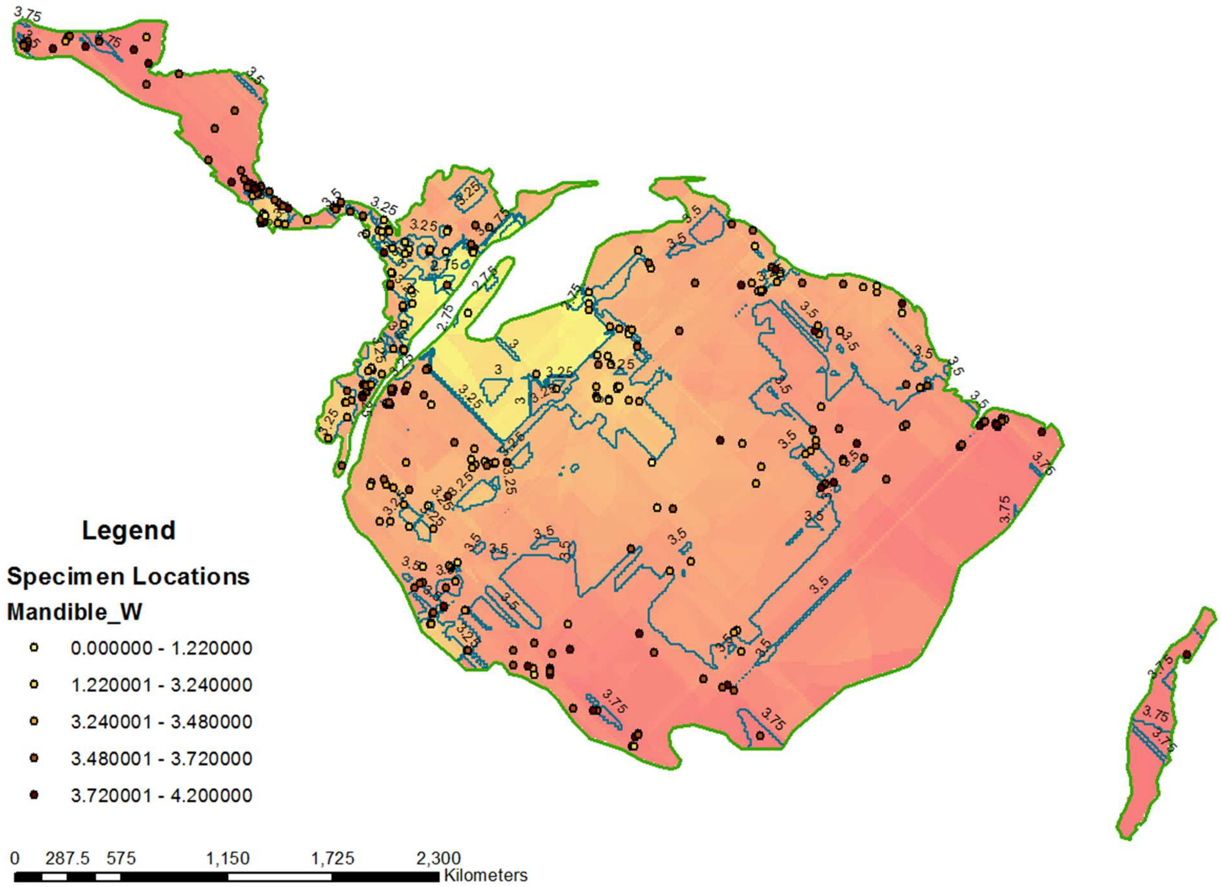


Figure A-3. Contour map for mandible width.

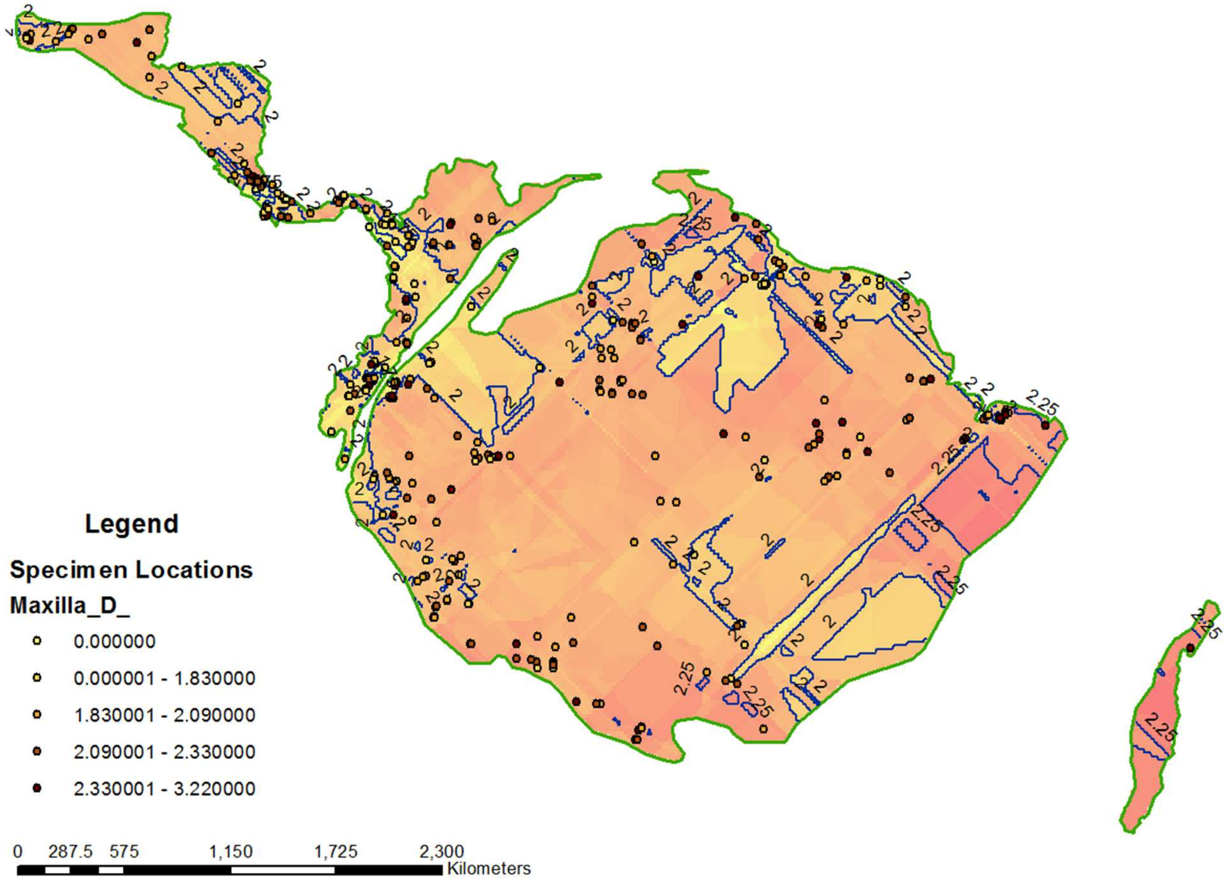


Figure A-4. Contour map for maxilla depth.

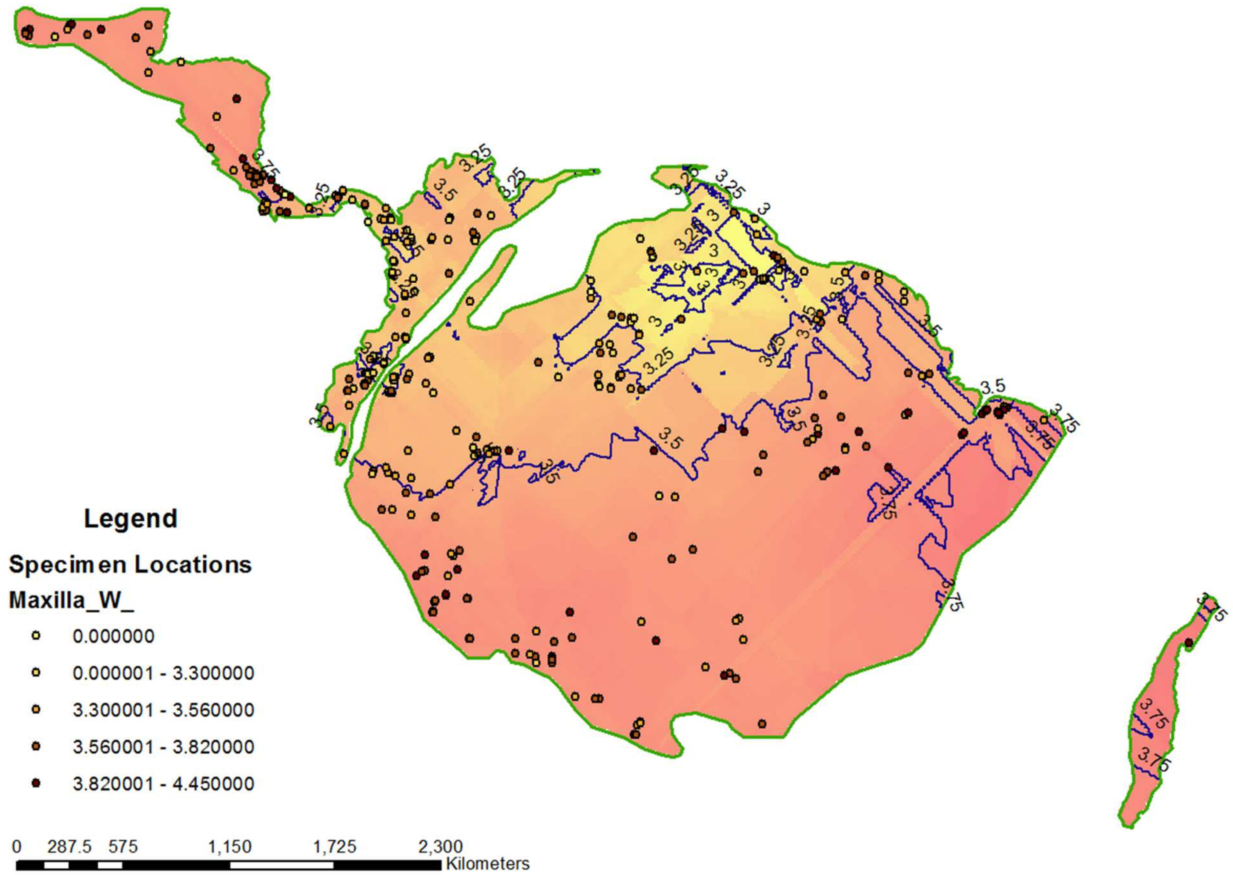


Figure A-5. Contour map for maxilla width.

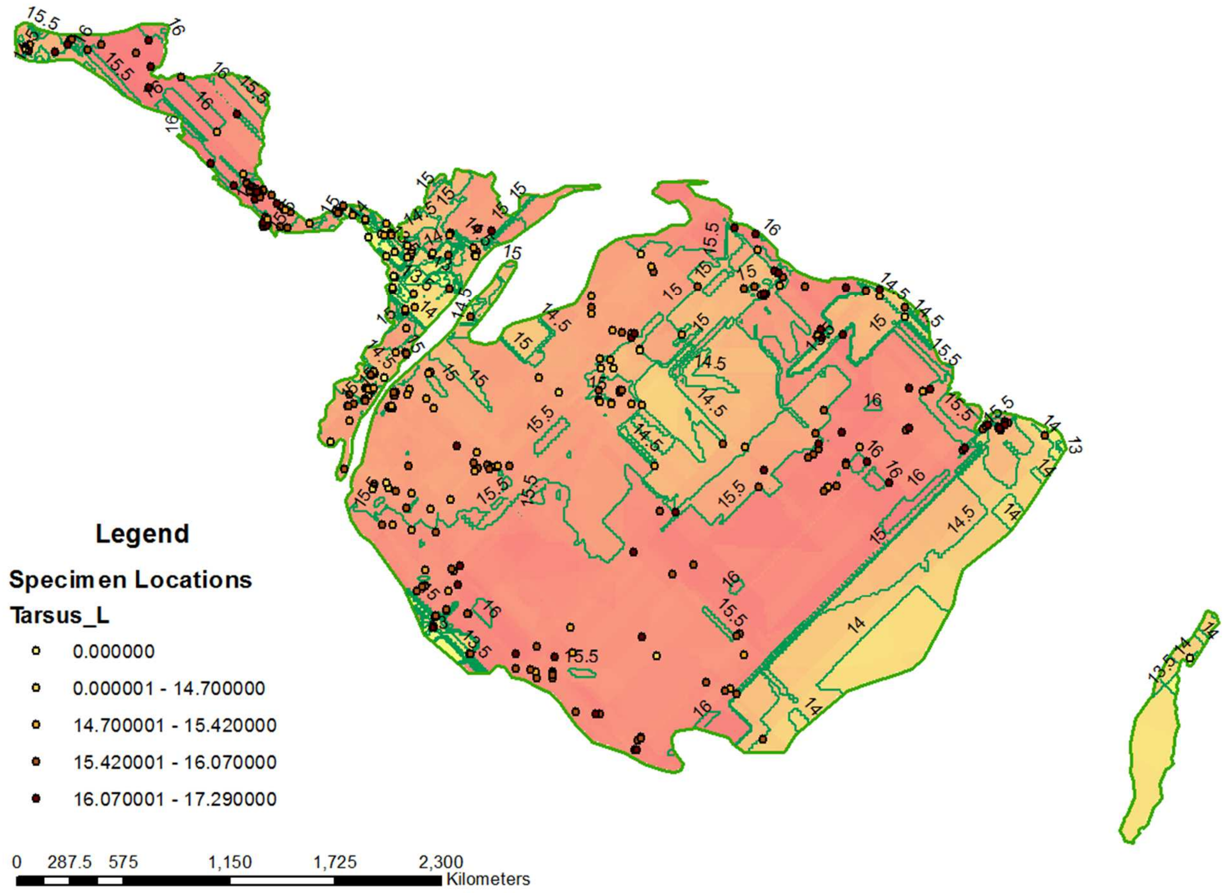


Figure A-6. Contour map for tarsus length.

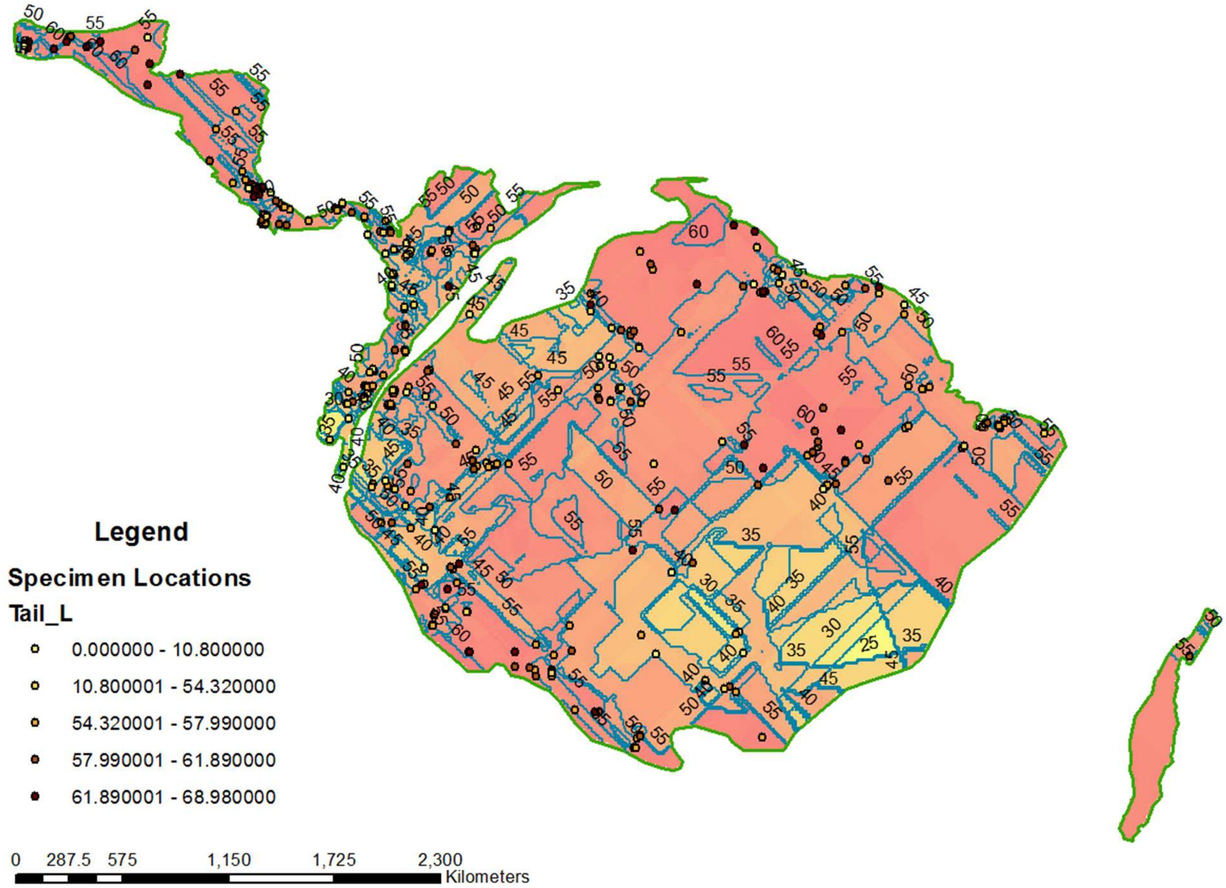


Figure A-7. Contour map for tail length.

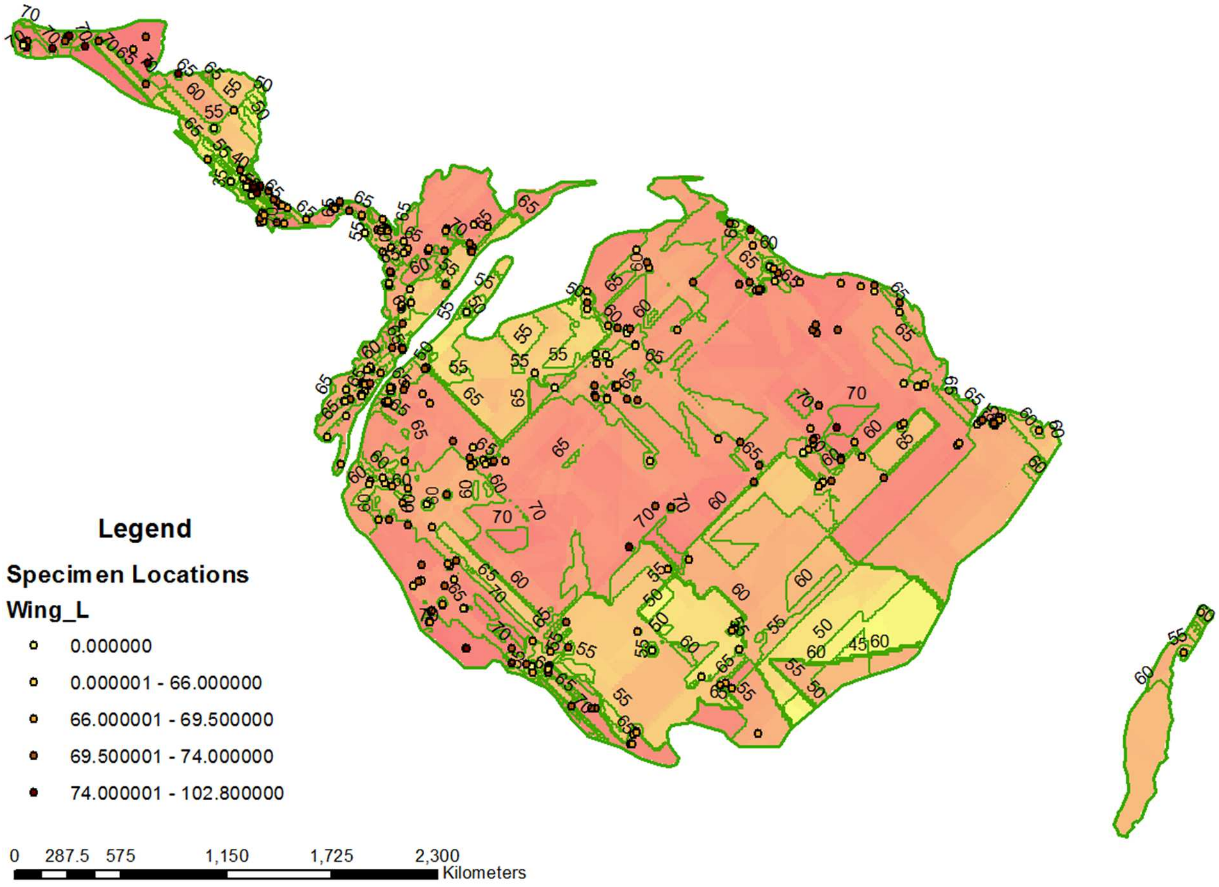


Figure A-8. Contour map for wing length.

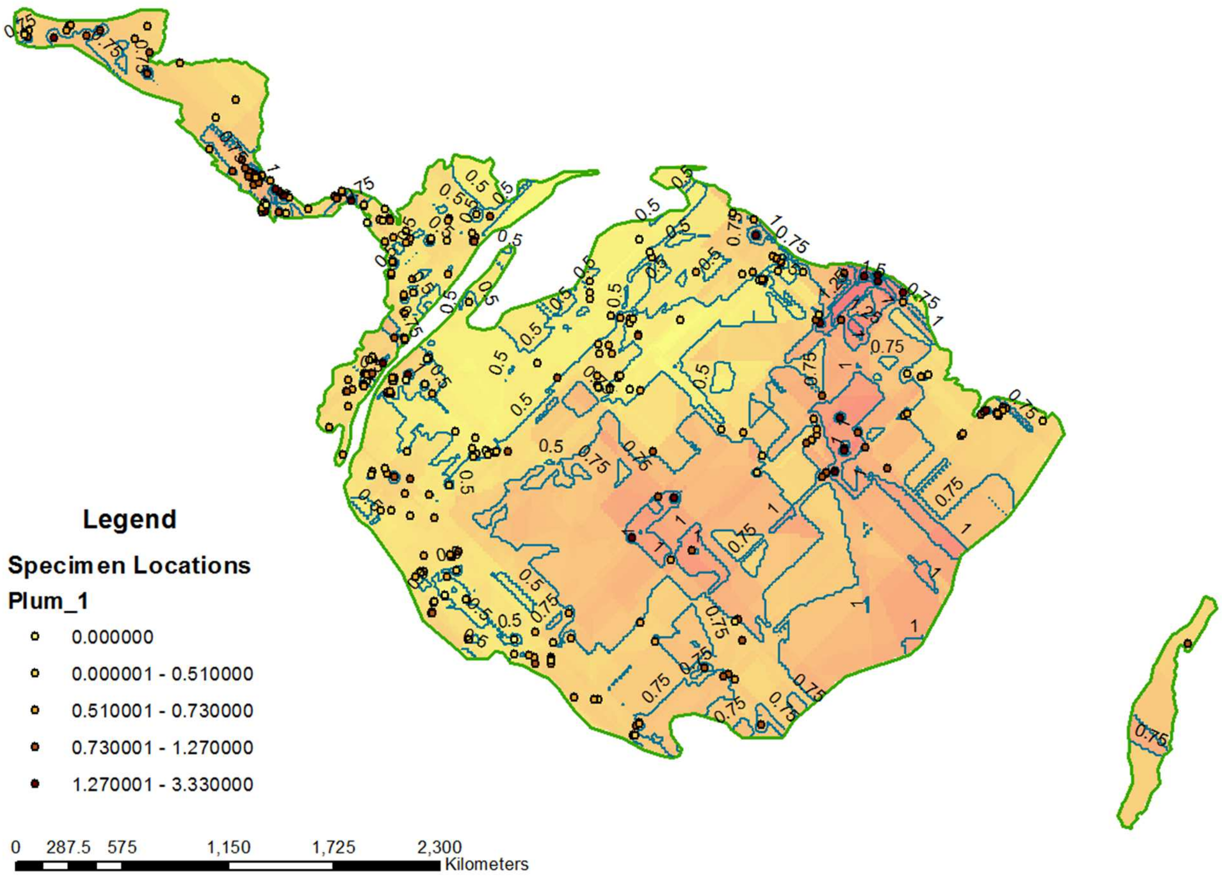


Figure A-9. Contour map for width of margin of center throat feather.

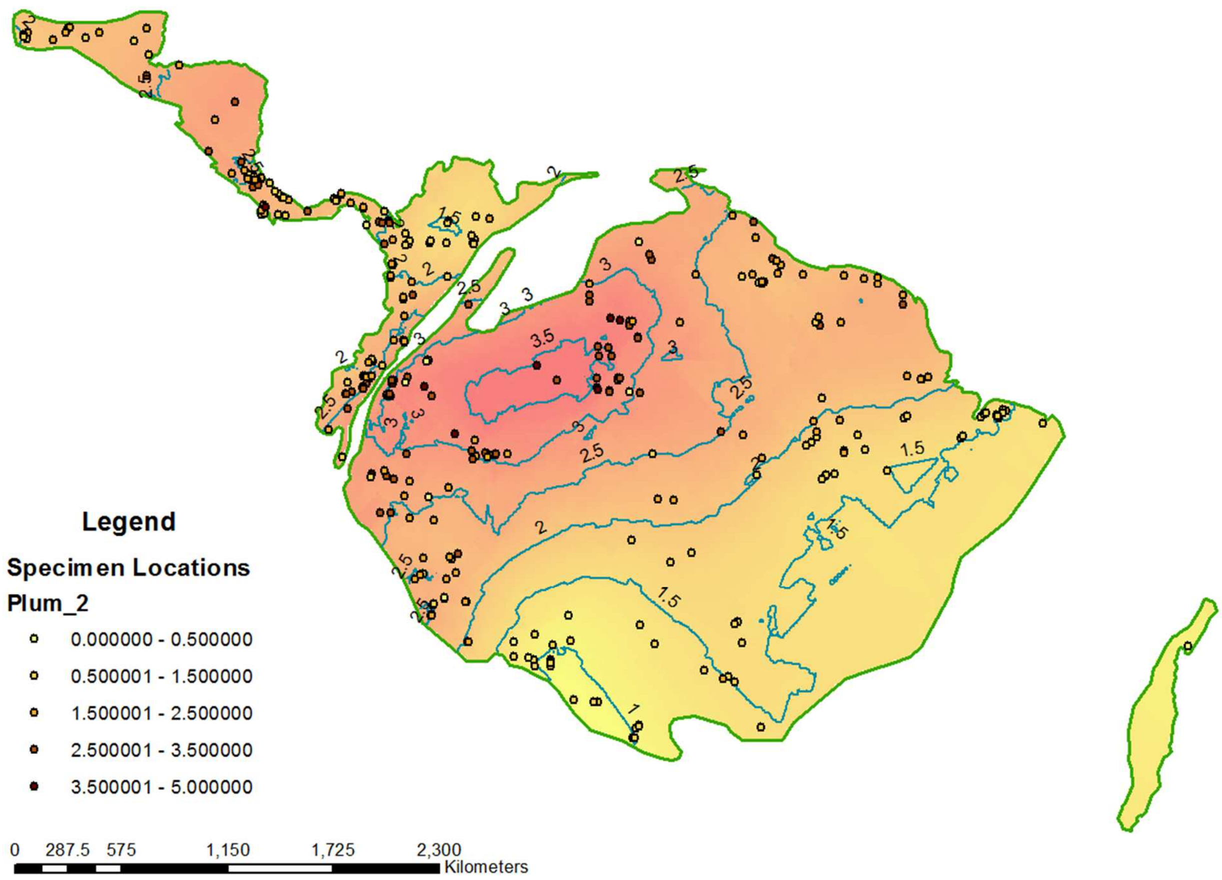


Figure A-10. Contour map for throat color. Lower scores mean whiter throat feathers, while higher scores mean more orange throat feathers.

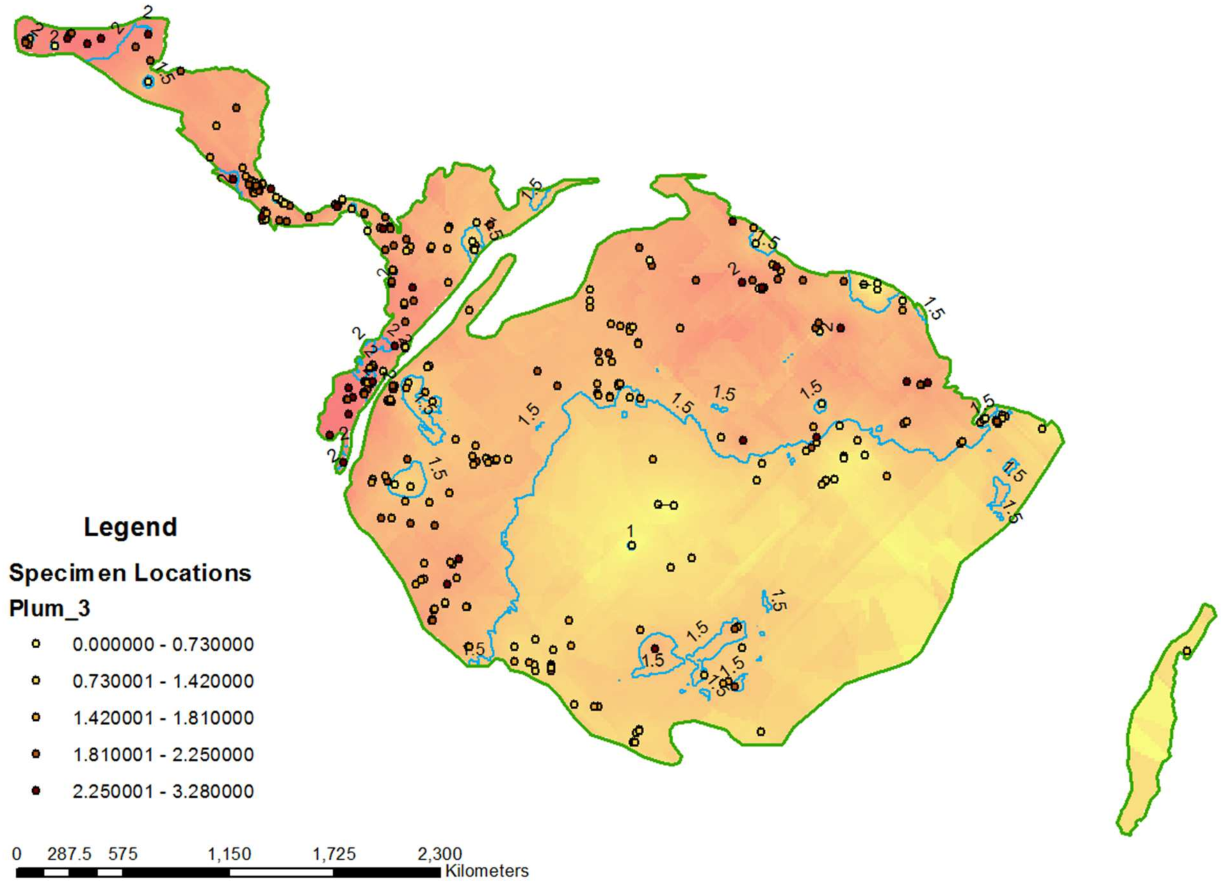


Figure A-11. Contour map of width of central light mark on breast feathers.

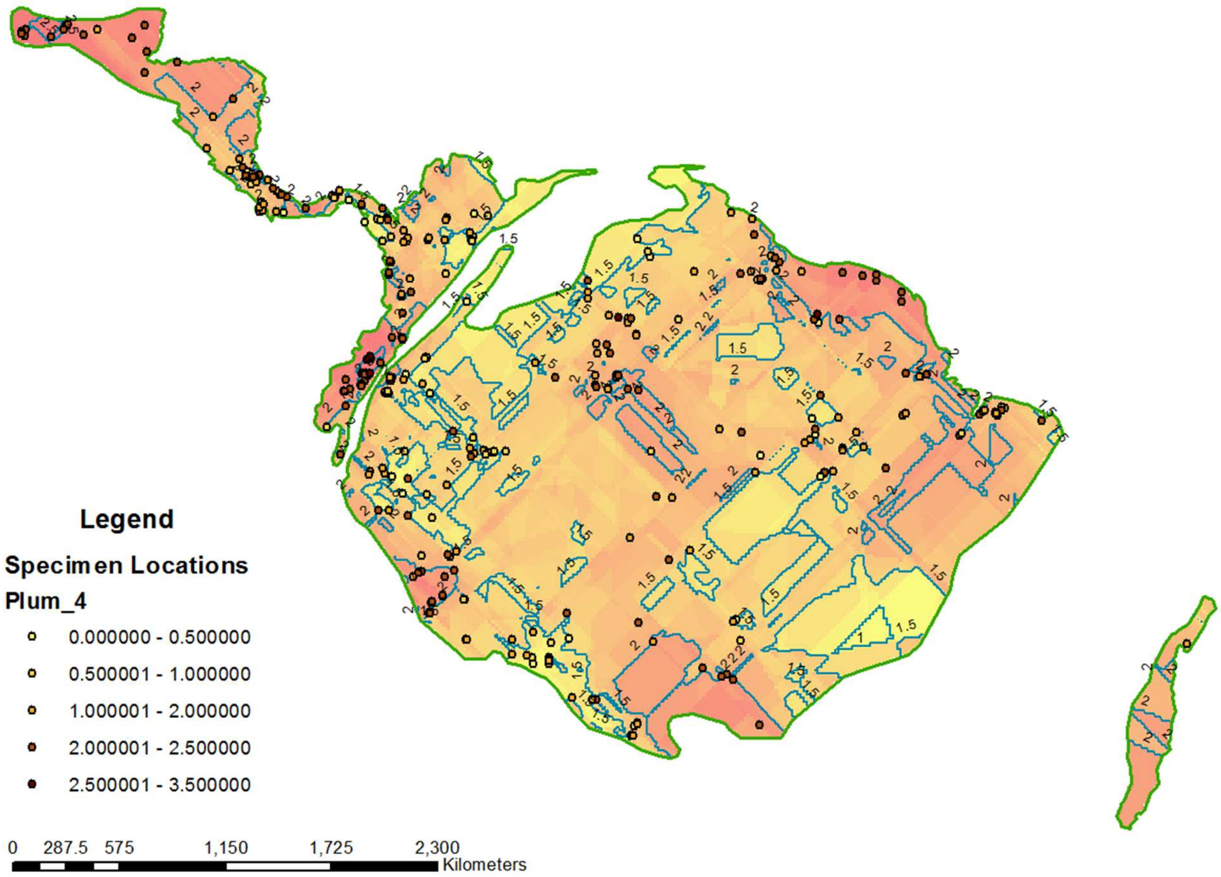


Figure A-12. Contour map of crown color. Higher scores signify darker brown and lower scores signify buffy.

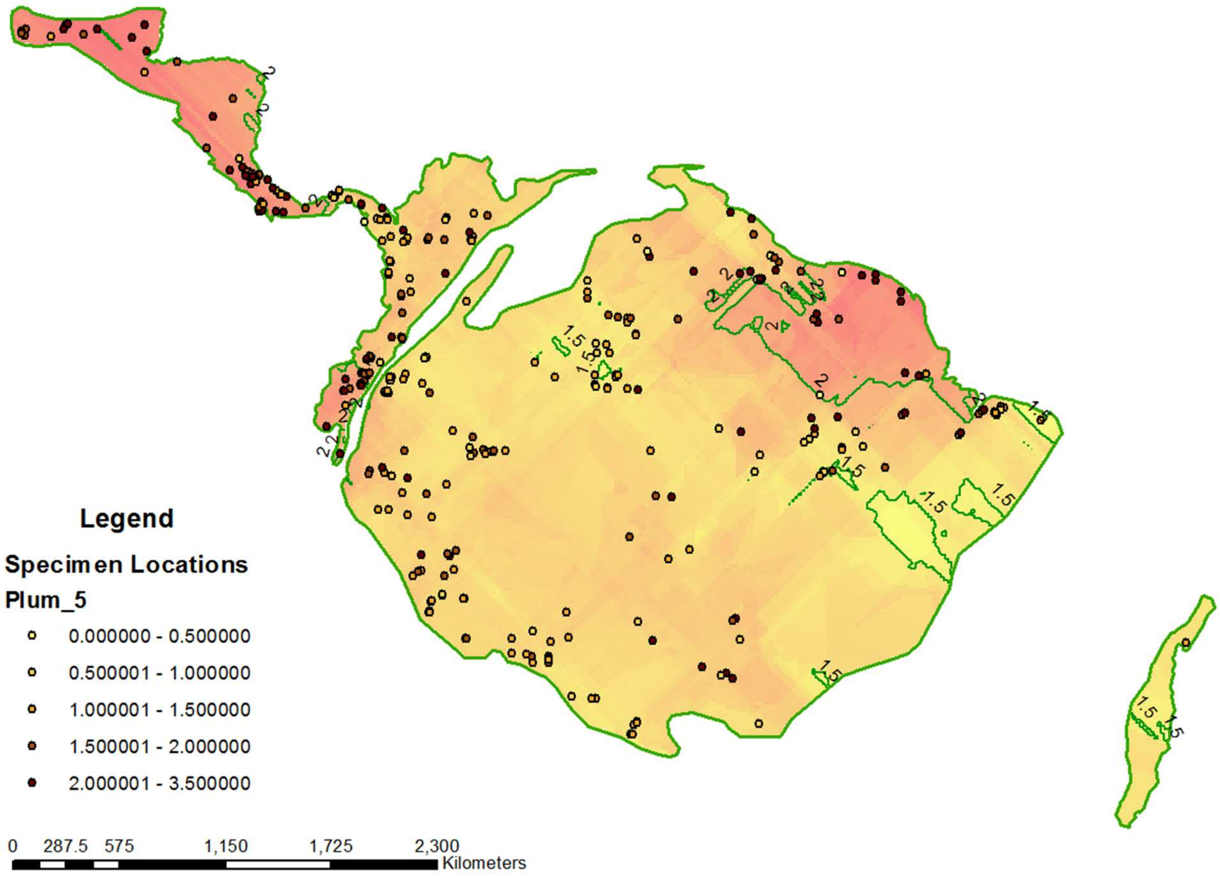


Figure A-13. Contour map for streaking on lower breast and upper belly. Higher scores mean more streaks.

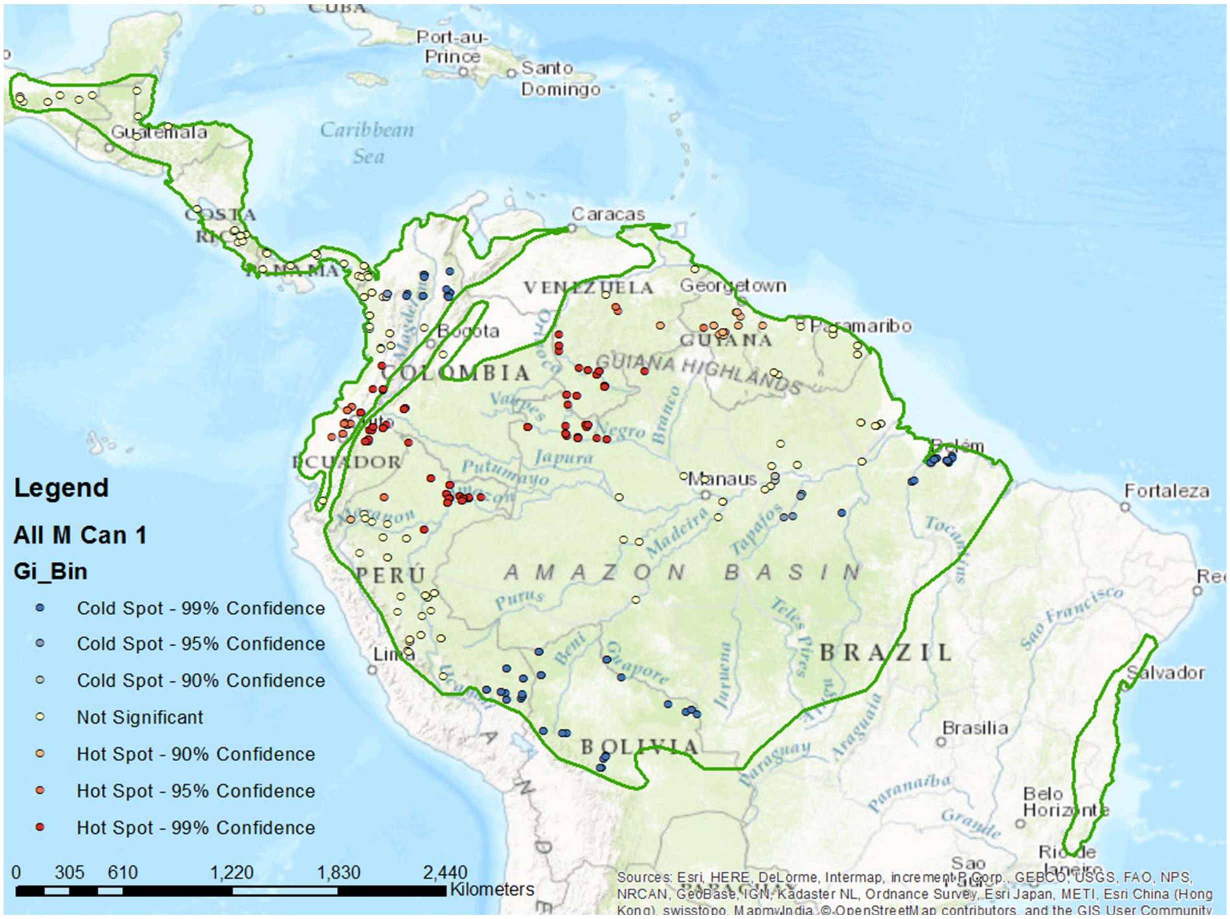


Figure A-14. Cluster analysis map for all males Can1

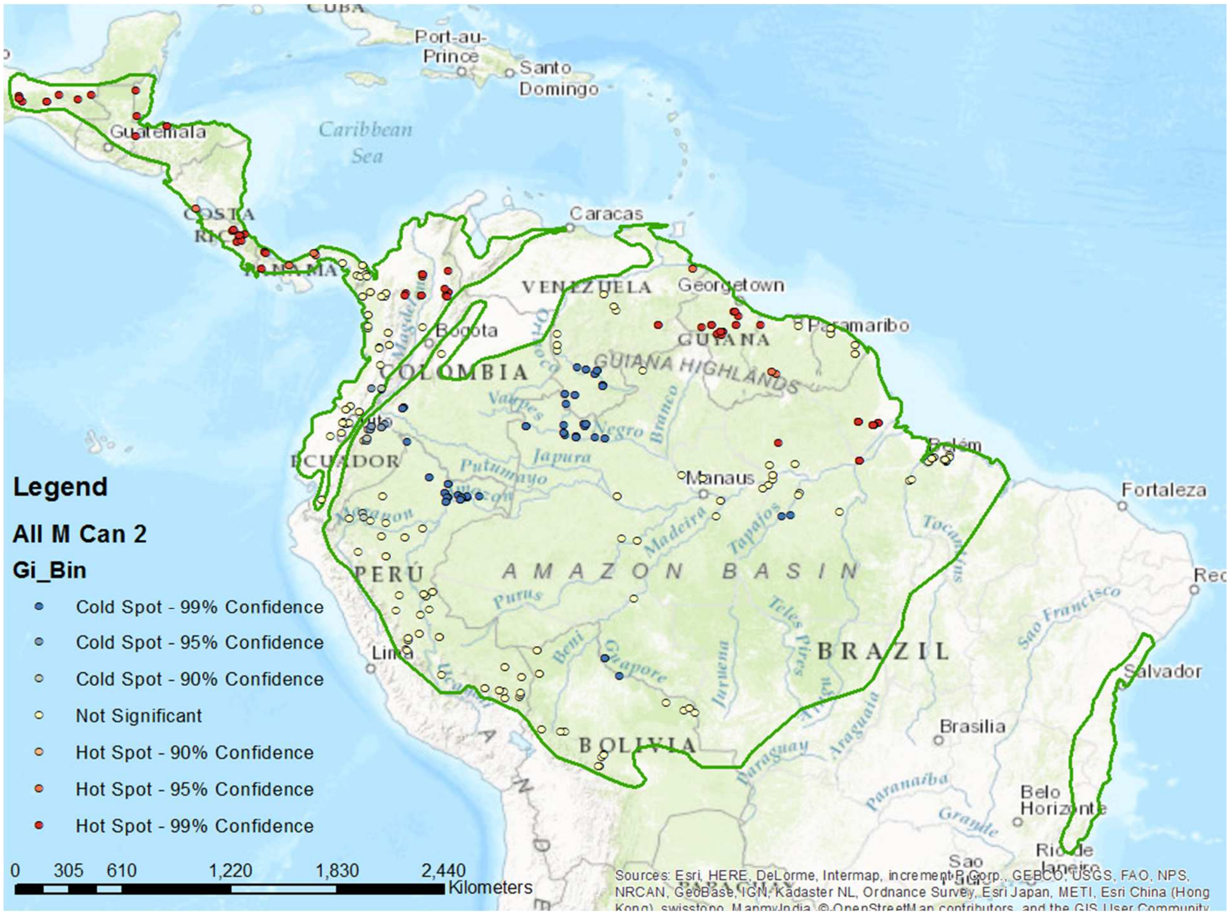


Figure A-15. Cluster analysis map for all males Can2

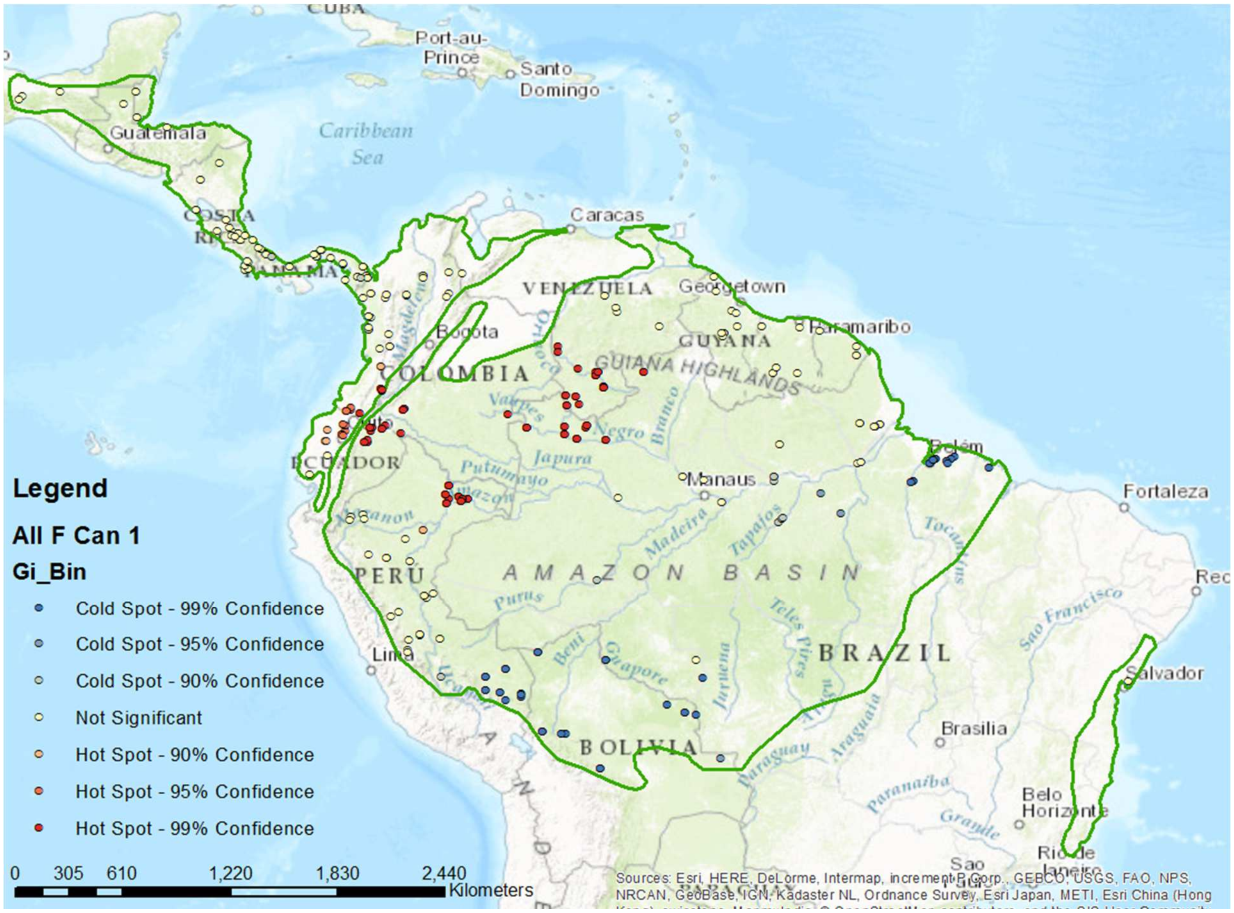


Figure A-16. Cluster analysis map for all females Can1

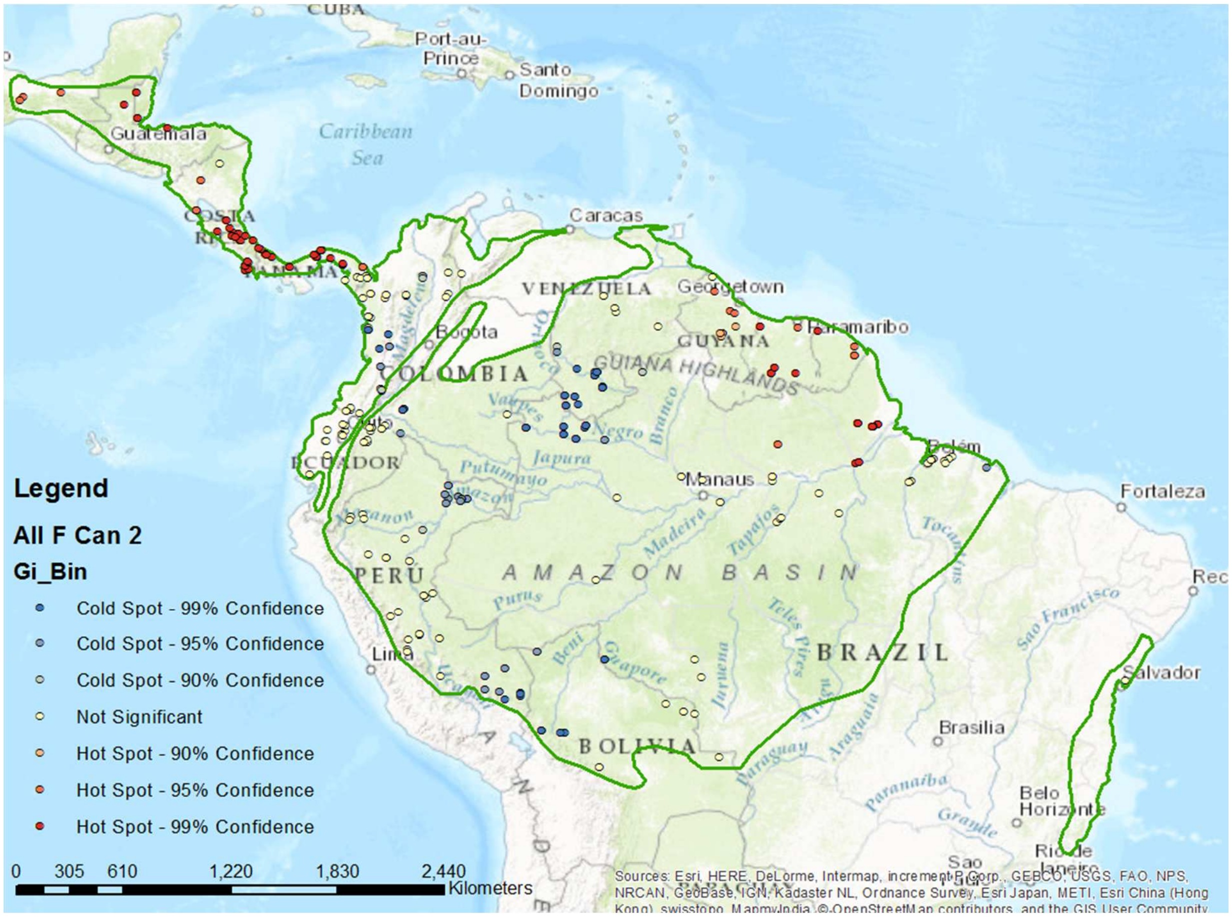


Figure A-17. Cluster analysis map for all females Can2

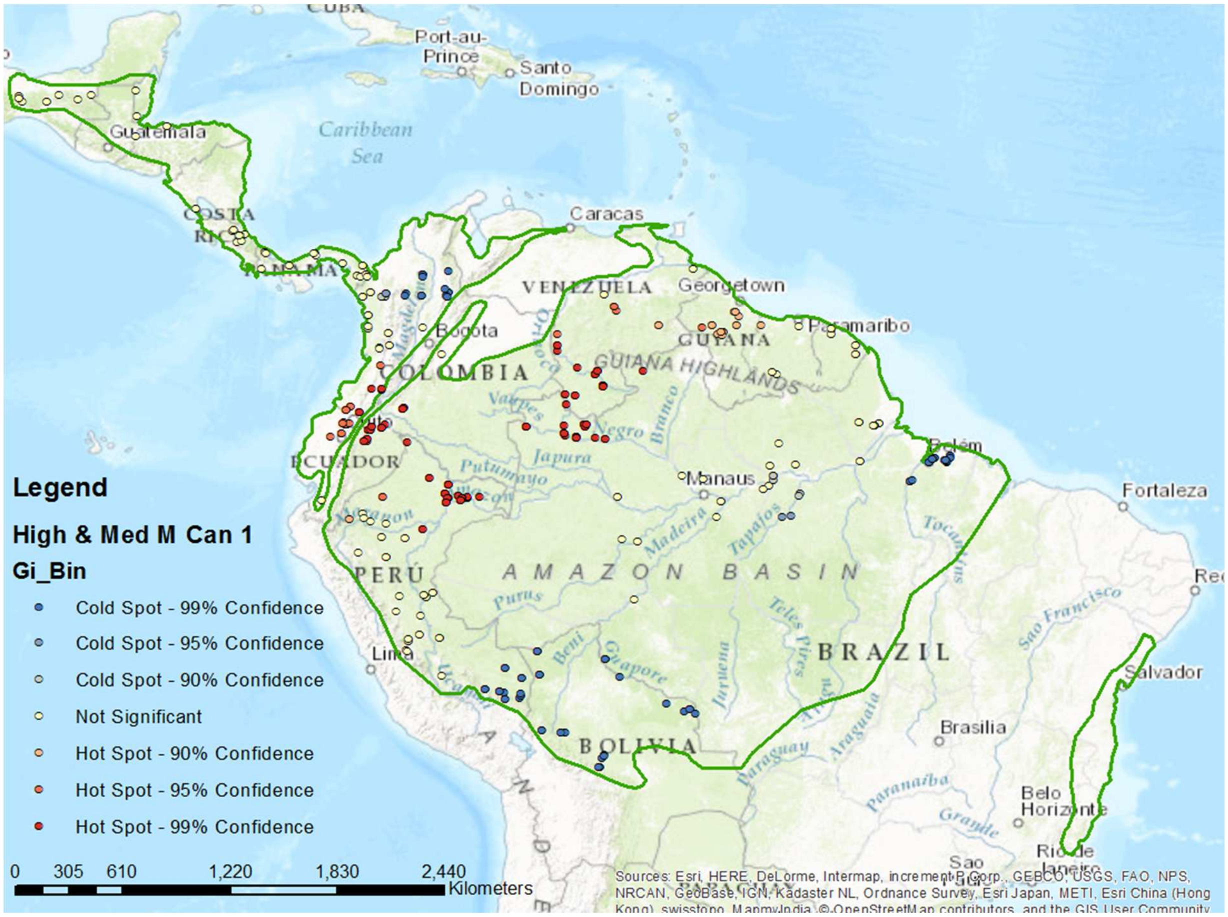


Figure A-18. Cluster analysis map for high and medium males Can1

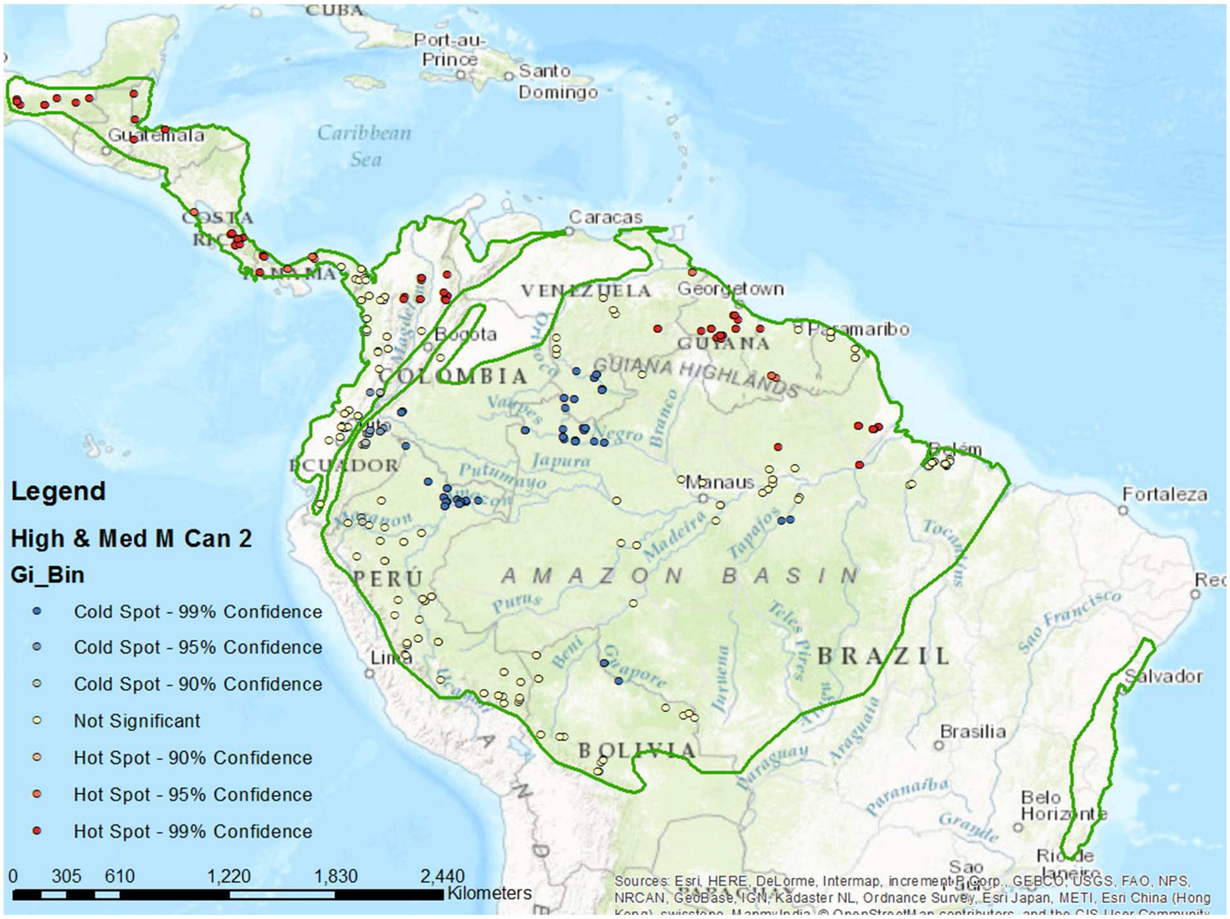


Figure A-19. Cluster analysis map for high and medium males Can2

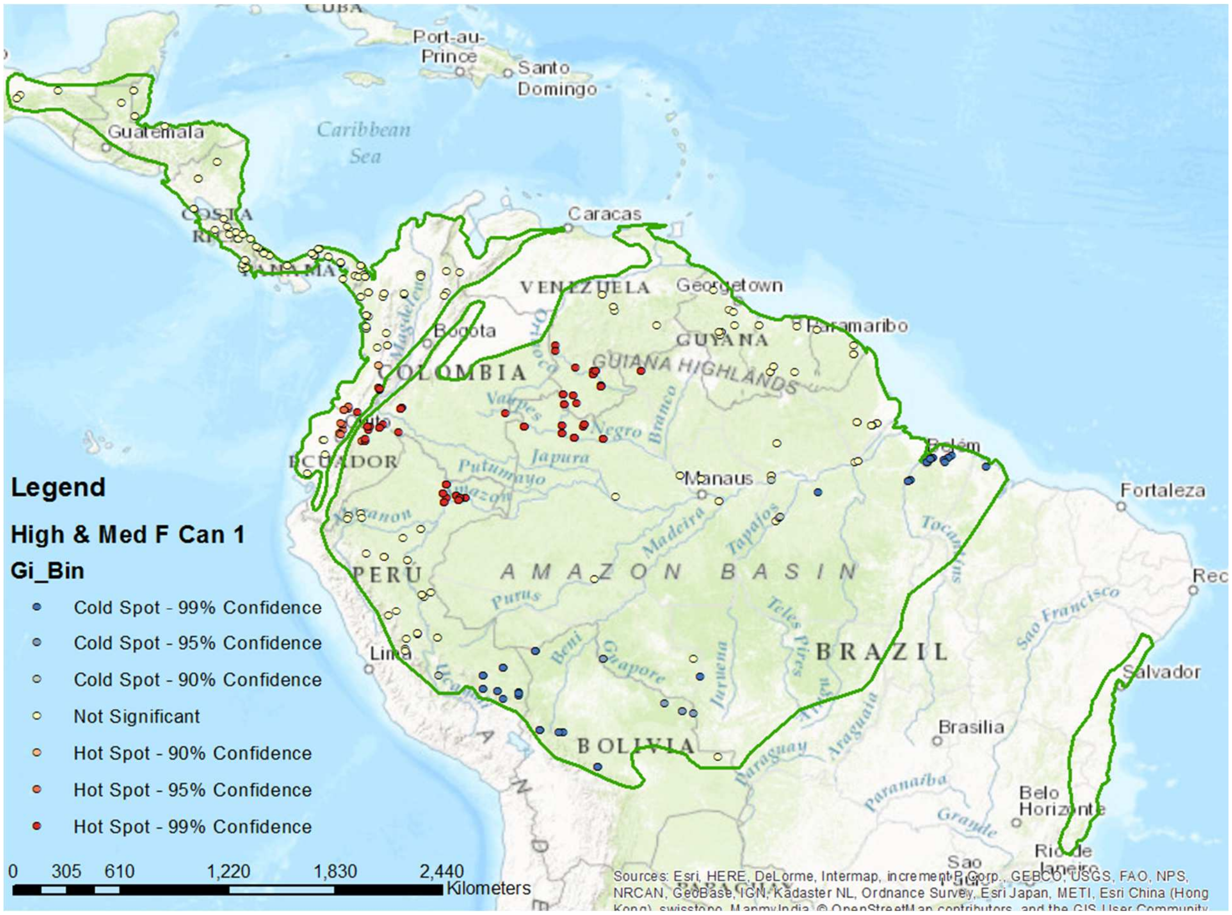
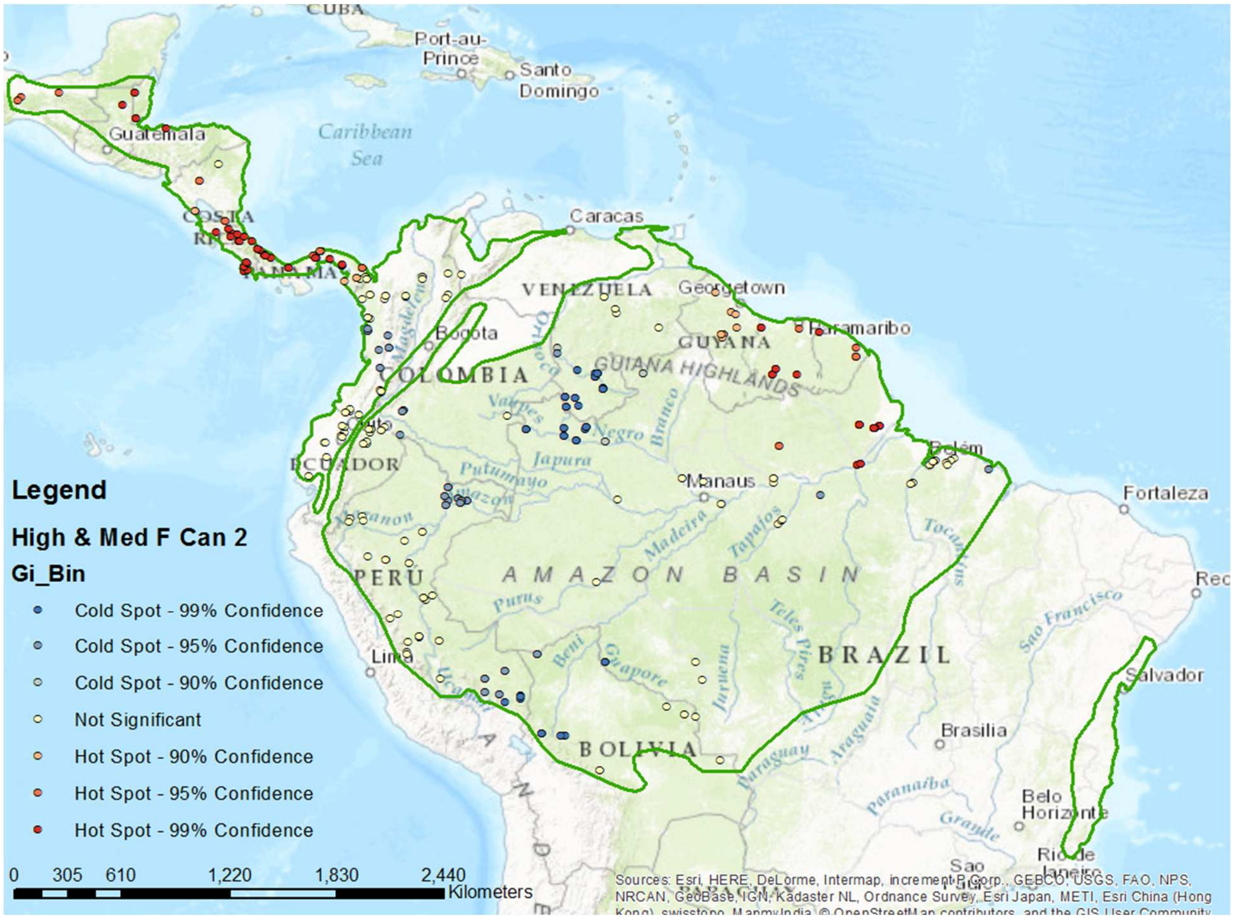
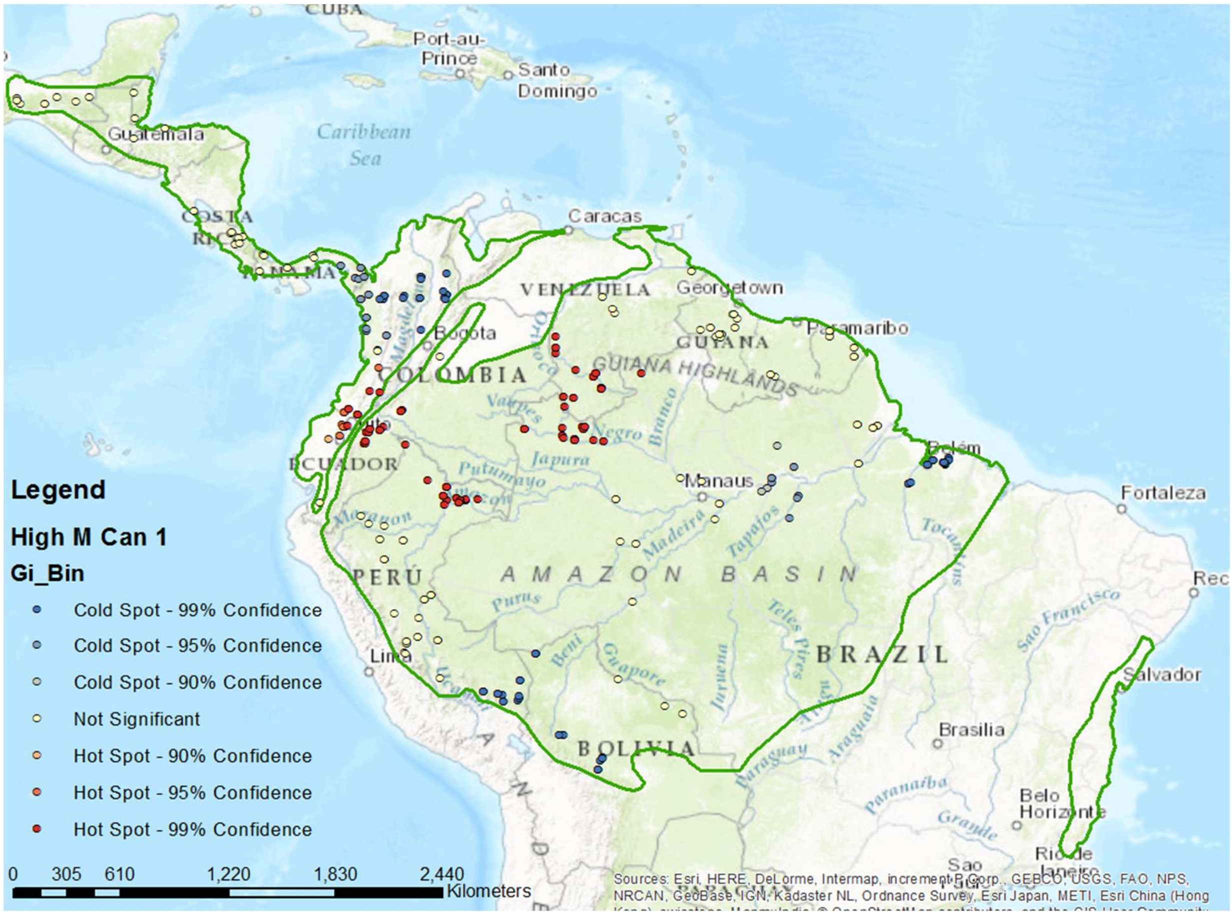


Figure A-20. Cluster analysis map for high and medium females Can1



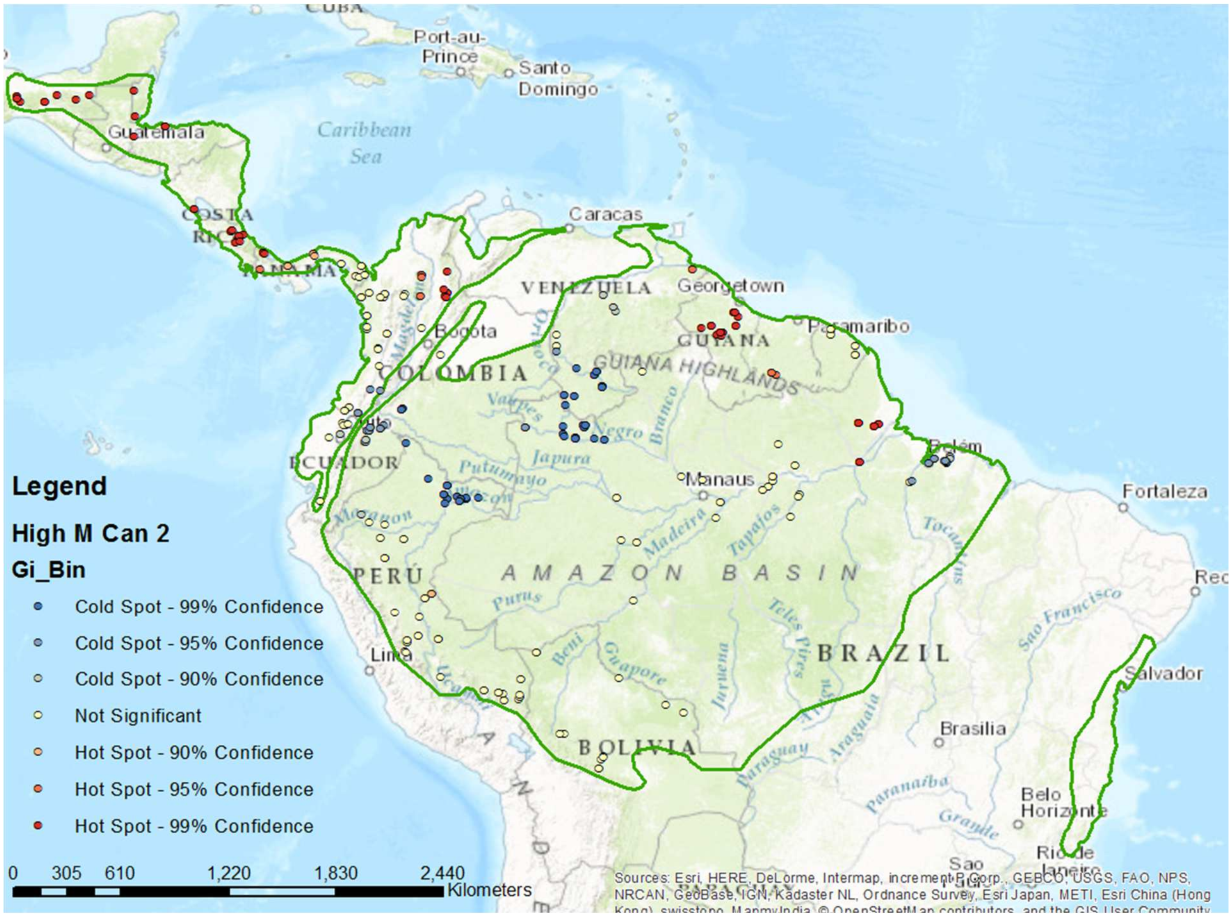
Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure A-21. Cluster analysis map for high and medium females Can2



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong

Figure A-22. Cluster analysis map for high males Can1



Sources: Esri, HERE, DeLorme, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community

Figure A-23. Cluster analysis map for high males Can2

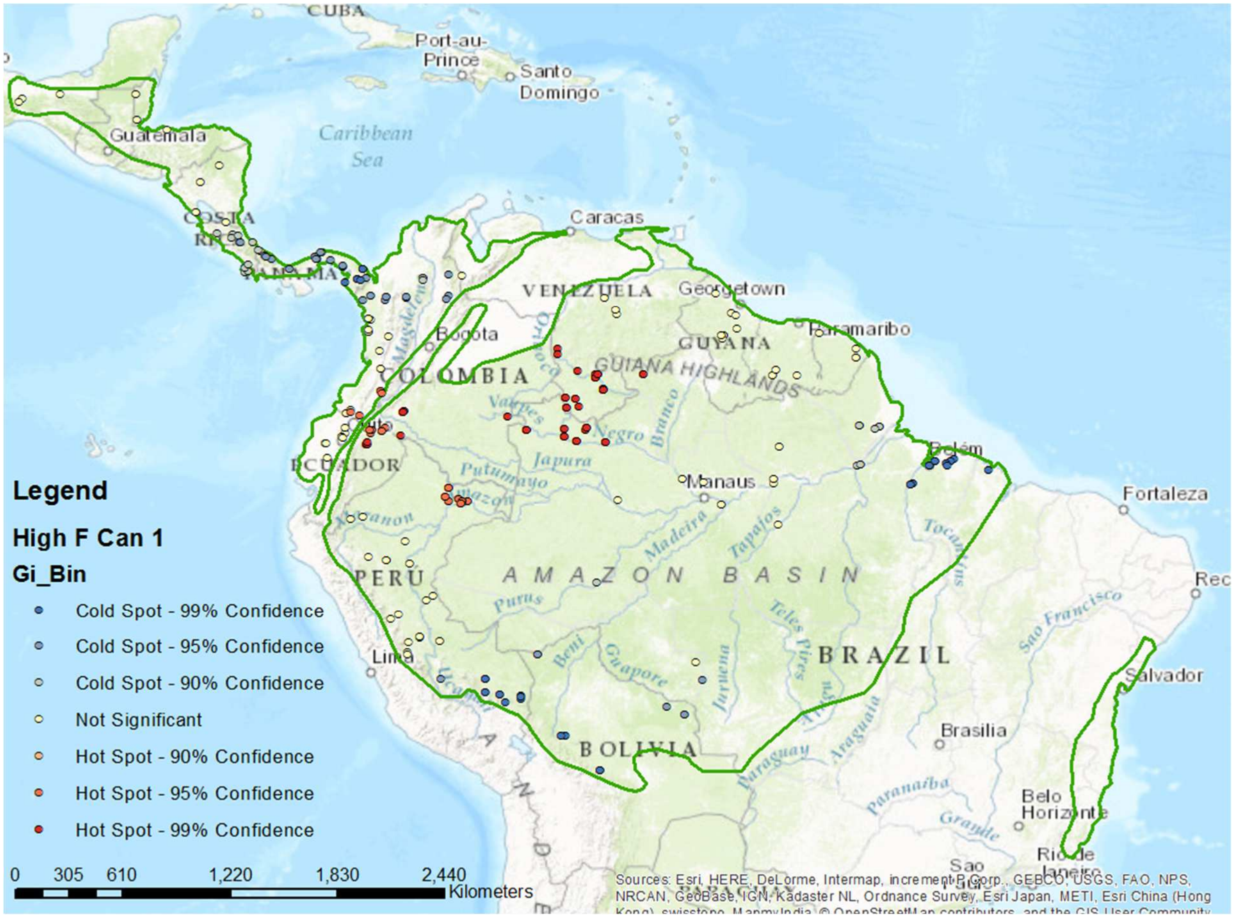


Figure A-24. Cluster analysis map for high females Can1

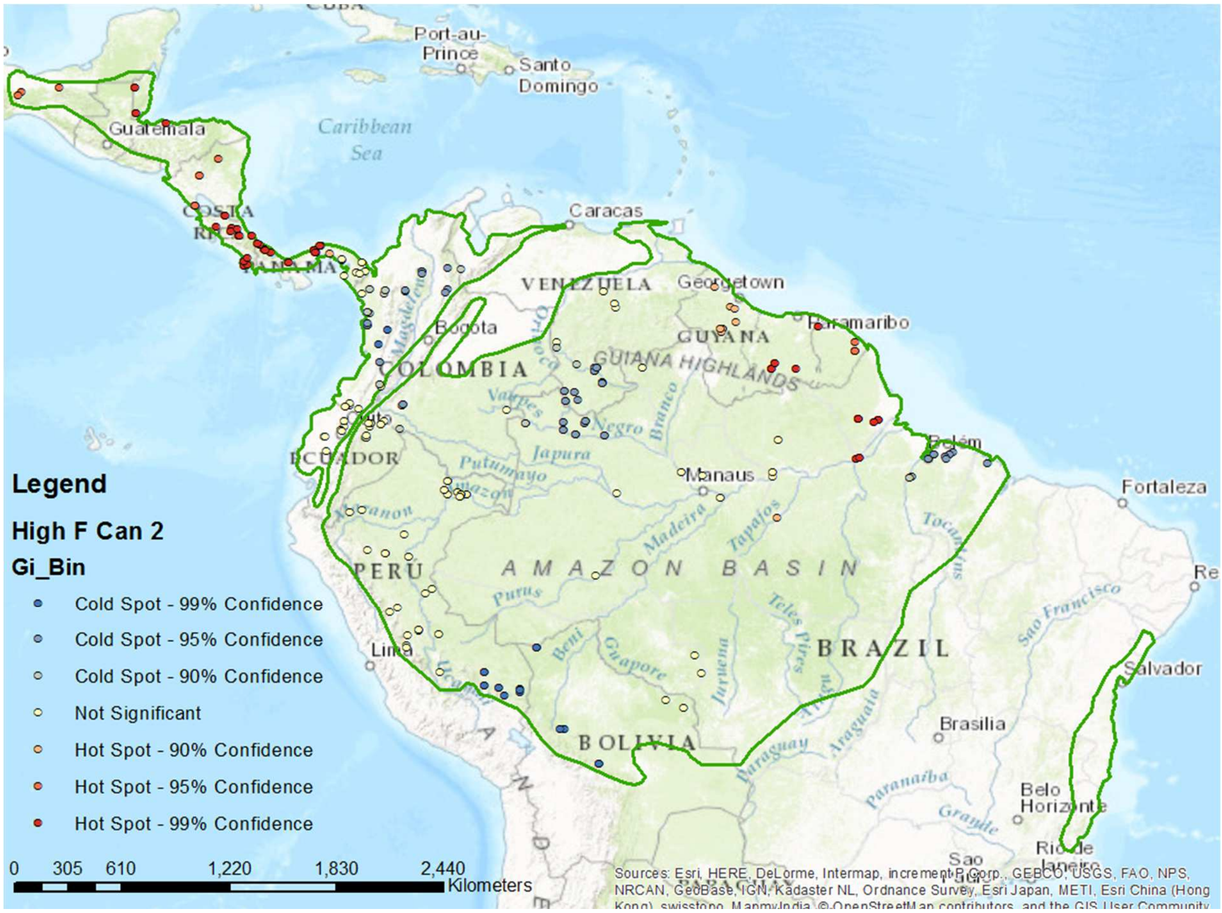


Figure A-25. Cluster analysis map for high females Can2

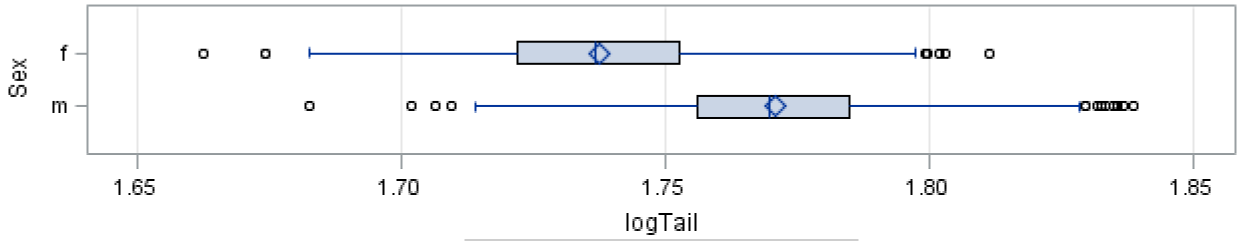


Figure A-26. Box and whisker plot showing differences in tail length between males and females. Males show longer tail lengths than females. The data were transformed using a log base 10 transformation and the units are in mm. The blue diamond represents the mean.

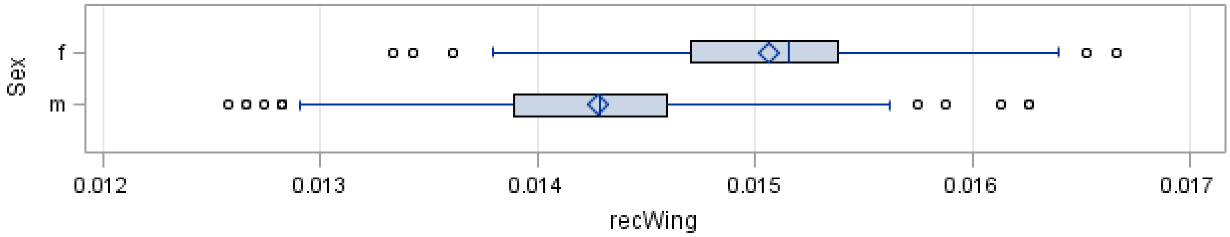


Figure A-27. Box and whisker plot showing differences in wing chord between males and females. Males show longer wing lengths than females (the data have undergone a reciprocal transformation). Units are in mm. The blue diamond represents the mean.

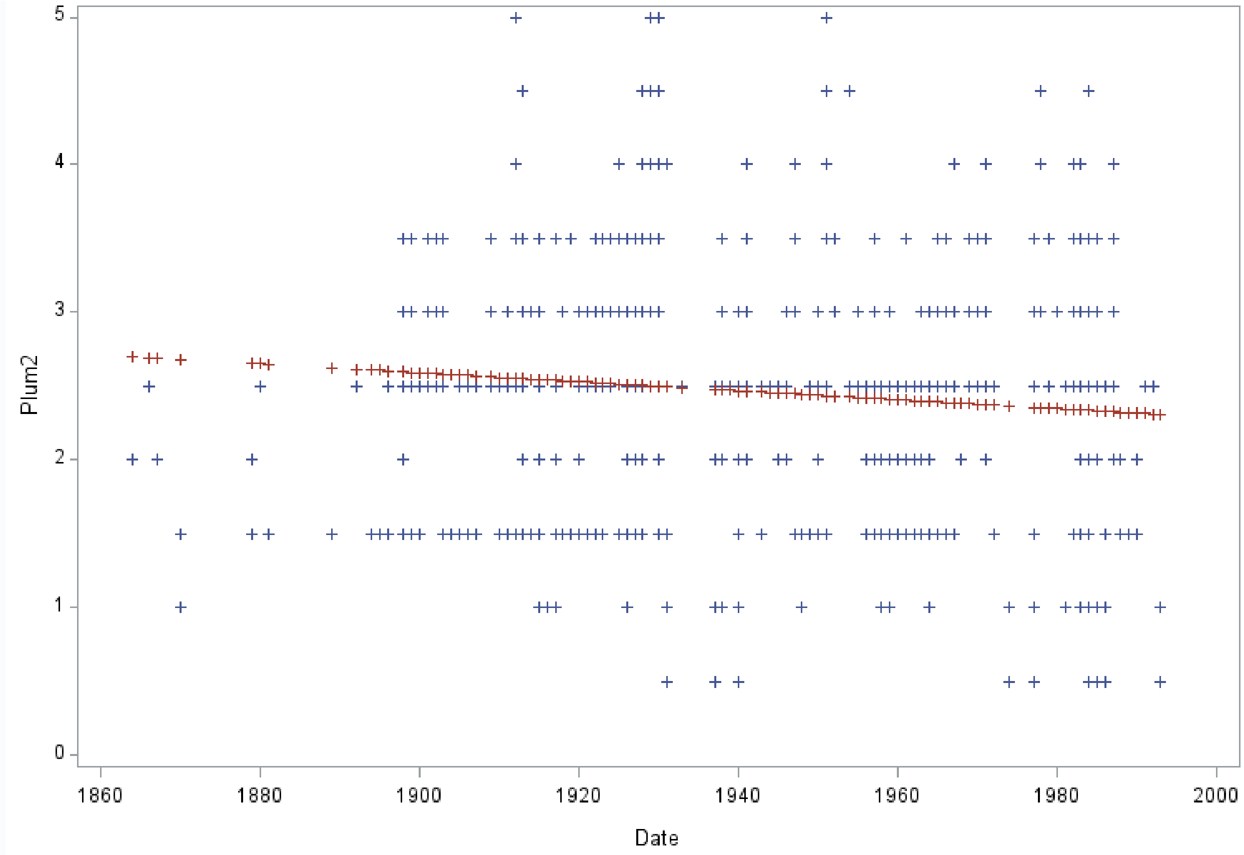


Figure A-28. Regression of throat color (Plum2) against specimen age. The blue crosses are the residuals and the red crosses show the regression line. Higher values of Plum2 represent more orange throats, while lower values represent whiter throats.

APPENDIX B: ADDITIONAL TABLES

Table B-1

Discriminant Function for All Males, Including Coefficients for All Variables

Ssp	Constant	ManW	ManD	MaxW	Plum2	Plum4	Plum5	Culm	MaxD	Tarsus	Tail	Wing	Plum3
alb	-15280	110.54	273.01	83.38	19.97	24.89	-36.85	10509	47.8	74.16	11986	423943	14.68
amac	-15763	108.08	285.94	83.64	23.82	24.74	-33.34	10950	50.81	76	12163	427843	21.04
cast	-15299	106.24	273.29	82.56	26.41	25.04	-35.63	10583	47.85	74.39	11993	423733	16.68
coro	-15276	104.67	265.41	88.95	31.46	28.19	-33.94	10664	51.68	73.21	11980	421272	16.33
inor	-15422	107.43	280	84.35	22.15	26.85	-37.97	10420	49.06	74.46	12043	426644	12.9
integ	-15242	107.82	264.59	80.45	21.67	25.47	-35.11	10584	50.64	71.95	12004	421798	18.61
intPI	-15343	107.55	285.94	86.29	22.21	25.99	-36.2	10390	48.17	74.59	12010	424233	11.45
intPS	-15354	112.85	242.56	85.9	27.96	25.05	-31.74	10874	44.22	75.15	12008	422255	18.62
pall	-15260	106.31	274.22	80.72	24.25	25.49	-34.76	10448	49.08	74.52	11982	423294	17.72
para	-15251	110.08	272.52	86.84	22.56	25.27	-35.41	10243	48.51	73.99	11970	424490	13.9
pect	-15583	114.12	259.64	79.62	24.11	26.86	-33.2	10612	46.99	75.46	12129	424609	19.03
rufi	-15337	103.49	275.93	82.1	27.36	25.15	-36.35	10629	50.51	74.05	12005	424943	16.53
spir	-15436	106.76	270.76	82.42	25.76	25.71	-32.05	10558	48.77	73.61	12052	426022	19.47
subl	-15403	108.82	269.14	84.14	23.94	25.99	-33.74	10645	47.86	74.41	12049	422763	17.7
subr	-15184	105.4	279	81.77	24.2	26.1	-35.74	10593	46.08	72.78	11953	422559	17.52

Table B-2

Discriminant Function for All Females, Including Coefficients for All Variables

Ssp	Constant	ManW	ManD	MaxW	Plum2	Plum4	Plum5	Culm	MaxD	Tarsus	Tail	Wing	Plum3
alb	-12604	138.15	137.06	-20.05	20.49	8.3	4.54	9450	-41.1	74.37	9883	362274	-8.23
cast	-12657	133.07	133.24	-18.81	26.99	8.35	6.13	9551	-38.59	74.69	9892	363663	-7.72
inor	-12644	135.55	149.45	-20.4	22.05	9.19	3.38	9194	-39.45	74.36	9907	363206	-9.83
integ	-12493	135.62	134.9	-24.81	23.73	8.09	4.68	9550	-39.43	72.98	9845	361017	-5.14
intPI	-12647	132.94	138.41	-18.52	22.73	9.27	5.3	9272	-37.88	77.49	9882	362864	-8.05
intPS	-12675	136.77	123.94	-14.37	29.53	8.38	6.94	9474	-40.92	75.47	9905	361326	-6.26
pall	-12592	129.93	130.43	-18.96	25.62	8.88	7.66	9350	-37.86	73.74	9900	361123	-4.81
para	-12596	136.31	135.23	-15.21	22.91	8.77	5.47	9178	-40.77	74.85	9868	363613	-8.44
pect	-12826	138.9	119.91	-19.69	25.77	9.55	9.13	9525	-40.69	75.64	9989	362233	-5.16
rufi	-12664	134.67	132.08	-20.88	29.61	8.04	5.44	9667	-38.14	73.9	9891	363962	-7.49
spir	-12724	132.76	133.13	-18.57	26.64	9.09	8.67	9555	-39.46	74.49	9934	362722	-4.59
sub	-12631	135.52	125.33	-19.62	26.17	8.65	7.67	9422	-37.72	74.92	9909	360500	-7.45
subr	-12507	133.08	137.77	-21.46	25.25	9.15	5.4	9513	-40.3	73.38	9845	361189	-5.53

Table B-3

Identity of Specimens and Collections Used in the Primary Data Set

Collection	Number
AMNH	525341
AMNH	390527
AMNH	390526
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AMNH	525345
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AMNH	278033
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AMNH	127761
AMNH	279693
AMNH	525311
AMNH	127760
AMNH	525305
AMNH	408597
AMNH	234748
AMNH	234747
AMNH	169078
AMNH	169771
AMNH	169772
AMNH	820900
AMNH	819712
AMNH	819741
AMNH	525315
AMNH	525312
AMNH	525313
AMNH	525314
AMNH	525317
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AMNH	130978

(Table Continues)

Collection	Number
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AMNH	239329
AMNH	239334
AMNH	239333
AMNH	239326
AMNH	239328
AMNH	239330
AMNH	239327
AMNH	23227
AMNH	240399
AMNH	240400
AMNH	240398
AMNH	240396
AMNH	240397
AMNH	231994

(Table Continues)

Collection	Number
AMNH	231995
AMNH	232230
AMNH	232229
AMNH	240401
AMNH	238303
AMNH	238302
AMNH	232228
AMNH	525321
AMNH	525325
AMNH	525324
AMNH	233663
AMNH	43232
AMNH	525328
AMNH	128570
AMNH	128569
AMNH	148480
AMNH	148481
AMNH	148479
AMNH	805792
AMNH	805793
AMNH	805791
AMNH	282206
AMNH	282205
AMNH	282207
AMNH	282209
AMNH	282204
AMNH	282208
AMNH	127759
AMNH	407162
AMNH	407163
AMNH	432910
AMNH	432913
AMNH	432911
AMNH	432912
AMNH	432914
AMNH	432916
AMNH	432924
AMNH	432921
AMNH	432925

(Table Continues)

Collection	Number
AMNH	432933
AMNH	432908
AMNH	432905
AMNH	432907
AMNH	432928
AMNH	432927
AMNH	274143
AMNH	274142
AMNH	274153
AMNH	274156
AMNH	274158
AMNH	432909
AMNH	432926
AMNH	432906
AMNH	432929
AMNH	432931
AMNH	432930
AMNH	432939
AMNH	432940
AMNH	432941
AMNH	432936
AMNH	432945
AMNH	432935
AMNH	432944
AMNH	432934
AMNH	120741
AMNH	432932
AMNH	432943
AMNH	432937
AMNH	432938
AMNH	432942
AMNH	525927
AMNH	274161
AMNH	271094
AMNH	274150
AMNH	274151
AMNH	274149
AMNH	274148
AMNH	271096

(Table Continues)

Collection	Number
AMNH	271095
AMNH	274144
AMNH	274167
AMNH	274166
AMNH	274163
AMNH	120743
AMNH	120742
AMNH	120744
AMNH	432917
AMNH	432918
AMNH	432915
AMNH	432922
AMNH	432920
AMNH	432923
AMNH	432919
AMNH	816674
AMNH	816677
AMNH	816676
AMNH	816675
AMNH	816671
AMNH	816672
AMNH	816673
AMNH	37354
AMNH	274154
AMNH	525277
AMNH	278030
AMNH	748392
AMNH	59991 Phelps
AMNH	49749 Phelps
AMNH	785885
AMNH	805789
AMNH	125749
AMNH	125752
AMNH	323733
AMNH	323736
AMNH	323734
AMNH	323732
AMNH	177393
AMNH	525280

(Table Continues)

Collection	Number
AMNH	525284
AMNH	525283
AMNH	525288
AMNH	525287
AMNH	43231
AMNH	125744
AMNH	805787
AMNH	805786
AMNH	805788
AMNH	805790
AMNH	821565
AMNH	821564
AMNH	176859
AMNH	176862
AMNH	95486
AMNH	125754
AMNH	125746
AMNH	125796
AMNH	125745
AMNH	125747
AMNH	125753
AMNH	125751
AMNH	125755
AMNH	125748
AMNH	125750
AMNH	125742
AMNH	525296
AMNH	313563
AMNH	125757
AMNH	176861
AMNH	116438
AMNH	116437
AMNH	116433
AMNH	116434
AMNH	122073
AMNH	116439
AMNH	434654
AMNH	434649
AMNH	434653

(Table Continues)

Collection	Number
AMNH	310780
AMNH	276110
AMNH	276113
AMNH	125759
AMNH	125758
AMNH	125736
AMNH	125743
AMNH	125739
AMNH	125740
AMNH	125738
AMNH	125737
AMNH	125741
AMNH	284016
AMNH	284012
AMNH	284010
AMNH	284009
AMNH	525309
AMNH	176860
AMNH	430975
AMNH	256123
AMNH	282200
AMNH	282203
AMNH	525300
AMNH	239335
AMNH	148482
AMNH	822252
AMNH	820148
AMNH	117907
AMNH	36374
AMNH	36375
AMNH	525322
AMNH	525327
AMNH	525326
AMNH	525323
AMNH	821369
AMNH	525282
AMNH	525286
AMNH	525285
AMNH	177395

(Table Continues)

Collection	Number
AMNH	525278
AMNH	525279
AMNH	177394
AMNH	525281
AMNH	119952
AMNH	148102
AMNH	274157
AMNH	274168
AMNH	274152
AMNH	274155
AMNH	274165
AMNH	274159
AMNH	274160
AMNH	274147
AMNH	274162
AMNH	274145
AMNH	274146
AMNH	120322
USNM	477715
USNM	477718
USNM	477716
USNM	477720
USNM	477717
USNM	477714
USNM	477713
USNM	477719
USNM	423468
USNM	423469
USNM	423467
USNM	423465
USNM	423466
USNM	484427
USNM	484426
USNM	484429
USNM	484430
USNM	484431
USNM	484428
USNM	206602
USNM	206604

(Table Continues)

Collection	Number
USNM	206607
USNM	229527
USNM	229528
USNM	229530
USNM	229531
USNM	229529
USNM	229526
USNM	401888
USNM	401886
USNM	401893
USNM	401894
USNM	401891
USNM	401889
USNM	401892
USNM	401887
USNM	401890
USNM	401895
USNM	411346
USNM	373385
USNM	411348
USNM	411345
USNM	411351
USNM	411344
USNM	411350
USNM	411343
USNM	373386
USNM	373387
USNM	401896
USNM	401897
USNM	514802
USNM	514803
USNM	514804
USNM	514805
USNM	514806
USNM	514807
USNM	514808
USNM	514809
USNM	514810
USNM	514811

(Table Continues)

Collection	Number
USNM	514812
USNM	514813
USNM	514814
USNM	514815
USNM	514816
USNM	514817
USNM	514818
USNM	514819
USNM	514820
USNM	514821
USNM	514822
USNM	514823
USNM	514824
USNM	514825
USNM	514826
USNM	514827
USNM	514828
USNM	515503
USNM	515504
USNM	515505
USNM	515506
USNM	515507
USNM	515508
USNM	515509
USNM	515510
USNM	515511
USNM	515512
USNM	515513
USNM	515514
USNM	515793
USNM	515794
USNM	515795
USNM	426227
USNM	426221
USNM	426222
USNM	426223
USNM	426225
USNM	426226
USNM	426219

(Table Continues)

Collection	Number
USNM	426224
USNM	443128
USNM	443132
USNM	443129
USNM	443131
USNM	443130
USNM	468471
USNM	468470
USNM	468469
USNM	468468
USNM	401905
USNM	401898
USNM	401904
USNM	401901
USNM	401903
USNM	401902
USNM	446581
USNM	446580
USNM	446582
USNM	326222
USNM	326219
USNM	326216
USNM	326217
USNM	326221
USNM	326223
USNM	327354
USNM	326218
USNM	326220
USNM	605270
USNM	513224
USNM	514102
USNM	513208
USNM	513209
USNM	513232
USNM	513205
USNM	514100
USNM	514101
USNM	514119
USNM	516281

(Table Continues)

Collection	Number
USNM	516283
USNM	516282
USNM	516284
USNM	516286
USNM	516285
USNM	513210
USNM	513211
USNM	513212
USNM	513216
USNM	513217
USNM	513218
USNM	514103
USNM	514104
USNM	514105
USNM	514106
USNM	514107
USNM	514108
USNM	514109
USNM	514110
USNM	513247
USNM	513248
USNM	514114
USNM	514113
USNM	514112
USNM	514111
USNM	513228
USNM	513254
LSUMNS	21077
LSUMNS	21079
LSUMNS	21078
LSUMNS	78227
LSUMNS	78228
LSUMNS	78230
LSUMNS	78231
LSUMNS	78234
LSUMNS	78233
LSUMNS	132407
LSUMNS	137564
LSUMNS	84629

(Table Continues)

Collection	Number
LSUMNS	84628
LSUMNS	84632
LSUMNS	84633
LSUMNS	84634
LSUMNS	67184
LSUMNS	67185
LSUMNS	71644
LSUMNS	67186
LSUMNS	67189
LSUMNS	67190
LSUMNS	132414
LSUMNS	132408
LSUMNS	132429
LSUMNS	132428
LSUMNS	123855
LSUMNS	123856
LSUMNS	101892
LSUMNS	101893
LSUMNS	67180
LSUMNS	87677
LSUMNS	87675
LSUMNS	87676
LSUMNS	132415
LSUMNS	132416
LSUMNS	132417
LSUMNS	132418
LSUMNS	132419
LSUMNS	132424
LSUMNS	34815
LSUMNS	67181
LSUMNS	67182
LSUMNS	67183
LSUMNS	34970
LSUMNS	34971
LSUMNS	33898
LSUMNS	32478
LSUMNS	67187
LSUMNS	67188
LSUMNS	50973

(Table Continues)

Collection	Number
LSUMNS	116739
LSUMNS	116740
LSUMNS	116741
LSUMNS	116742
LSUMNS	116744
LSUMNS	116745
LSUMNS	116746
LSUMNS	116747
LSUMNS	116749
LSUMNS	116751
LSUMNS	116752
LSUMNS	116753
LSUMNS	116754
LSUMNS	116755
LSUMNS	116756
LSUMNS	116757
LSUMNS	116758
LSUMNS	116759
LSUMNS	116760
LSUMNS	116761
LSUMNS	84624
LSUMNS	92107
LSUMNS	92106
LSUMNS	119582
LSUMNS	119583
LSUMNS	119585
LSUMNS	119590
LSUMNS	114967
LSUMNS	114969
LSUMNS	114973
LSUMNS	114974
LSUMNS	114976
LSUMNS	114979
LSUMNS	114980
LSUMNS	16586
LSUMNS	40562
LSUMNS	51153
LSUMNS	51155
LSUMNS	51154

(Table Continues)

Collection	Number
LSUMNS	40561
LSUMNS	27184
LSUMNS	22891
LSUMNS	22890
LSUMNS	23957
LSUMNS	61547
LSUMNS	40563
LSUMNS	140145
LSUMNS	30586
LSUMNS	51157
LSUMNS	38634
LSUMNS	51156
LSUMNS	20620
LSUMNS	20621
LSUMNS	21873
LSUMNS	38636
LSUMNS	51158
LSUMNS	109651
LSUMNS	109652
LSUMNS	109660
LSUMNS	109661
LSUMNS	109668
LSUMNS	109670
LSUMNS	109653
LSUMNS	109656
LSUMNS	109645
LSUMNS	109646
LSUMNS	109647
LSUMNS	109648
LSUMNS	109649
LSUMNS	105853
LSUMNS	105854
LSUMNS	105855
LSUMNS	130215
LSUMNS	130216
LSUMNS	130217
LSUMNS	109594
LSUMNS	109599
LSUMNS	109601

(Table Continues)

Collection	Number
LSUMNS	109607
LSUMNS	109617
LSUMNS	109620
LSUMNS	109621
LSUMNS	109622
LSUMNS	109624
LSUMNS	109625
LSUMNS	109627
LSUMNS	109641
LSUMNS	109626
LSUMNS	105852
LSUMNS	109629
LSUMNS	119536
LSUMNS	119537
LSUMNS	119538
LSUMNS	119539
LSUMNS	119540
LSUMNS	119541
LSUMNS	119542
LSUMNS	119543
LSUMNS	119548
LSUMNS	119549
LSUMNS	119551
LSUMNS	119552
LSUMNS	119557
LSUMNS	119559
LSUMNS	119545
LSUMNS	119546
LSUMNS	119560
LSUMNS	119564
LSUMNS	119565
LSUMNS	119572
LSUMNS	119576
LSUMNS	119577
LSUMNS	114940
LSUMNS	114941
LSUMNS	114943
LSUMNS	114944
LSUMNS	114914

(Table Continues)

Collection	Number
LSUMNS	114915
LSUMNS	114916
LSUMNS	114917
LSUMNS	114919
LSUMNS	114920
LSUMNS	114921
LSUMNS	114922
LSUMNS	114923
LSUMNS	114924
LSUMNS	114925
LSUMNS	114947
LSUMNS	114949
LSUMNS	114950
LSUMNS	114952
LSUMNS	114954
LSUMNS	114957
LSUMNS	114960
LSUMNS	115010
LSUMNS	115011
LSUMNS	115012
LSUMNS	64089
LSUMNS	84623
LSUMNS	84625
LSUMNS	28367
LSUMNS	72349
LSUMNS	114986
LSUMNS	114987
LSUMNS	114990
LSUMNS	114992
LSUMNS	114993
LSUMNS	114994
LSUMNS	114995
LSUMNS	114998
LSUMNS	115000
LSUMNS	115001
LSUMNS	115005
LSUMNS	114963
LSUMNS	114964
LSUMNS	114965

(Table Continues)

Collection	Number
LSUMNS	MCG551
LSUMNS	MCG487
LSUMNS	DCS5075
LSUMNS	MCG507
LSUMNS	MCG479
LSUMNS	JMB388
LSUMNS	MCG508
LSUMNS	MCG518
LSUMNS	DCS5167
LSUMNS	MCG491
LSUMNS	JMB430
LSUMNS	CGS5081
LSUMNS	MCG490
LSUMNS	MCG562
LSUMNS	DCS4905
LSUMNS	DCS4739
LSUMNS	DCS4818
LSUMNS	CGS4931
LSUMNS	DCS4808
LSUMNS	CGS4907
LSUMNS	DCS4591
LSUMNS	DCS4629
LSUMNS	DCS4646
LSUMNS	APC3178
LSUMNS	DCS4634
LSUMNS	APC2961
LSUMNS	PPM286
LSUMNS	PPM90
LSUMNS	APC2941
LSUMNS	APC2945
LSUMNS	PPM101
LSUMNS	APC2911
LSUMNS	PPM113
LSUMNS	JPO7326
LSUMNS	MSS3093
LSUMNS	DCS4554
LSUMNS	GC84
LSUMNS	ISS3504
LSUMNS	MCH285

(Table Continues)

Collection	Number
LSUMNS	AC6034
LSUMNS	MCH314
LSUMNS	IOM15
LSUMNS	153299
LSUMNS	153300
LSUMNS	153301
LSUMNS	RSV6
LSUMNS	MCH45
LSUMNS	MCH48
LSUMNS	APC3348
LSUMNS	JMB573
LSUMNS	APC3520
LSUMNS	APC3521
ANSP	76906
ANSP	76912
ANSP	76908
ANSP	76911
ANSP	76909
ANSP	76910
ANSP	76907
ANSP	76913
ANSP	90711
ANSP	167869
ANSP	63864
ANSP	177217
ANSP	148382
ANSP	147837
ANSP	147838
ANSP	147419
ANSP	148380
ANSP	147836
ANSP	150650
ANSP	150653
ANSP	164964
ANSP	164956
ANSP	164957
ANSP	164962
ANSP	164961
ANSP	164960

(Table Continues)

Collection	Number
ANSP	164968
ANSP	152640
ANSP	152641
ANSP	151341
ANSP	152642
ANSP	152636
ANSP	152639
ANSP	152638
ANSP	152635
ANSP	151337
ANSP	151339
ANSP	151340
ANSP	6959
ANSP	143186
ANSP	157931
ANSP	157945
ANSP	157944
ANSP	131619
ANSP	157940
ANSP	157936
ANSP	157937
ANSP	157942
ANSP	147417
ANSP	157933
ANSP	146101
ANSP	146994
ANSP	157946
ANSP	157938
ANSP	148378
ANSP	157941
ANSP	150655
ANSP	329137
ANSP	151338
ANSP	152637
ANSP	103538
ANSP	103539
ANSP	103536
ANSP	103540
ANSP	103535

(Table Continues)

Collection	Number
ANSP	103534
ANSP	103537
ANSP	140923
ANSP	140920
ANSP	140921
ANSP	140918
ANSP	140919
ANSP	140922
ANSP	80611
ANSP	80610
ANSP	80612
ANSP	80613
ANSP	92546
ANSP	92545
ANSP	92544
ANSP	92548
ANSP	83397
ANSP	180292
ANSP	180293
ANSP	180294
ANSP	177740
ANSP	177743
ANSP	177742
ANSP	177741
ANSP	147420
ANSP	146992
ANSP	146993
ANSP	146318
ANSP	147416
ANSP	151124
ANSP	151126
ANSP	151125
ANSP	173221
ANSP	173223
ANSP	146320
ANSP	148377
ANSP	146317
ANSP	150651
ANSP	150654

(Table Continues)

Collection	Number
ANSP	150652
ANSP	149624
ANSP	148375
ANSP	150924
ANSP	148381
ANSP	157370
ANSP	147418
ANSP	146100
ANSP	146105
ANSP	157943
ANSP	144325
ANSP	146104
ANSP	175506
ANSP	170649
ANSP	64802
ANSP	64801
ANSP	150172
ANSP	150173
ANSP	163355
ANSP	175734
YPM	40406
YPM	40407
YPM	32097
YPM	32098
YPM	25514
YPM	29267
YPM	29269
YPM	29268
YPM	29270
YPM	27390
YPM	7705
YPM	81637
YPM	81636
YPM	29277
YPM	29278
YPM	29276
YPM	29275
YPM	29273
YPM	29279

(Table Continues)

Collection	Number
YPM	29272
YPM	29271
YPM	29274
YPM	56468
YPM	56472
YPM	56471
YPM	56467
YPM	58700
YPM	58701
YPM	32099
YPM	32100
YPM	32360
YPM	55026
YPM	55027
YPM	55029
YPM	55028
FMNH	293136
FMNH	293137
FMNH	293138
FMNH	292818
FMNH	292821
FMNH	292820
FMNH	292822
FMNH	286999
FMNH	287002
FMNH	287001
FMNH	286994
FMNH	286998
FMNH	287003
FMNH	287000
FMNH	286997
FMNH	286996
FMNH	292819
FMNH	292817
FMNH	292815
FMNH	249670
FMNH	249671
FMNH	249669
FMNH	249668

(Table Continues)

Collection	Number
FMNH	249672
FMNH	250790
FMNH	250791
FMNH	250792
FMNH	286995
FMNH	292816
FMNH	292567
FMNH	292568
FMNH	315473
FMNH	315474
FMNH	315476
FMNH	315468
FMNH	315469
FMNH	315471
FMNH	251782
FMNH	251784
FMNH	251785
FMNH	321285
FMNH	321284
FMNH	321284bis
FMNH	281220
FMNH	281218
FMNH	281217
FMNH	281219
FMNH	281216
FMNH	311278
FMNH	311277
FMNH	311279
FMNH	311282
FMNH	311281
FMNH	315475
FMNH	278567
FMNH	278566
FMNH	66226
FMNH	66227
FMNH	66225
FMNH	108317
FMNH	108316
FMNH	108315

(Table Continues)

Collection	Number
FMNH	295667
FMNH	295663
FMNH	63901
FMNH	318957
FMNH	318958
FMNH	318959
FMNH	318960
FMNH	318961
FMNH	318962
FMNH	318963
FMNH	318964
FMNH	318965
FMNH	264360
FMNH	260336
FMNH	260333
FMNH	260337
FMNH	260334
FMNH	260335
FMNH	260332
FMNH	264361
FMNH	262280
FMNH	120185
FMNH	120186
FMNH	120187
FMNH	179911
FMNH	179912
UM	199605
UM	199606
UM	199604
UM	132548
UM	150233
UM	210618
UM	132549
UM	58521
UM	56325
UM	56324
UM	153672
UM	222739
UM	88042

(Table Continues)

Collection	Number
UM	98158
UM	216343
UM	215367
UM	215366
UM	1501
UM	1501bis

Table B-4

Identity of Specimens from the AMNH Used in the Secondary Data Set

Collection	Number
AMNH	125737
AMNH	125738
AMNH	125753
AMNH	125736
AMNH	125796
AMNH	176859
AMNH	176862
AMNH	805786
AMNH	125741
AMNH	525288
AMNH	525283
AMNH	177393
AMNH	525278
AMNH	177395
AMNH	821369
AMNH	12895
AMNH	177394
AMNH	323732
AMNH	323734
AMNH	323736
AMNH	122073
AMNH	434665
AMNH	434659
AMNH	310775
AMNH	312077
AMNH	434648
AMNH	434646
AMNH	274150
AMNH	274159
AMNH	274147
AMNH	274160
AMNH	274163
AMNH	432933
AMNH	432928
AMNH	432921

(Table Continues)

Collection	Number
AMNH	432942
AMNH	432938
AMNH	432929
AMNH	432926
AMNH	11944
AMNH	231986
AMNH	231991
AMNH	184184
AMNH	256128
AMNH	231995
AMNH	232230
AMNH	240400
AMNH	240398
AMNH	239331
AMNH	239330
AMNH	239333
AMNH	239334
AMNH	407162
AMNH	819712
AMNH	819741
AMNH	820900
AMNH	820148
AMNH	169078
AMNH	234748
AMNH	234747
AMNH	459610
AMNH	459607
AMNH	459608
AMNH	459609
AMNH	459603
AMNH	459602
AMNH	459606
AMNH	459604
AMNH	459605
AMNH	430974
AMNH	430973
AMNH	430970
AMNH	430972
AMNH	430970bis

(Table Continues)

Collection	Number
AMNH	430975
AMNH	430969
AMNH	430977
AMNH	525323
AMNH	525327
AMNH	525322
AMNH	148482
AMNH	148483
AMNH	146194
AMNH	146193
AMNH	132724
AMNH	132726
AMNH	132725
AMNH	147722
AMNH	146196
AMNH	791935
AMNH	278028
AMNH	279693
AMNH	127761
AMNH	286854
AMNH	278033
AMNH	430976
AMNH	278029
AMNH	278031
AMNH	278032
AMNH	278026
AMNH	278027
AMNH	117910
AMNH	117909
AMNH	117908
AMNH	109688
AMNH	107482
AMNH	108066
AMNH	133588
AMNH	108061
AMNH	133583
AMNH	133587
AMNH	133586
AMNH	184188

(Table Continues)

Collection	Number
AMNH	184189
AMNH	525339
AMNH	525329
AMNH	525335
AMNH	525330
AMNH	525334
AMNH	525333
AMNH	787084
AMNH	390521
AMNH	390528
AMNH	390527
AMNH	134927
AMNH	136631
AMNH	136629
AMNH	134925
AMNH	134929
AMNH	134928
AMNH	246781
AMNH	246780
AMNH	246782
AMNH	246779
AMNH	246780bis
AMNH	247591
AMNH	247588
AMNH	247587
AMNH	776017
AMNH	787534
AMNH	74729