

2008

Phylogeography of Nothoprocta Tinamous and the the Phylogeny of the Tinamidae

Thomas Valqui

Louisiana State University and Agricultural and Mechanical College, tvalqui@corbidi.org

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PHYLOGEOGAPHY OF *NOTHOPROCTA* TINAMOUS
AND THE PHYLOGENY OF THE TINAMIDAE

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Biological Sciences

by

Thomas Valqui

B.S. Universidad Nacional Agraria-La Molina, Peru, 1992

Ing. Universidad Nacional Agraria- La Molina, Peru, 1997

M.A. Princeton University, New Jersey, 1998

May, 2009

ACKNOWLEDGMENTS

First of all, I want to thank my main advisor J. “Van” Remsen, for taking me in as his student, for his guidance and for being always there when I needed it. When my dissertation contracted a genetic twist Robb Brumfield generously accepted co-advisorship and helped me more than I could have expected. My other committee members, Fred Sheldon, Bruce Williamson and Alan Afton, offered lots of their time and were very patient during all these many years.

For advice on many aspects of my fieldwork and methods, for information natural history of Andean tinamous and much help in the collecting process, I especially thank Jose Antonio Otero. José Ignacio Otero, Mark Sokol, Abraham Urbay, Demetrio Huachaca, and Oliverio Diaz also accompanied us on several trips. Aquira, Isabel and Sagal were invaluable companions who were key to successful field-work with tinamous.

The field trip to Argentina was only possible thanks to Daniel Winizky. Daniel Gonzales made data collecting in Chile possible. Many trips in Peru happened thanks to Kevin McCracken of UAF-Alaska. Rob Wilson, Mariana Bulgarella, Chris Barger, Maria Jose Fernandez and Patricia Brennan participated in some of these trips.

Special thanks also go to Dan Lane and John O’Neill for helping out throughout the years. For general guidance and preparing techniques I want to thank Steve Cardiff.

For the work on niche modeling, my gratitude goes to Carolina Tovar. Pilar Hernández, Pedro Vásquez, Claudia Vega and Fernando Regal offered lots of help in the CDC- La Molina. Mark Pearman generously offered information on distribution for Argentina.

For help in the genetics lab I first have to thank Robb Brumfield, Zac Chevron, Elizabeth Derryberry and Donna Dittman. Always helpful when methodological questions arose in the lab where Ben Marks, Alex Aleixo, Andrés Cuervo, Jessica Eberhard, Luciano Naka, Matt Carling. Rebecca Kimball provided important information from her line of research.

Jason Weckstein talked me into collecting lice long time ago and conducted the louse research for this dissertation. His assistant Holly Lutz worked hard on the sequencing.

For being able to visit AMNH, I especially thank Joel Cracraft, José Tello and Paul Sweet. Pablo Tubaru, Darío Lijtmaer, Cecilia Kopuchian helped tremendously during my visit to the collection in Buenos Aires. Gary Graves and Terry Chesser assisted during my visit to the collection in the Smithsonian Institution, Washington. For information from the Bolivian collection in La Paz I thank Isabel Gómez and Kazuya Naoki. Irma Franke and Letty Salinas earn my thanks for permission to visit the collection in the Museo de Historia Natural de San Marcos, Lima.

Tissue loans came from the Smithsonian Institution, Washington, Peabody Museum in Yale, Museum of Southwestern Biology in the University of New Mexico,

People at CORBIDI were always keen to help in many aspects of my work. Particularly Dora Susanibar, but also Javier Barrio, Willy Nájuez, Jano Núñez and Alessandra Quiñonez.

For general help and advice during my time at LSU, I also want to thank faculty members Mark Hafner and Phillip Stouffer, and the following alumni: Mario Cohn-Haft, Chris Witt, Kazuya Naoki, Alex Aleixo, Ben Marks. These fellow current graduates were also of great help: Curt Burney, Gustavo Bravo, James Maley, Santiago Claramunt, Richard Gibbons, Haw Chuan, Verity Mathis, Brian O'Shea, Jesús Fernandez.

Last not least I want to thank my wife Verónica who always stood by my side and supported me in many ways during this journey.

Funding for this project was provided by the Museum of Natural Sciences, Louisiana State University (various sources), the Center for the Study of Tropical Birds, the University of Alaska – Fairbanks, Apeco (Asociación para la Conservación de la Naturaleza) and the Collections Study Grant from AMNH.

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ABSTRACT

Understanding how diversity is attained and maintained is one of the central questions in biology. In the Neotropics most attention has centered on the Amazonian lowlands, despite the recognized importance of the role of the Andes in South American diversity. In this dissertation, I address the question by using *Nothoprocta* tinamous as a model case for examining diversification in the Andes. As a group, they are a manageable size, they exhibit near-restriction to the Andes, they show multi-species parapatric distributions, and they have presumed limited dispersal ability. These are all useful attributes for a system to study speciation and diversification.

First, I constructed the phylogenetic framework with a molecular phylogeny based on one nuclear and two mitochondrial genes. This phylogeny has the richest taxon-sampling of any yet produced for tinamous. High Bayesian posterior probabilities (>0.95) for all of the higher-level relationships supported the traditional subfamily division as well as the monophyly of all genera. Within *Nothoprocta*, the main finding was the paraphyly of *Nothoprocta pentlandii*, which requires that the northern populations (*Nothoprocta oustaleti*) be elevated to species rank.

Second, I analyzed the distributions of all *Nothoprocta* taxa using niche modeling. With 407 different existing localities and 100 new localities obtained during my fieldwork, I used Maxent to produce a likelihood of occurrence for each species using seven environmental variables. Six of the species show “parapatric stratified distributions.” The current distribution pattern in *Nothoprocta* at the specific and subspecific levels is not characterized by isolation by geographical barriers or distance, but rather by extensively parapatric distributions.

Finally, I combined the data presented in the previous chapters in an effort to find explanations to the striking parapatric stratified diversity pattern of *Nothoprocta*. I analyzed this pattern of distribution with respect to the evolutionary relationships within clades, species, and subspecies. I did not find evidence of parapatric speciation among members of *Nothoprocta* and concluded that the most likely mechanism driving speciation in this group is the fracturing of long, narrow, montane distributions, followed by diversification in allopatry and possibly through posterior secondary contact.

CHAPTER 1. INTRODUCTION

1.1. Diversity and Speciation

A central question in biology has been how diversity is attained (Haffer 1969; Mittelbach et al. 2007; Nores 1999; Terborgh 1980) and maintained (Karr and Roth 1971; Klopfer and MacArthur 1961; MacArthur and Horn 1969; Terborgh 1992). This question has proven particularly challenging in the Neotropics, where diversity and diversity patterns seem to be particularly rich and of mixed origins. Most studies of diversity in the Neotropics have concentrated on the more striking alpha (or point) diversity. However, beta diversity (Whittaker 1975) is not only (considerably) higher in the Neotropics than in temperate zones, but also the mechanisms producing beta diversity are an important or necessary step to understand alpha diversity. Most models of speciation analyze allopatric or parapatric distributions within a group of species because these kinds of patterns are assumed still to bear the fingerprints of the mechanisms creating the necessary isolation for speciation. When groups of related species replace one another geographically, they are each assumed to be in, or close to, their areas of origin. These areas of speciation are assumed to have been isolated, because the most widely accepted -- often the only accepted (Futuyma and Mayer 1980) -- mechanism of speciation among animals is that of allopatric speciation. For species groups that evolve within a region, this means that the development of beta diversity is a necessary step for increasing overall diversity, including alpha diversity.

1.2. The Phylogenetic Framework

In recent years, the ability to sequence genes has added a new perspective to the analysis of diversity (Cheviron et al. 2005; Graham et al. 2004), particularly in two aspects: a) making it possible to incorporate genetic structure into current patterns of diversity, and b) significantly strengthening the historical component of evolutionary relationships by the use of phylogenetic hypotheses based on genetic information.

Predicting evolutionary relationships among species, estimating the timing of speciation events, and comparing the evolutionary histories of one organismal group with those of other groups exhibiting congruent distribution patterns are all useful tools for unraveling current diversity patterns and predicting the mechanisms that lead to them. A solid phylogenetic framework is a foundation for the study of the distribution patterns and speciation models of a group of related species or among the inhabitants of a region.

1.3. Importance of Current Distribution

A fundamental component in studying distribution patterns is, of course, the proper mapping of the distribution of each of the species. It is important to recognize that in the

temporal axis given by phylogenies, the current pattern of population distribution and structure is the only one that can be measured precisely. Proper sampling combined with the rather recently developed niche-modeling (Elith et al. 2006; Guisan and Zimmermann 2000; Peterson 2001) would seem a good approach to estimating current distributions. Niche-modeling also allows predictions about past and future conditions and distributions (Pearson and Dawson 2003; Ruegg et al. 2006).

In this study I use both phylogenetic reconstruction and niche modeling, to analyze the possible mechanism resulting in the current distribution of *Nothoprocta* tinamous.

1.4. Study Taxa: Tinamous with Emphasis on *Nothoprocta*

Evolutionarily, tinamous are members of the paleognath lineage, a basal split in the avian evolutionary tree (Hackett et al. 2008). Within the paleognaths they represent the only major evolutionary branch containing a large number (47) of species (Davies 2002). In South America, they occur in most habitats, making them an interesting and historically independent branch to the neognaths.

The phylogeny of the tinamous is still controversial at various levels. Only recently, a study proposed a new position of the tinamous within the class Aves. With exhaustive sampling both of taxa and genes, this robust study places tinamous within the ratites (Hackett et al. 2008; Harshman et al. 2008). Relationships among tinamous, however, were still incompletely known. Although there are previously two morphological studies (integument [Bertelli et al. 2002]) and osteology [Bertelli and Chiappe 2005]), a taxon-poor, mitochondrial-based molecular study (Porzecanski 2003), and a combined analysis of the previous two data sets (Bertelli and Porzecanski 2004), the many missing taxa in the molecular study prevented a comprehensive analysis. A fundamental reason for the lack of genetic studies within tinamous is the scarcity of tissues samples. Even though the focus of my own study is of one genus (*Nothoprocta*), the lack of an uncontroversial outgroup forced me to produce a full phylogeny of the Tinamidae.

Relative to other birds, tinamous can be considered poor dispersers because they are only capable of short flights to escape imminent danger. Their limited dispersal ability increases the likelihood that tinamou taxa have remained in their “birthplaces” (i.e., that distribution patterns are relatively stable temporally), a topic of concern when studying population structure among birds, given that most fly and disperse well. Considering that they are possibly as old as any neognath lineage (Hackett et al. 2008), their homogeneity is striking compared to neognath groups of comparable age and diversity. Constraints on their cranial kinesis has been invoked to explain the minimal diversification in feeding behavior (Bock 1964; Zusi 1984), despite having colonized most habitats of the Neotropics. This lack of differentiation might also partly explain the apparent lack of syntopy in some groups of tinamous, thus limiting the likelihood of speciation by adaptive radiation.

The genus *Nothoprocta* consists of seven species of tinamous and eleven additional subspecies (Davies 2002). *Nothoprocta* species are restricted to the Andes or the base of the Andes (Fjeldså and Krabbe 1990). Their distribution is apparently parapatric with up to three species showing altitudinal replacement where they co-occur (pers. obs.). Their manageable group size, phylogenetic independence from the neognaths, near-restriction to the Andes, multi-species parapatric distribution, and presumed limited dispersal ability are all useful attributes for a system to study speciation and diversification. They made excellent candidates for my study of an avian group that had undergone vicariant and dispersal-barrier related speciation.

1.5. Geographical Setting: The Andes

The Andean cordillera extends for over 5000 km along the western coast of the continent of South America. It is a result of plate tectonics dating as far back as 200 MYA (Chew et al. 2005), but with most of its dynamics occurring in the last 27 MYA (Gregory-Wodzicki 2000). The Andes of South America and the mountains of western Antarctica were continuous into the Palaeogene as a reduced version of present day cordillera (Ramos 1999). The continental continuity for terrestrial biotas may have persisted as far as the Oligocene. After the separation of these continents, nearly orthogonal, rapid plate subduction along the western coasts of South America gave rise to the modern Andean cordillera, around 27 MYA (still in the Oligocene) (Gregory-Wodzicki 2000). Even though the uplift is known to have been uneven in time and space, an estimate for the rise of the mountains of 0.25 mm/year is often cited. The Altiplano was at sea level until the Eocene (ca. 35 MYA) and reached half of its present height (over 3500 m elevation) only 7 My ago (Gregory-Wodzicki 2000).

1.6. Speciation in the Andes

Three modes of origin have been hypothesized for Andean faunas: a) lowland origin of species that disperse repeatedly to the Andes (Monasterio and Vuilleumier 1986), b) lowland-to-highland climatic interaction based on topography (Brumfield and Edwards 2007), and c) passive upwards transportation of populations during Andean uplift (Ribas et al. 2007). All these hypotheses assume a strong interaction of the Andes with the lowlands and consider the lowlands to be the source of species. However, the opposite has also been proposed. Fjeldså (1995) considered certain ecologically stable areas in the Andes to act as “species pumps” that produce species for the “museums” of the lowlands.

When compared to the Amazonian lowlands, the Andes have a lower alpha diversity, but some of the patterns of distribution in the Andes are more striking than in the lowlands: multiple species with extremely narrow elevational distributions replacing one another along altitudinal gradients (Remsen and Graves 1995a; Terborgh 1971), leapfrog

patterns, where two more similar morphotypes are geographically “interrupted” by an intervening dissimilar, but related, population (Remsen 1984), sandwiched distributions, in which a species is in between two populations of another species along an altitudinal gradient (Remsen and Graves 1995b) and ‘niche switch,’ in which a species changes altitudinal preference along the latitudinal axis of its distribution (Remsen and Cardiff 1990).

Even though the above distributional patterns have been described carefully for some species, the possible underlying mechanisms producing those patterns have not been tested for generality. In general, hypotheses for the speciation of Andean organisms has received far less attention than hypotheses for speciation of Amazonian organisms. Amazonian speciation has spawned several hypotheses: refugia (Haffer 1969), Andean foreland dynamics (Gascon et al. 2000; Loughheed et al. 1999; Rasanen et al. 1990), oceanic intrusion (Nores 1999), river barrier (Gascon, 2000; Wallace, 1852; Capparella, 1987), and gradient (Endler 1977; Smith et al. 2001) hypotheses.

The Andes themselves, by their virtue of dramatic topography, could be seen as the barrier-rich species pump. First, the Andean massif splits several sister taxa on opposite slopes (Restall et al. 2006; Ridgely and Tudor 1994), and many deep valleys create broad habitat and elevation barriers, both across and along the Andean massive. High peaks, parallel cordilleras, and isolated mountain ranges, would also likely promote population isolation.

Four major hypotheses are candidates for general speciation modes in the Andes. Three are adapted from lowland scenarios:

a) a deep valley hypothesis, similar to the river hypothesis in Amazonia. Deep valleys in the Andes represent regional breaks that isolate populations. Original connections between these populations were either before the barrier arose or based on dispersal and founder populations.

b) a Pleistocene hypothesis (Chesser 2000), similar to the refugia hypothesis in the lowlands. Even though the Andes have not changed much since the late Pleistocene (Gregory-Wodzicki 2000; Hooghiemstra et al. 2006), during that period heavy climatic oscillations made the Andean topography play an important and dynamic role in the biogeography of its biotas (Chesser 2000). In that climatic scenario, the Andes were responsible, passively, for dramatic reductions, expansion and shifts of microclimates and habitats. This created ample opportunities for population isolation, which is usually considered fundamental in the diversification of the Andes.

c.) linearity of geographical range hypothesis (Graves 1988), which states that speciation in the Andes is based on the high likelihood of disruption of long and linear ranges of many Andean organisms. This speciation mode would be exclusive to the Andean setting.

d.) gradient hypothesis (Endler 1977), which is the only hypothesis that does not require population isolation. The gradient hypothesis, which proposes that a continuously distributed population becomes divided by gradual specialization at two resource peaks along a gradient (such as elevation) and that selection against intermediate individuals causes a cessation of gene flow even though the two populations are never separated. This hypothesis (reviewed by Smith et al.[2001]), is particularly appealing with respect to elevational gradients as suggested by (Terborgh 1977).

With time, more studies will test these hypotheses, and possibly additional ones, with different species groups and will show which ones best explain the speciation of Andean birds. Note that hypotheses a, b, and c are not mutually exclusive.

1.7. Chapter Summaries

Nothoprocta tinamous provide an excellent model for the study of beta diversity and speciation models in the Andes. In this dissertation I first contribute a considerable amount of new sampling data, both taxonomic and geographic. In chapter 2, I will construct a phylogeny of the tinamous. Besides contributing the first well-supported phylogeny of the family, this provides a solid phylogenetic framework for my study of distribution patterns of the *Nothoprocta* tinamous. In chapter 3, I will use niche-modeling to predict the distribution of the taxa (species and subspecies) within *Nothoprocta*. In many instances, the comparison of the distributional predictions and actual known occurrence allow for some interpretation of possible causes for distributional limits. Chapter 4, ties chapter 2 and 3 together. I will use the information produced in the two previous chapters to analyze the distribution patterns in a phylogenetic framework. I will start by addressing the possible lowland origin of this Andean group. Then I will analyze the distribution patterns of sister clades to see which speciation mode might best explain the pattern. Finally, using a separate phylogeny of chewing lice collected from their *Nothoprocta* tinamou hosts, I will analyze general distribution patterns trying to find congruencies between lice and tinamous that might suggest a underlying mode of speciation.

CHAPTER 2. A PHYLOGENY OF TINAMIFORMES WITH SPECIAL EMPHASIS ON *NOTHOPROCTA*

2.1 Introduction

2.1.1. Placement of Tinamiformes

The phylogenetic placement of the tinamous has long been controversial. Historically, tinamous were hypothesized to be sister to the Galliformes (Chandler 1916; Glenny 1946; Lesson 1931). This placement was based on an overall resemblance to partridges, and similarities in the sternum, feather structure (Chandler 1916), and arterial system (Glenny 1946). Other workers argued that these similarities were homoplasious and suggested instead that the Tinamiformes was an ancient, basal lineage within birds (Mayr and Amadon 1951; Wetmore 1930). Others have shown that tinamous are very similar to ratites in several morphological and behavioral characters, including a palaeognathous palate (Huxley 1867), rhynchokinetic skull (McDowell 1978; Zusi 1984), other skull anatomy features (Bock 1963; Bock 1964; Starck 1993), tarsal morphology (McGowan 1985), egg shell structure (Tyler and Simkiss 1959), bill shape in the downy young (Kenneth and Clark 1966), and a polyandrous reproductive system. In addition several tinamou species have cloacas with ureters that open into the coprudeum, a character shared with crocodylians (Oliveira et al. 2004). Studying the Emu and two *Nothoprocta* species, Sillman et al. (1981) found an identical oil globule system in the retina, which is much simpler than the typical system for neognathous birds. Ausio et al. (1999) found that the protamines of Ostrich and a *Nothoprocta* tinamou sperm display a higher electrophoretic mobility and a significantly different amino acid composition and protein sequence when compared to neognathous birds.

With the advent of molecular techniques, more powerful analytical tools were expected to clarify the relationships, but disagreement is considerable among several phylogenies reconstructed from molecular data. The DNA-DNA hybridization classification of Sibley and Ahlquist (1990) placed tinamous as sister to the ratites, a relationship corroborated by a later mitochondrial study (van Tuinen et al. 1998). That the origin of Tinamous was deep in the evolutionary history of birds makes it difficult, even for molecular data, to recover their evolutionary relationships (Hackett et al. 2008). For example, using a phylogeny inferred from mitochondrial gene sequences, Harlid and Arnason (1999) disputed the basal split between paleognaths and neognaths, putting some ratites (Rhea and Ostrich) inside Passeriformes.

The consensus of an accumulating number of studies suggests that the Tinamiformes is the sister group to the ratites (Struthioniformes), and that these two groups, known

collectively as the Paleognathae, are the sister to all other living birds, which are known as the Neognathae (e.g. Braun and Kimball 2002; Cracraft 1988; Van Tuinen et al. 2000).

The most comprehensive molecular study to date that examined higher-level relationships across the entire class Aves (Hackett et al. 2008) resulted in a highly supported, yet novel, hypothesis regarding the placement of Tinamiformes (Fig.1). Evidence from 19 independent loci spanning 15 different chromosomes (totaling 32 kilobases of DNA sequences for 169 species of birds representing all major lineages) found that Tinamiformes is nested within ratites. Despite high support for Tinamiformes monophyly and for *Struthio* (Ostrich) as the outgroup of the rest of the ratites plus Tinamiformes, the exact placement of tinamous within the ratites remained unresolved. Maximum likelihood and Bayesian analyses placed tinamous as sister to Australian ratites, whereas maximum parsimony and RY-coded maximum likelihood placed them as sister to rheas, both with low bootstrap support (<65%). The latter hypothesis is biogeographically more parsimonious because rheas and tinamous are exclusively Neotropical.

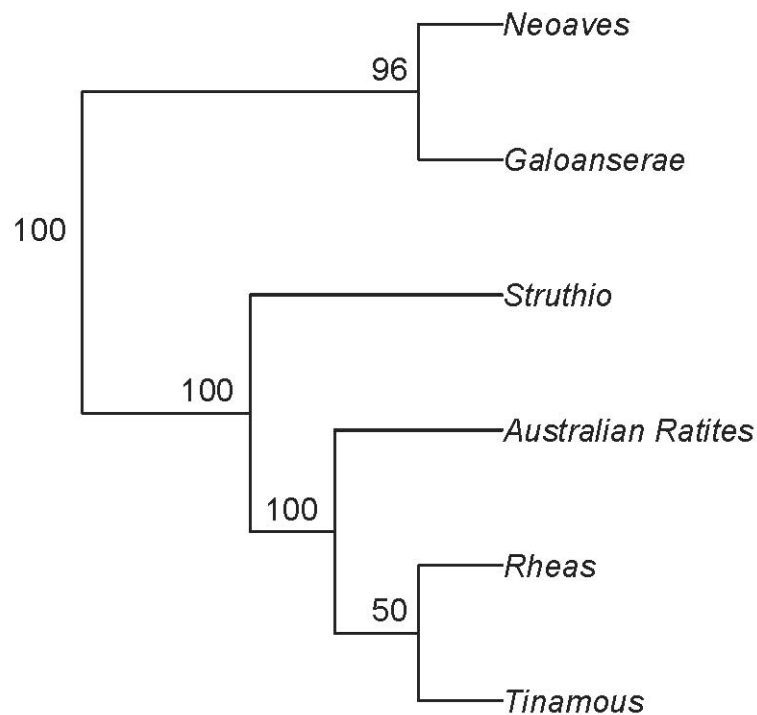


Figure 1. Summary of avian phylogeny according to Hackett et al (2008) and Harshman et al. (2008). Values on nodes represent ML bootstrap support. Rheas, tinamous, and Australian ratites should be treated as a polytomy. Bootstrap support for tinamous and Australian ratites as sisters was actually a little bit higher for some analyses. Rheas and tinamous shown here together as the alleged more biogeographically parsimonious hypothesis.

2.1.2. The Subfamilies of Tinamidae

Monophyly of the order Tinamiformes, and its only family the Tinamidae, has overwhelming support from morphological and molecular data (Bertelli and Chiappe 2005; Hackett et al. 2008; Harshman et al. 2008; Jehl 1971). The relationships among tinamous, however, remain largely unresolved. In the first attempt to classify tinamous into subfamilies, Salvadori (1895) named the Tinamotidinae (*Eudromia* and *Tinamotis*), a group missing the hallux, and the Tinaminae, formed by the rest of the tinamous. In a subsequent classification attempt, von Boettischer (1934) proposed a three-way partition with *Eudromia* and *Tinamotis* as Eudrominae (equivalent to Salvadori's Tinamotidinae) and by further dividing Tinaminae (with only *Nothocercus*, *Tinamus*, and *Crypturellus*), taking out what he named Rhynchotinae (*Rhynchotus*, *Nothura*, *Taoniscus*, and *Nothoprocta*). Miranda-Ribero (1937) followed with a classification that merged Eudrominae and Rhynchotinae into the Nothurinae. Perhaps the most distinctive character supporting this division was the open habitat used by Nothurinae and the forest interior by Tinaminae (Miranda-Ribero 1937). Morphologically, the position of the nares in the bill (close to the tip for Tinaminae) was also a clear distinguishing character.

The first study to reconstruct a tinamou phylogeny was Bertelli et al. (2002). They performed exhaustive morphological analyses, measuring 80 integumentary characters in almost all species. They found high support for the monophyly of open-land tinamous (Nothurinae). Monophyly of open-land tinamous was also supported by a cladistic analysis of 63 osteological characters that included extant (24 species) as well as fossil tinamous (10 species) (Bertelli and Chiappe 2005). The main distinguishing characters between the subfamilies, in addition to the position of the nares, were the complexity of the plumage pattern on the back of adult birds, the number of scutes at the base of the toes, the natal plumage patterns, and iris color, which is brownish only in the Nothurinae (Bertelli et al. 2002). Neither of the Bertelli studies found high support for the monophyly of the Tinaminae, however. The forest tinamous formed a paraphyletic group with respect to the Nothurinae, with *Nothocercus* as sister to all other tinamous. Thus, Bertelli and Chiappe (2005) recommended eliminating the subfamily division within the tinamous.

In a study using mitochondrial markers, Porzecanski (2003) found high bootstrap support for the family Nothurinae, even though the cytochrome-*b* (Cyt-B) data were considered to be saturated at the deep distances found among tinamous. In a combined analysis of morphological and Cyt-B characters, Bertelli and Chiappe (2005) found the subfamily Tinaminae monophyletic, albeit with very low (13%) Bremer support.

The comprehensive molecular work done by Hackett et al. (2008), with 169 representative bird taxa, including two members of each subfamily within the Tinamidae (*Eudromia* and *Nothoprocta* for Nothurinae, and *Tinamus* and *Crypturellus* for Tinaminae), did find 100% bootstrap support for the Tinaminae and 97% for the Nothurinae in maximum likelihood and maximum parsimony analyses. With the same data set, but focusing on the ratites and tinamous (with *Anas*, *Gallus*, *Buteo* and *Ciconia*

as outgroups), Harshman et al. (2008) found support for the monophyly of Tinaminae but not Nothurinae, in contrast to Bertelli (2004), Bertelli and Chiappe (2005). and Bertelli et al. (2002). The *Eudromia-Nothoprocta* clade received only 66% bootstrap support. Although the bootstrap support was higher (but still less than <95%) in other analyses, Harshman et al. (2008) presented their most likely tree as a polytomy for Tinaminae (“supporting information” in Harshman et al. [2008]).

2.1.3. Taxonomy of Subfamily Tinaminae

Only three publications treat specific relations within the subfamilies. First, Bertelli et al. (2002), with the integumentary dataset mentioned above, proposed two hypotheses for the precursor of the family according to where they rooted their tree: a precursor similar to *Tinamous osgoodi*, with little feather pattern tending to more complex feather pattern, with the latest branching event forming the Nothurinae; and (2) bicolored, barred birds such as *Nothocercus*, with two evolutionary trends, one towards no pattern (such as *Crypturellus*) and one towards more complex pattern, with the latest branching event being Nothurinae. Bertelli and Chiappe (2005), using osteological data, found both *Nothocercus* and *Tinamus* to be monophyletic, but found *Crypturellus* to be paraphyletic. Bertelli and Chiappe (2005) considered *Nothocercus* to be the basal lineage, with successive branching from *Tinamus*, two *Crypturellus* clades, *Taoniscus*, a *Nothura* polytomy and, finally, Nothurinae. The combined tree of Bertelli (2004) has Tinaminae as monophyletic, with *Tinamus* and *Crypturellus* as sister taxa.

2.1.4. Taxonomy of Nothurinae

Relationships within the Nothurinae are challenging to study morphologically because of their overall similarity in size and coloration. The genera within the subfamily are relatively distinctive and include *Eudromia* (2 species), *Tinamotis* (2 species), *Rhynchotus* (2 species), *Nothura* (5 species), *Taoniscus* (1 species), and *Nothoprocta* (6 species). Of these, the only clade well-supported by consensus is that of *Eudromia* and *Tinamotis* (Bertelli and Chiappe 2005; Porzecanski 2003; Salvadori 1895). The other group generally accepted as monophyletic is *Nothoprocta*, but mitochondrial data published by Porzecanski (2003) conflicted with other studies by placing *Rhynchotus* inside *Nothoprocta* with *N. cinerascens* as its sister. The higher relationships among these clades and the other members of the subfamily have not been resolved. Bertelli et al. (2002) and Bertelli and Chiappe (2005) found *Rhynchotus* to be sister to the *Eudromia-Tinamotis* clade, which then groups with *Nothoprocta*. Basal to this larger clade are two clades of *Nothura* with *Taoniscus nanus* the most basal branch within the subfamily. For the molecular tree (Porzecanski 2003) and the combined tree of Bertelli and Porzecanski (2004), *Nothoprocta* (including *Rhynchotus*) forms a clade with *Nothura*, with *Taoniscus* basal to them. These taxa then group with the *Eudromia-Tinamotis* clade.

As I mentioned above, the monophyly of *Nothoprocta* has been challenged by a single genetic tree, using Cyt-B, by Porzecanski (2003), in which *Rhynchotus* was sister to *Nothoprocta cinerascens*, the resulting clade basal to the rest of *Nothoprocta*.

Porzecanski (2003) placed *Nothoprocta* as sister to a group containing, *Tinamotis*, and *Eudromia*. Basal to this group is *Nothura*. However, some characters put *Nothura* closer to *Nothoprocta*: they both share the presence of distal coracoidal pneumatization near to the scar of musculus sternocoracoidei, a character that, according to Bertelli and Chiappe (2005) could have been acquired by early Nothurinae (after split from *Taoniscus*) and lost at the split between *Nothoprocta* and the rest of Nothurinae. Morphologically *Nothura* differs from all other tinamous in the size and shape of the bill: *Nothura* has a short and almost straight bill.

2.1.5. Within *Nothoprocta*

Within *Nothoprocta* the morphological tree placed *N. taczanowskii* as basal (76% jackknife support), given its overall different look, than the rest of the genus (Bertelli and Chiappe 2005). The combined (morphological and mitochondrial) tree has *N. cinerascens* as basal (relative Bremer support 100) and overall bears little resemblance to the morphological tree (Bertelli and Porzecanski 2004).

2.1.6. Age of Paleognaths, Tinamidae, Nothurinae and *Nothoprocta*

The divergence of paleognath and neognath birds has been placed by “Tertiary Big-Bang” proponents (*sensu* Feduccia (2003)) as an early split in the appearance of modern bird orders starting at the K-T boundary (around 65 MYA). Given the lack of fossil records, Feduccia (2003) proposed that there is no evidence of phyletic continuity of Neornithes, including ratites, across the K-T boundary. If this is correct, then only one or (at most) a few lineages, which could have included paleognaths, can trace their origins to the Cretaceous. In a molecular clock calibrated with fossil records of penguins, Slack et al. (2006) placed paleognaths considerably earlier, in the early Cretaceous, around 100 MYA. Van Tuinen and Hedges (2001), who used several fossils to calibrate their estimates, placed the origins of Paleognaths at 100-120 MYA. The oldest neognath fossil was described by Clarke et al. (2005) and dated at 66 MYA, so the neognath-paleognath split has to be older.

The first split among extant paleognaths is thought to have been the divergence of the Tinamidae and the ratites, and has been placed in the late Cretaceous (70-80 MYA) by Cracraft (2000) and Slack et al. (2006). Slack et al. (2006) placed the divergence between *Eudromia* and *Tinamus* at about 38 to 47 MYA (Eocene), which would, by extension, represent the split of Nothurinae and Tinaminae. Bertelli and Chiappe (2005) stated that the monophyly of Nothurinae is consistent with a single event for the radiation of tinamous into open areas. They suggested that a group of fossils from the Santa Cruz

formation represents the earliest branch of the Nothurinae. This formation is also considered to predate a period of expansion of open habitats, and thus these fossils might represent the earliest tinamous inhabiting open areas, dated to the Miocene (ca. 26 MYA).

Porzecanski (2003) used fossil data to shed light on the timing of diversification within the family Tinamidae. Based on alternative calibrations of the nuclear distances, she postulated that the earliest divergences within Tinamidae occurred in the early Eocene, and that most of the subsequent diversification within the family occurred between the Oligocene and Miocene. Within the Nothurinae, Tambussi (1987) reported fossil records of *Eudromia* from the late Miocene (ca. 7 MYA), and Tambussi and Tony (1985) reported fossils for the genus *Nothura* and *Eudromia* from the upper Pliocene (4 MYA).

2.2. Methods

Mitochondrial markers are still the most commonly used markers for phylogenetic reconstruction. Several characteristics in the methodology to sequence them make them practical markers to use. Among mitochondrial markers, Cyt-B and ND2 are commonly used. However, within the last few years the use of mitochondrial DNA as a sole genetic marker has been criticized, and evidence of incongruence between mitochondrial and nuclear gene trees is now becoming documented with increasing frequency (Ballard and Whitlock 2004; Funk and Omland 2003; Ting et al. 2000). Several hypotheses have been proposed to explain gene tree discordance between mitochondrial and nuclear markers, e.g., differential lineage sorting, in which one marker retains its polymorphism through the speciation event and is randomly sorted into patterns of allelic relationships that do not match the organismal phylogeny (Avice 2000). Another cause for discordance between mitochondrial gene trees and species trees is ancient hybridization the signal of which shows up in some genes but not others.

To test for possible discordance, the inclusion of at least one nuclear marker is recommended when constructing phylogenies. CLTC is a clarathin, heavy chain (HC) that occurs in chromosome 19 of the chicken genome. It is a noncoding intron with two sections (intron 6 and intron 7) and a total of 1930 base pairs in the chicken genome, 22% of which are coding. For this study a section of 737 base pairs of intron 6 was sequenced.

An intron was considered appropriate to resolve deeper nodes, given that introns, particularly CLTC, have been found to be better suited for determining closely spaced branching events such as the base of Neoaves: Chojnowski et al. (2008) suggested that large intron datasets have the best potential to resolve relationships among avian orders, and they indicated that the utility of intron data for other phylogenetic questions should be examined.

In addition to the base pair sequence data, indels are often used in phylogenetic reconstruction. Indels are rare genomic changes that are considered to be valuable phylogenetic markers, free from a number of caveats that apply to nucleotide

substitutions (Rokas and Holland 2000). Harshman et al. (2008) found homoplasy with one 1 base pair indel but larger indels (e.g. <5 base pairs) were shown to be consistent with their overall phylogeny and homoplasy in them has proven to be highly unlikely .

The Appendix presents locality information for the 168 individuals sampled for this study. Twenty-five tissues were borrowed from the Louisiana State University Museum of Natural Science Collection of Genetic Resources (LSUMNS), 27 from other North American collections, and 103 were collected specifically for this study and are deposited at the LSUMNS tissue collection. Thirteen additional sequences were downloaded from GenBank.

Total genomic DNA was extracted with a DNeasy Kit (Qiagen, Inc.). The final extraction product was stored at -20°C until further analyses. PCRs were performed in 25 μl volumes and contained 16.4 μl dH₂O, 2.5 μl 10X buffer, 1.5 μl dNTPs (10 mM), 1 μl of each primer (10 μM), 0.1 μl *Taq* polymerase, and 2.5 μl template (~50 ng). For Cyt-B, the primers used were L14990 and H16065. Thermal amplification profiles for both mitochondrial genes were 35 cycles of 94°C (30 sec), 50°C (30 sec), and 72°C (1 min). The thermal profile of amplification for used 35 cycles of 94°C (30 sec) denaturation, 53°C (30 sec) annealing and 72°C extension (30sec).

PCR products were cleaned using a PEG purification protocol. Cycle sequencing was performed in 7 μl volumes containing 1.75 μl dH₂O, 1.5 μl buffer 5X, 1 μl primer (10 μM), 0.25 μl Big Dye 3.1 (Applied Biosystems, Inc), and 2.5 μl purified PCR product. The amount of template PCR product was varied slightly in some cases. Cycle sequencing reactions were cleaned with Sephadex and visualized on an ABI Prism 3100 Genetic Analyzer.

Sequences were imported into Sequencher 4.7 (Genecodes, Inc) and aligned visually. In some cases, alignments were performed visually using a text editor (TextWrangler). All cytochrome-b sequences in this analyses start at position 13,737 of the gene (compared to *Eudromia elegans* AF338710 from GenBank). The sequence length used in the analysis is 1048 base pairs. ND2 sequences start at position 3933 of the mitochondrial genome (compared with *Eudromia elegans* AF338710 from GenBank). The sequence length used in the analysis is 1098 base pairs. The aligned sequence length of the CLTC gene used in the analysis was 740 base pairs. A 6 base pair long region of difficult to align sequence was excluded prior to all phylogenetic analyses. Not all individuals amplified with the same ease for each gene. As a result some genes were not obtained for some of the individuals. The appendix shows individuals for which sequences of all genes were available.

Protein-coding mitochondrial sequences were translated into amino acids to verify the absence of stop codons or other anomalous residues. All phylogenetic analyses were performed using a portable UNIX version of PAUP*4.0b10 on Macintosh G5 computers with two parallel processors (Swofford 2003). Maximum likelihood and Bayesian

methods were the primary methods of phylogenetic analysis. To determine the optimal ML model for each data set (each locus plus combined), I used the Akaike Information Criterion implemented in the program ModelTest 3.5 (Posada and Buckley 2004; Posada and Crandall 1998). Using PAUP*, likelihood scores for input into ModelTest were estimated on neighbor-joining trees inferred for each data set from an uncorrected “*p*” distance matrix. The best-fit ML model (Table 1) for CLTC was TVM + Γ , and for Cyt-*b*, ND2, and the combined data set was best model was GTR + Γ + INV (Swofford et al. 1996). A PAUP* search was first performed under the “minimum evolution” criterion of Rzhetsky and Nei (1987) (originally described as “LS-length” by Kidd and Sgaramella-Zonta (1971) using maximum-likelihood genetic distances.

Table 1. Parameters for maximum-likelihood finite-sites DNA substitution model

	Maximum-likelihood			
	ND2	Cyt- <i>b</i>	CLTC	Combined
# bp	1098	1048	735	2881
$-\ln L$	14953.3	11474.9	4217.2	29348.1
r_{AC}	0.185	0.273	1.109	0.823
r_{AG}	9.194	9.468	5.622	7.069
r_{AT}	0.596	1.089	0.785	1.806
r_{CG}	0.539	0.499	1.938	0.611
r_{CT}	4.219	6.709	5.622	10.784
α	0.784	0.795	1.348	0.593
p_{iv}	0.0313	0.368	-	0.270
freq(A)	0.335	0.323	0.296	0.309
freq(C)	0.374	0.391	0.186	0.289
freq(G)	0.053	0.058	0.201	0.140
freq(T)	0.238	0.228	0.317	0.263

Using the optimal ML model inferred from the AIC tests, Bayesian analyses were performed on each data set using the program MrBayes (version 3.0b4, Huelsenbeck and Ronquist 2001). Because the TVM + Γ substitution model is not implemented in MrBayes, I replaced it with GTR for the analysis of CLTC. On the combined data set, the data were partitioned by gene and analyzed under the best-fit ML model for each gene. Uniform interval priors were assumed for the parameters, except for base frequencies, which were assigned a Dirichlet prior (Huelsenbeck and Ronquist 2001). Four heated chains were run for 2.0×10^6 generations and sampled every 1000 generations. After visually examining burn-in plots from each run using Tracer

(Rambaut and Drummond 2003) to insure the chain had reached stationarity, trees from the first 100,000 generations were discarded, with the remaining trees used to estimate posterior probabilities of tree topology and other ML parameters. Three independent runs with different random seeds were performed to ensure the posterior probabilities were stable.

2.3. Results and Discussion

2.3.1. Indels in the Intron CLTC Section 6

The nuclear gene used for this study a non-coding intron, contained many indels, (table 2). Some of these indels have important phylogenetic implications because they occur across several species. None show a pattern that conflicts fundamentally with accepted basal clades. One important, large indels (28 base pairs), groups all *Nothoprocta* with *Rhynchotus* and *Nothura* and excludes *Tinamotis* and *Eudromia*. These latter have two independent indels that group them together. This partitioning coincides exactly with von Boettischer's (1934) classification of the current Nothurinae into Rhynchotinae and Eudrominae.

A rather long indel (10 base pairs), groups *N. cinerascens* with *N. pentlandii*, *N. patriciae* and *N. taczanowskii*. This grouping contradicts current phylogenies (where either *N. taczanowskii* or *N. cinerascens* are outgroups to the rest of *Nothoprocta*), but more importantly, does not include the subspecies *oustaleti* of *N. pentlandii*. Within the Tinaminae, the only large indel (118 base pairs) groups all *Crypturellus*.

2.3.2. The Subfamily Partition

As discussed in the Introduction, the subfamily partition (Tinaminae-Nothurinae) has been long debated. In this study, all three genes independently had problems recovering the monophyly of these groups. Analysis of the nuclear CLTC gene placed the Nothurinae inside the Tinaminae and closest to *Nothocercus*. In the Cyt-B analysis, the *Tinamotis-Eudromia* clade fell out of the Nothurinae and formed a polytomy with the rest of the tinamous at the root of the tree (*Pterocnemia*). Analysis of ND2 placed the Nothurinae close to the *Tinamus-Crypturellus* clade. The incongruence among genes suggests some difficulty in recovering deep nodes that might have diverged in relatively short periods of time. The combined analysis (Fig. 2) of all three genes recovered reciprocal monophyly with 100% Bayesian support. More nuclear genes than used in this study and better taxon sampling will needed to further confirm this nodes.

Table 2: Indels in the CLTC intron 6 and species in which they occurred. Only indels included in all individuals of the species are considered in this table

Indel length (# of base pairs)		2	1				*	1										
		8	5	0	1	1	1	4	8	1	4	1	1	3	2	6	1	4
Indel position		2	4	1	1		5	4	3	4	5	5	4	5	4	5		5
Taxa	n=	6	0	9	4	6	3	9	1	6	0	7	1	0	8	1	4	6
		5	5	3	3	3		7	7	7	1	4	3	2		2	6	1
<i>Nothoprocta ornata ornata</i>	13	■	■															
<i>Nothoprocta ornata branickii</i>	13	■	■															
<i>Nothoprocta ornata</i> ssp. nov.	3	■	■															
<i>Nothoprocta curvirostris</i>	4	■																
<i>Nothoprocta p. oustaleti</i>	15	■																■
<i>Nothoprocta p. pentlandii</i>	2	■		■														
<i>Nothoprocta p. patriciae</i>	10	■		■														
<i>Nothoprocta perdicaria</i>	7	■		■														
<i>Nothoprocta taczanowskii</i>	1	■		■							■							
<i>Nothoprocta cinerascens</i>	3	■		■														
<i>Rhynchotus rufescens</i>	1	■			■	■							■					
<i>Nothura darwinii</i>	4	■			■	■												
<i>Tinamotis pentlandii</i>	2						■	■							■			t
<i>Eudromia elegans</i>	2						■	■						■				
<i>Crypturellus bartletti</i>	1								■									
<i>Crypturellus soui</i>	2								■									
<i>Crypturellus tataupa</i>	1								■									
<i>Crypturellus undulates</i>	1							■	■	■								
<i>Crypturellus atrocapillus</i>	1							■	■	■								
<i>Crypturellus parvirostris</i>	1								■									
<i>Crypturellus obsoletus</i>	2								■									
<i>Nothocercus julius</i>	2																	■

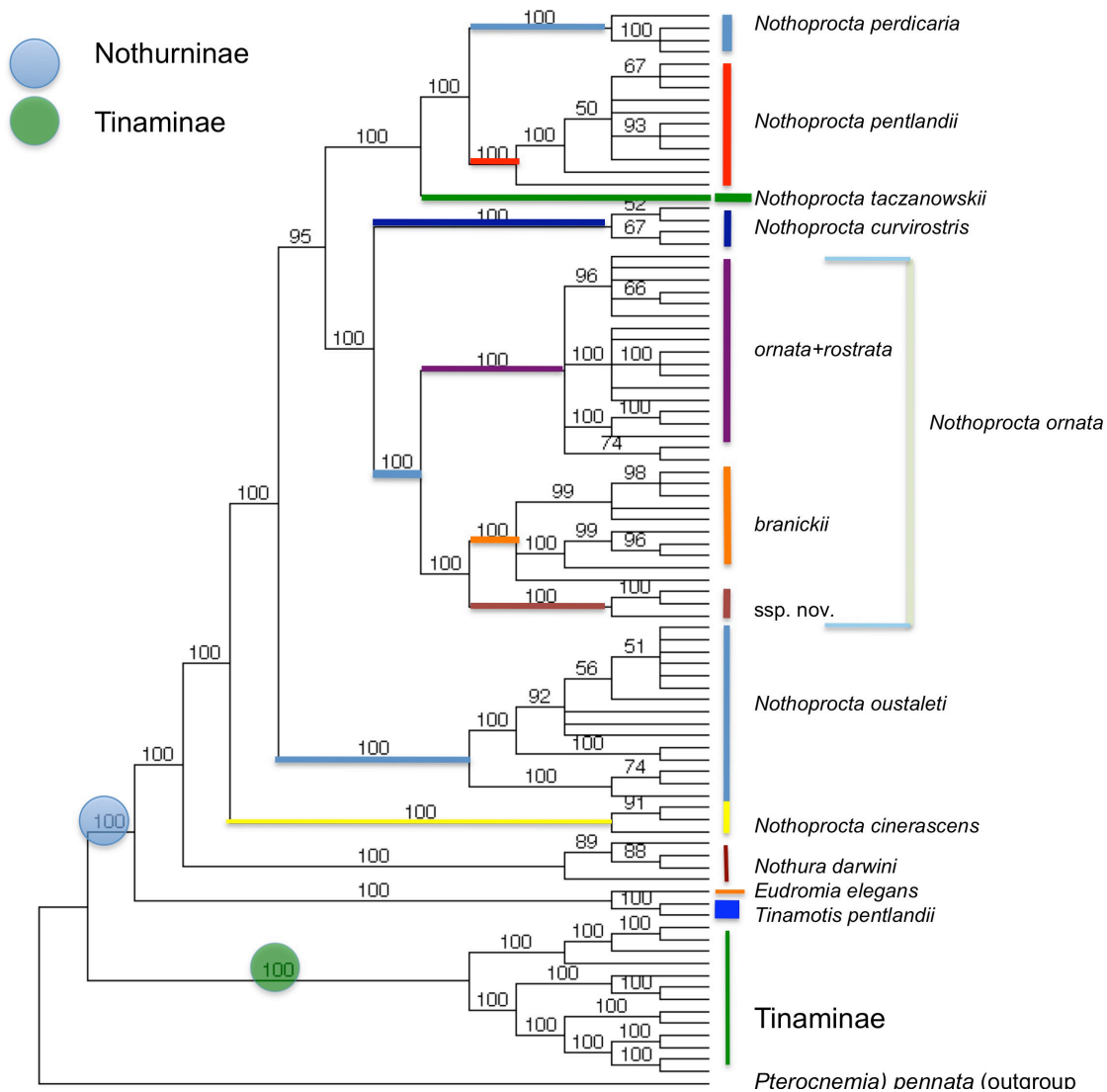


Figure. 2 Phylogeny based on Bayesian analysis. Values are posterior probability (x100).

All higher-level clades in the combined Bayesian tree have posterior probabilities of 1.00 (shown at the generic level in Fig.2). Within the Tinaminae subfamily, the three traditional clades, the genera *Crypturellus* (supported in addition by an indel of 118 base pairs), *Tinamus*, and *Nothocercus* are monophyletic using any combination of these data, contrary to the results of Bertelli et. al. (2005), who found that *Crypturellus* was a basal and paraphyletic. Within the Nothurninae, the clade *Eudromia* and *Tinamotis* (the Tinamotidinae of Salvadori [1895]) always were sister genera. However, the position of this pair of genera lacked consensus. Generally they were placed as basal in the Nothurninae, but Cyt-B alone, and Cyt-B combined with nuclear CLTC, placed them as basal to all other tinamous. The final combined Bayesian tree puts *Eudromia* and

Tinamotis as basal to Nothurinae. The only other inconsistency with the Nothurinae is based on the difficulty in placing the genus *Rhynchotus*. Mitochondrial genes analyzed using neighbor-joining (not shown), maximum likelihood, and simple evolutionary models group *Rhynchotus rufescens* with *Nothoprocta cinerascens*, the same as Porzekanski (2003), with high bootstrap support, either as the basal clade to *Nothoprocta* (ND2), or well inside (Cyt-B). More parameterized models of evolution (e.g., for Cyt-B), recover the *Nothoprocta* monophyly but make *Rhynchotus* basal to *Nothoprocta*, and *Nothura* basal to these. The nuclear gene alone puts *Rhynchotus* as sister to *Nothura* and basal to *Nothoprocta*. The closeness of *Nothura* and *Rhynchotus* is supported by two independent indels of size one base pair, and the closeness of these to genera to the rest of *Nothoprocta* is supported by an indel of size 28 base pairs. This would suggest that the strong sister relationship of *Nothoprocta cinerascens* and *Rhynchotus rufescens* in mitochondrial genes is based on long branch attraction. Simple evolution models have difficulty handling the saturation level of these particular deep branches.

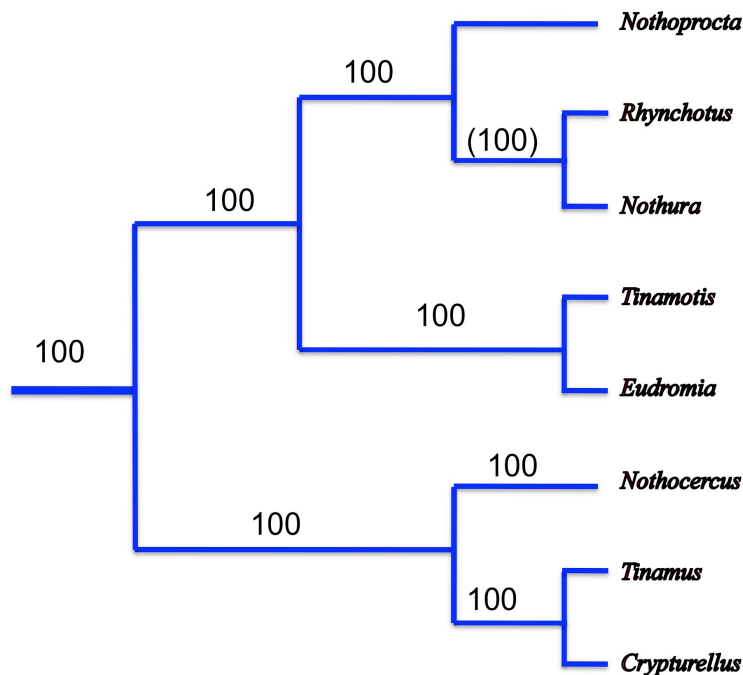


Figure 3. Tinamou phylogeny collapsed to the genus level. Samples of *Taoniscus* were not available. Values show Bayesian posterior probabilities (x100). In parenthesis probability not based on all three genes.

2.3.3. Within Genera Relationships

As seen in Fig. 4., *Nothocercus nigrocapillus* and *N. bonapartei* are sisters, consistent with morphology (Bertelli et al. 2002). This clade represents a geographic split in the Marañon depression with *N. nigrocapillus* to the north and *N. bonapartei* to the south.

The more widespread *N. julius* is from a higher elevation and is probably elevationally parapatric to the two species in this clade.

Crypturellus is the most diverse genus in the Tinamidae and species limits within the genus taxonomy remains uncertain. As mentioned previously all *Crypturellus* sampled for CLTC in this phylogeny have a 128 base pair indel in the nuclear gene. Even though the species sampling was weak, some congruent groupings provide some idea of the relations in the genus. Two well-supported groups are revealed within *Crypturellus*. One consists of *C. parvirostris* and *C. tataupa* as sisters, with *C. obsoletus* sister to this pair; this grouping is consistent with morphological similarity (Bertelli et al. 2002). The other consists of *C. atrocapillus* and *C. undulatus* (supported by three indels size 1,4,4), sister to *C. soui* and *C. bartletti*. Three indels of base pair size 1,4 and 4, occurs in these two species. The group of these latter four species was paraphyletic in the Bertelli et al. (2002) phylogeny. However resolving this group will require much better species (and subspecies) sampling.

In *Tinamus*, the sister relationship between *T. tao* and *T. solitarius* is well supported. Less supported, is a sister relationship between *T. major* and *T. guttatus*. *Tinamous osgoodi*, missing from my analysis, was placed outside *Tinamus* by Bertelli et al. (2002).

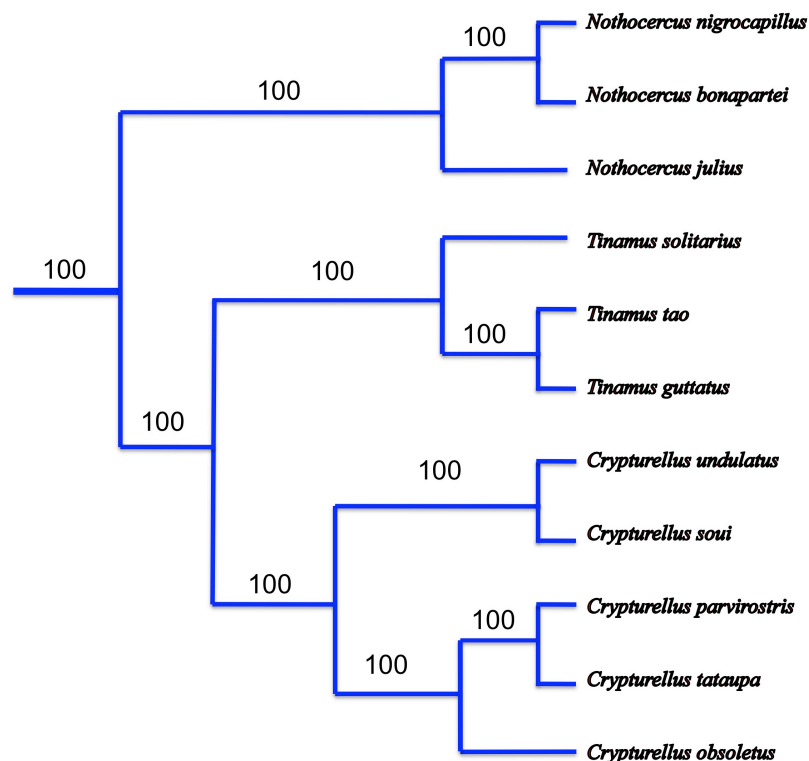


Figure 4. Phylogeny of the Tinaminae with posterior probabilities (x 100)

2.3.4. The Phylogeny of *Nothoprocta*

My data produce a substantially different phylogeny (fig. 5) from any other proposed for *Nothoprocta*. The most divergent result is the paraphyly of *Nothoprocta pentlandii*. The clade composed of *N. pentlandii* (races *pentlandii* and *patriciae*, and allegedly *doeringi* and *mendozae*) with *N. perdicaria*, is sister to *N. taczanowskii* in every recovered tree with high (1.00) Bayesian posterior probability. The group of *N. pentlandii oustaleti* (with races *fulvescens* and allegedly *ambigua* and *niethammeri*) is not even basal to this group, and therefore needs to be considered a different species by any phylogenetic criterion. As seen in section 2.3.1., (table 2) this split is also supported by indels. Although the morphological tree of Bertelli et al. (2002) did not recover the clade (*N. pentlandii*, *N. perdicaria*, *N. taczanowskii*), the combined tree of Bertelli & Porzekanski (2005) did find *N. pentlandii* and *N. taczanowskii* to be sisters, but put *N. perdicaria* outside the group, sister to *N. curvirostris*. They lacked samples of *N. p. oustaleti*. The next branch to join the group is another clade with strong support that has not previously been detected: the *N. ornata* -*N. curvirostris* clade. This is also well supported in the complete gene consensus tree (0.99 Bayesian posterior probability).

The CLTC gene alone, and in combination with Cyt-B, put *N. cinerascens* as sister to that group. The *N. oustaleti* group (nominate *oustaleti* and *fulvescens*) appears either as basal to all *Nothoprocta* besides *N. cinerascens*, or basal to all *Nothoprocta*. At the subspecific level three subspecies groups are also differentiated: *N. ornata branickii*, *N. o. ssp. nov.*, and the nominate *ornata* + *N. o. rostrata* clade.

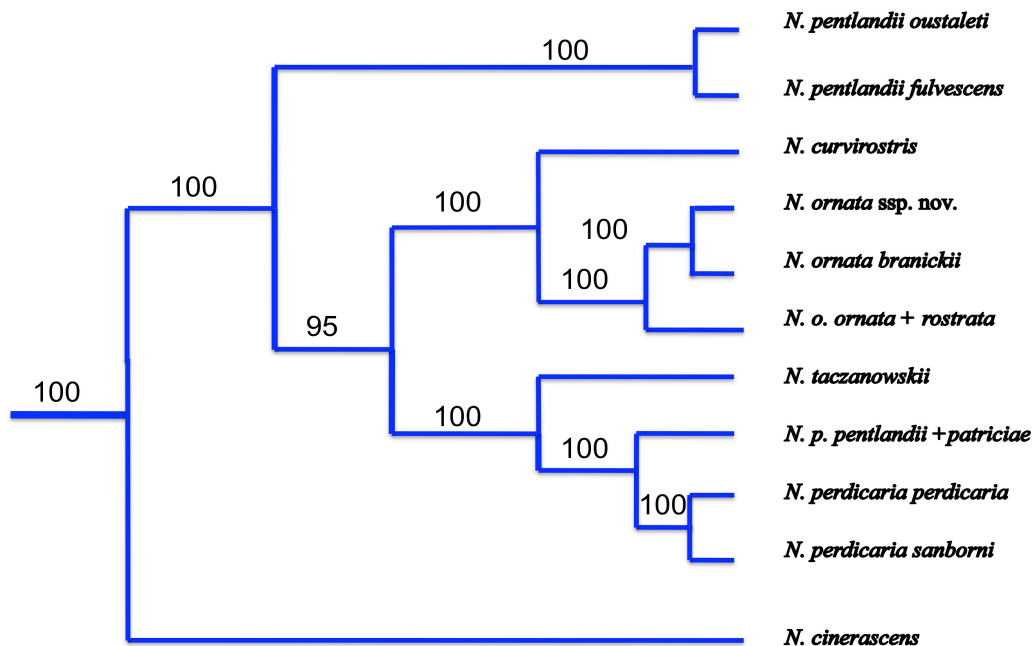


Figure 5. *Nothoprocta* consensus tree, with three genes (ND2, Cyt-B and CLTC), for a Bayesian analysis. Numbers above nodes are Bayesian probability scores (x100).

CHAPTER 3. THE DISTRIBUTION PATTERNS OF *NOTHOPROCTA* SPECIES AND SUBSPECIES, AND IMPLICATIONS FOR TAXONOMY

3.1. Introduction

Distribution past and present provides important information for understanding the evolutionary history of a group of related species. It is important to recognize that the current pattern of distribution is the only one that can be measured precisely; however, sampling is seldom sufficiently thorough to map accurately a species' true distribution. Proper geographic sampling combined with multivariable niche-modeling is a powerful approach that allows estimating true current distributions from known localities (Ortega and Peterson 2008; Peterson 2001; Phillips et al. 2006).

3.1.1 Why Niche Modeling?

To predict the presence of a species in an area, we would need to understand its dynamic response to the environment. This requires a considerable volume of complex data on both the organism and the environment. Given limited information, static-statistical distribution modeling has been developed as an alternative method for predicting the potential distribution of a species.

Niche modeling is not really a new concept. For a long time, distributions have been mapped manually using presence-absence information for a species and then extrapolating to the area considered suitable for the species, based on knowledge of geography and habitat availability. Understandably the number of variables, as well as the mental algorithms used to rank their importance and determine likelihood of occurrence, had to be kept simple. With the availability of increasingly detailed global environmental data, the increased power of computer analyses, and the advent of new statistical and GIS techniques, the statistical prediction of species' distribution has become a powerful tool used increasingly in conservation (Elith et al. 2006; Fielding and Bell 1997; Young 2007), ecology (Ortega and Peterson 2008), and evolution (Graham et al. 2004).

The statistical integration of the species' occurrence data and the environmental variables associated with those points of occurrence is expected to summarize useful niche dimensions of the species. Therefore, a niche-based model should represent an approximation of a species' ecological niche in the environmental dimensions examined (Phillips et al. 2006) and can be used to predict the potential geographical distribution of the modeled species. Traditionally in ecology, fundamental niche is distinguished from realized niche. The first is the set of environmental conditions that allow long-term survival of the species, whereas the realized niche is the subset of the fundamental niche

that the species actually occupies (Hutchinson 1957). Although some of the variables that could restrict the fundamental niche to the realized niche (e.g. human habitat alteration, biotic interactions, competitive exclusion, etc.) could be specifically added to the environmental layers, generally they are not available and thus not used. Therefore, niche models predict the fundamental niche of a species, despite the fact that occurrence data that feed the model can only come from the realized niche, namely the species' current distribution. Both, actual and potential distribution, are important when analyzing distribution patterns.

3.1.2. Sampling Biases

A potential problem with static models is the assumption of population equilibrium between the environment and observed species patterns. This type of model is unable to cope with non-equilibrium situations. Given some aspects of the natural history of tinamous and the antiquity of the lineage, an assumption of equilibrium at the coarse scale seems reasonable. At the local scale, however, special care must be taken when interpreting data because *Nothoprocta* populations fluctuate dramatically, apparently tied to precipitation phenomena (pers. obs.). The large population increases after good rainy seasons could produce sink populations in marginal areas. In a similar manner, local migration to artificial food sources such as agricultural areas outside their natural habitat or beyond their natural elevation could create problematic presence data.

Another problem with the use of specimen records is sampling bias. Rather than a random sample of a species' distribution, presence (or absence) records might be biased by field logistics such as roads and other access conduits (Reedy and Davalos 2003) and autocorrelation among those sites that are accessible. Given the scale of the modeled distributions, such biases are probably minor, except perhaps for taxa with small distributions, such as *Nothoprocta taczanowskii*, for which there are few known localities and for which access to its habitat is limited. Bias can also be introduced during my sampling by not collecting in a predetermined grid but rather in sites subjectively considered the best for *Nothoprocta* in a given area, thus leaving some area unsurveyed. Given the area sampled and the time available, sampling in a predetermined grid was not feasible.

A final problem that should be mentioned is the use of specimen records from older locality data that tend to be less accurate and thus may introduce error into data used for niche modeling. In fact, as noted later, localities that fell outside predicted distributions were often from such older locality records.

3.1.3. Model Used: MAXENT

Maxent is a general purpose machine-learning method with a simple and precise mathematical formulation; a number of its features make it well-suited for species distribution modeling (Phillips et al. 2006). It is a presence-only model that has been shown to perform among the better than 16 other such models (Elith et al. 2006), including widely used ones such as Garp (Phillips et al. 2006). For small sample sizes in particular, it performs better than more established models such as Bioclim and Domain (Hernandez et al. 2008; Hernandez et al. 2006).

For Maxent, presence data represent a sampling from the modeled distribution that is used to calculate an empirical average of the environmental conditions. The predicted presence of the species will depend on the match of this empirical average with the values of the environmental variables at each pixel. Maxent estimates a species' probability distribution by finding the probability distribution of maximum entropy (i.e. most spread-out or closest to uniform), subject to the constraint of a match of empirical and real data of environmental layers (Phillips et al. 2006). It uses algorithms developed for other sciences, and always converges on the optimal (maximum entropy) probability distribution (Phillips et al. 2006). Its use of presence-only data could be viewed as an advantage, because the validity of also using absence data requires confidence that the species was not missed in a survey. Another advantage of Maxent is that the output is given as a continuous probability of occurrence, which allows flexibility in choosing the threshold for converting the probability map to the final product, a binary presence/absence map.

A disadvantage of Maxent is that despite using rather straightforward mathematical techniques, the mechanism by which the variables interact to construct the model is difficult to interpret biologically. Therefore, Maxent results are evaluated based on the fit of the predicted area to known localities, rather than on the mechanism in which the variables produce the output. However, this is also true for many of the more advanced models.

3.1.4. Environmental Variables

Distribution modeling is based on the environmental variables for the potential area to be modeled. These are not easy to produce, because they must meet several prerequisites, starting with uniformity in coverage and resolution. Because climatic stations are few, particularly in the Andes, bioclimatic maps are developed by elevation-sensitive spatial interpolations of climate station data. This introduces spatial uncertainties, for example because of interpolation error and lack of a good geographic sampling. Nevertheless, they represent the only available data for this type of large-scale modeling. In contrast, available digital elevation models (Bates and Demos 2001) tend to be relatively accurate. Thus, predictive vegetation models developed for mountainous terrain are based partially

or even completely on topographic factors (Brown 1994; Fischer 1990; Moore and Noble 1991).

Implicit ecological assumptions in the variables used for modeling (Phillips et al. 2006) require careful selection of variables. Mackey and Lindenmayer (2001), who pointed out that not all variables are effective at the same scale, defined three scales at which each type of variable was assumed to work best: climatic at “global” scales, vegetation at “meso” scales, and topographic at “topo” scales. In the Andes, climatic variables vary strongly over short distances because of complex topography, and they are highly correlated with elevation. Therefore, in the Andes these climatic variables are of meso or topo scale rather than global.

Some authors (Austin 1980; Austin 1985; Austin et al. 1984; Austin and Smith 1989), define three types of ecological gradients: (1) “Resource” (nutrients, water, light, plants, food); (2) “Direct” (temperature, pH); and (3) “Indirect” (slope, aspect, elevation, topographic position, habitat type, geology). “Indirect” variables are most easily measured and are the ones typically used in niche modeling because of their good correlation with observed species patterns. Particularly in the Andes, “indirect” topographic gradients are strongly correlated with “resource” and “direct” gradients (e.g., temperature). One drawback of using “indirect” parameters is their limited geographical applicability, because the same topographic position in two different regions can have different combinations of “direct” and “resource” gradients.

Because Maxent produces a probability of occurrence for each pixel, one has to decide the threshold probability level above which the species is predicted to be present. Many methods have been proposed to determine thresholds (Fielding and Bell 1997; Freeman and Moisen 2008; Liu et al. 2005; Manel et al. 2001), and the lack of an objective way to set a threshold is a drawback (Phillips et al. 2006). This problem is particularly acute with presence-only models, in which predictability of absence cannot be tested without bias, because those are chosen randomly from the background.

3. 2. Methods

3.2.1. Data Sources

3. 2.1.1. Overall *Nothoprocta* Distribution

The overall distribution of the genus *Nothoprocta* covers an area of about 3000 km² (see fig. 6) and is restricted to mostly open habitats. Although some species or subspecies reach low elevations, all populations are near the Andes. In particular, that part of the Andean cordillera with continuous areas above 4000 m coincides well with the core of the distribution of the genus (from latitude 0° to 40° N, and longitude 57 to 81 W.)

The basic unit for determining distributions, manually or by niche modeling, is reliable georeferenced points of the species' presence. Specimen localities were taken initially from specimen labels. The mapping of those points in combination with preliminary niche modeling generated overall distributions that were then used to plan further field sampling. Given the extent of the distributions, this could not be done for all species or for all geographic areas that needed confirmation of presence.

3. 2.1.2 Data Collection

Of 964 specimens, 724 provided useful locality data for 407 unique localities, the ones used for niche modeling. Georeferenced locations for 307 localities were taken directly from museum specimens, or georeferenced by using gazetteers (Paynter 1988; Paynter 1989; Paynter 1992; Paynter 1993; Paynter 1995; Stephens and Traynor 1983), 1/100 000 maps, or Google Earth. I collected specimens and sight records at an additional 100 localities, all with relatively precise (± 20 m) geographic positions. These were the points where the bird was detected by a pointing dog before flushing or where an undisturbed bird was seen by me or other experienced observers. As seen on Fig. 6, they are highly concentrated in Peru.



Figure 6. Map of georeferenced record data used for this study. Gray dots represent museum or literature records, blue dots are LSUMZ specimen records from prior to the study, and red dots represent records collected specifically for this study.

Table 3: Unique locality data used for niche modeling for each species.

Species of <i>Nothoprocta</i>	Total localities	Museum specimen localities	New localities from this study
<i>ornata</i>	136	90	46
<i>curvirostris</i>	38	19	14
<i>cinerascens</i>	77	76	2
<i>oustaleti</i>	61	29	32
<i>pentlandii</i>	65	62	3
<i>perdicaria</i>	22	20	2
<i>taczanowskii</i>	8	7	1
TOTAL	407	307	100

3. 2.1.3. Data Reliability

Each georeferenced position was assigned a rather arbitrary confidence value of 10, 50, 80, or 100, depending on the expected accuracy of the position. The scale of 10, 50, 80, and 100 has no particular meaning and should be seen as discrete qualitative variables. It started as a subjective % confidence in a coordinate and is a reduction of a once broader range of values. Localities that referred only to a major city only were discarded, but for towns, proximity to the town was assumed, but a low confidence value (10) was assigned. The same value (10) was given to localities found in the gazetteers but for which variation in the names left some doubt about the correct interpretation of the locality. A value of 50 was given for good matches between label data and gazetteers or maps, but the specific site was uncertain. A value of 80 was given to recently collected specimens for which the coordinates were taken by a collector unknown to me; these coordinates typically refer to a specific locality from which specimens may have been collected as far away as 1 km. A confidence value of 100 was given to specimen localities gathered during this study, for which GPS readings were taken within 20 m of where the bird was seen.

3.2.2 Environmental Variables

3.2.2.1 Variable Definition

In niche modeling, variables are raster layers that need to be standardized so that they all cover the exact same area and have the same resolution (pixel size). The first step for defining the variables was to define the geographic area to be covered by the models. This was done by using all unique data points for *Nothoprocta* and adding enough surrounding area as to make sure to encompass all potential habitat. This included all of Ecuador, Peru, Bolivia, Chile, most of Argentina, and part of Paraguay. The second step

was to find environmental variables that would cover that area. Three types of variables are typically used and publicly available for large scales: climatic, topographic, and vegetation.

Climatic variables available at the WORLDCLIM website were used. These have been processed from analyses of climatic data from the 1950 to 2000. Most are based on temperature (maximum, minimum, and mean) and monthly precipitation. As a result of various combinations of those, 19 variables are available (table 4). Four topographic variables, also available at WORLDCLIM, were obtained from calculations from the Digital Elevation Model (Bates and Demos). Using the MODIS GLCF images, a percent coverage for each of the following vegetation types was initially calculated: herbs, bare ground, and trees in three individual layers.

Table 4. Source for the environmental variables before standardization.

Variable	Source	Resol.
Climatic	WORLDCLIM http://www.worldclim.org/current.htm	1 km
Topographic	WORLDCLIM http://www.worldclim.org/current.htm	1 km
Vegetation	Global Land Cover Facilities MODIS http://glcf.umiacs.umd.edu/data/modis/vcf/data.shtml	500 m

Because most of these variables have been constructed from other variables, autocorrelation is expected. To minimize autocorrelation, my final selection included variables of all three types. I also tried to use that have biological meaning to facilitate interpretation.

3.2.2.2. Final Selection of Variables

After 28 variables had been standardized for the area and to the same resolution (1 km² pixel size), I decided to use the three topographic variables (given their relative accuracy and assumed importance in Andean topography), the vegetation layer on herbs, and three climatic variables. I used the following criteria to select those three climatic variables: (a) Relevant spatial structure. To be useful, a variable had to show geographic variation within the distribution of the *Nothoprocta* (this had to be true for all variables, of course); (b) Low autocorrelation. A correlation matrix using Pearson's index was constructed (appendix) to exclude climatic variables that were highly autocorrelated (i.e., Pearson coefficient > 0.05) with other variables, including the topographic and vegetation variables. This first selection left 12 variables; (c) For the final selection, I discarded an

Table 5. Final variables used for the environmental envelope.

Type = type of variable: Clim=climatic, Topo= topographic, Veg=Vegetation. Shaded rows highlight the seven variables used in all models.

Type	Name of variable	File name	Units	Source
Clim	Mean annual temperature	BIO1	°C x 10	Worldclim
Clim	Mean daily range (monthly mean(max T° - min T°))	BIO2	°C x 10	Worldclim
Clim	Isothermality (mean daily T° range/annual T° range) x 100	BIO3	-	Worldclim
Clim	Seasonality of T (standard deviation x 100)	BIO4	-	Worldclim
Clim	Maximum T° of the hottest month	BIO5	°C x 10	Worldclim
Clim	Minimum T° of the coldest month	BIO6	°C x 10	Worldclim
Clim	Annual T° range (BIO5-BIO6)	BIO7	°C x 10	Worldclim
Clim	Mean T° of the wettest trimester	BIO8	°C x 10	Worldclim
Clim	Mean T° of the driest trimester	BIO9	°C x 10	Worldclim
Clim	Mean T° of the hottest trimester	BIO10	°C x 10	Worldclim
Clim	Mean T° of the coldest trimester	BIO11	°C x 10	Worldclim
Clim	Annual precipitation	BIO12	Mm	Worldclim
Clim	Precipitation of the wettest month	BIO13	Mm	Worldclim
Clim	Precipitation of the driest month	BIO14	Mm	Worldclim
Clim	Seasonality of precipitation (coefficient of variance)	BIO15	-	Worldclim
Clim	Precipitation of the wettest trimester	BIO16	Mm	Worldclim
Clim	Precipitation of the driest trimester	BIO17	Mm	Worldclim
Clim	Precipitation of the warmest trimester	BIO18	Mm	Worldclim
Clim	Precipitation of the coldest trimester	BIO19	Mm	Worldclim
Clim	Ombrothermic Index	Bio20		Derived from T° & pp
Topo	Elevation above sea level	alt	M	Worldclim
Topo	Slope	Slope	degrees	derived from elevation
Topo	Aspect (orientation)	Aspect	degrees	derived from elevation
Topo	Relative position of a point on a hillslope (valley bottom, toe slope, slope and ridge)	Tono-scale	-	derived from elevation
Veg	Percentage of herbs covering the ground	herb.	%	MODIS
Veg	Percentage of trees	Tree2001_g	%	MODIS
Veg	Percentage of herbs	Herb2001_g	%	MODIS

additional 5 climatic variables, with similar correlation patterns, by using an “ecological relevance” criterion that gave priority to presumably more-relevant variables. Knowing which variables are ecologically relevant to *Nothoprocta tinamous* can only be weakly inferred from the meager data available on the biology of the genus. The final seven variables were not used to draw conclusions concerning their individual effects on tinamous, so the subjective nature of this last step had no impact on the results of the modeling, but was designed to make the climatic layers as interpretable as possible.

Table 6. Rationale for selecting the final variables and their ecological relevance.

Variable	Value	Rationale
Alt	9	Elevation can be measured precisely. <i>Nothoprocta</i> distribution in Andes strongly associated with elevation. Other variables including climatic ones are derived from elevation.
Slope	9	Predator-escape strategy of <i>Nothoprocta tinamous</i> is mostly downhill escape flights, for which slope might be important; see Barrio (2004).
Herb	8	Because <i>Nothoprocta</i> restricted to open habitats, presence of herbaceous vegetation should be a good habitat indicator.
Bio11	8	Mean temperature of the coldest trimester could be a good predictor excessive thermal stress.
Asp	7	Orientation of a slope has microclimatic implications because of length and time of day ground exposed to sun.
Bio4	7	Temperature seasonality should predict the range of extreme conditions
Bio19	7	Precipitation of coldest trimester is another measure of extreme conditions. At high elevations, this should indicate the presence of snow. At low elevations, this is an index of dryness, because the coldest trimester is typically in the dry season.

3.2.3 Determining the Threshold Probability of Occurrence

As a first step the Receiver Operating Curve (ROC) and Area Under the Curve (AUC) output from Maxent were checked for each model for problems with the models, such as the behavior of their precision errors. A ROC curve without a curvature would represent bad discrimination of true positives (predicted area with records) and true negatives (unpredicted area with known absence). An AUC of 0.5 or less indicates random discrimination. The better the model discriminates the predictions of presence and absence, the larger the AUC, conceivably up to 1 in a perfect model. The use of pseudo negatives, given the lack of negatives in the Maxent models, means that values of 1 cannot be achieved. To evaluate the importance of each variable, Jackknifing was performed by deleting one variable at a time and rerunning the model to monitor the impact of the missing variable. If the model was considered to be acceptable given its

ROC and AUC curves and jackknife results, then the selection of a threshold probability of occurrence was the next step.

I followed the manual procedure used by (Young 2007) for choosing the threshold by increasing the threshold progressively to the highest possible value that minimizes the number of presence records and minimizes the areas of known overprediction. However, rather than setting a fixed number of unwanted false negatives, the decision to accept the threshold depended on the precision of that point. If the false negative had a confidence value of 10 or 50 (see section 3.2.1.3), then it was ignored for a decision, particularly if it was close to the predicted area. Points with a confidence of 80 or 100, however, were never left out without considering a problem in the threshold.

These models were run for each species and its subspecies independently, as well as with some combination of taxa that were known to be closely related. The model representing the final species could be chosen from the model of the species as a whole, or as an aggregate of its subspecies (or of a combination of these). To choose which model (species or subspecies models) was the best, the criteria was to minimize “interspecific false positives”. These false positives were defined as those points where a different species (or subspecies) occurred in the predicted modeled distribution (see table in appendix). Because the model could be correctly predicting the distribution range in an area of another species (as unused fundamental niche), this is a somewhat biased way to look at error. However, if the area “over-predicted” is correct, a reduction in the threshold should not eliminate that area without creating false positives. Because the false positives are the main criteria used to choose a threshold, such overprediction could never be avoided, as expected, for example, under condition of interspecific competition.

All models performed well, with all AUC curves above 0.95. Jackknifing of variables showed that some contributed little to the model. Models rerun without those variables resulted in very similar distributions, but for consistency all seven variables were retained in each model. The variables identified as not important varied among models without an apparent pattern, so I decided to run all models with all seven environmental variables for consistency.

3.3. Results

3.3.1. General Distribution Pattern of *Nothoprocta*

Published distribution maps and range statements of *Nothoprocta tinamous* (Cabot 1992; Davies 2002) portray their distributions as independent and do not discuss overall patterns. However, all species except *N. perdicaria* are parapatric with at least two

congeners (Table 7). A high degree of parapatry thus characterizes species' distributions in the genus.

Table 7. Number of parapatric congeners for each *Nothoprocta* species.

Species (code)	Number of parapatric congeners
<i>Nothoprocta ornata</i> (Nor)	5 (Ncu, Npe, Nou, Nta, Nci)
<i>Nothoprocta curvirostris</i> (Ncu)	3 Nor, Nou, Nta
<i>Nothoprocta oustaleti</i> (Nou)	3 Nor, Ncu, Nta
<i>Nothoprocta taczanowskii</i> (Nta)	3 Nor, Ncu, Nou
<i>Nothoprocta pentlandii</i> (Npe)	2 Nor, Nci
<i>Nothoprocta cinerascens</i> (Nci)	2 Nor, Npe
<i>Nothoprocta perdicaria</i> (Npr)	0

Although Fig. 7 also suggests some sympatry, no more than one species has ever been collected at the same locality. This was also my personal experience in the field. The apparent overlap is an artifact of the meandering nature of elevation curves. A locality for one species might appear to be in between those of another species or embedded in

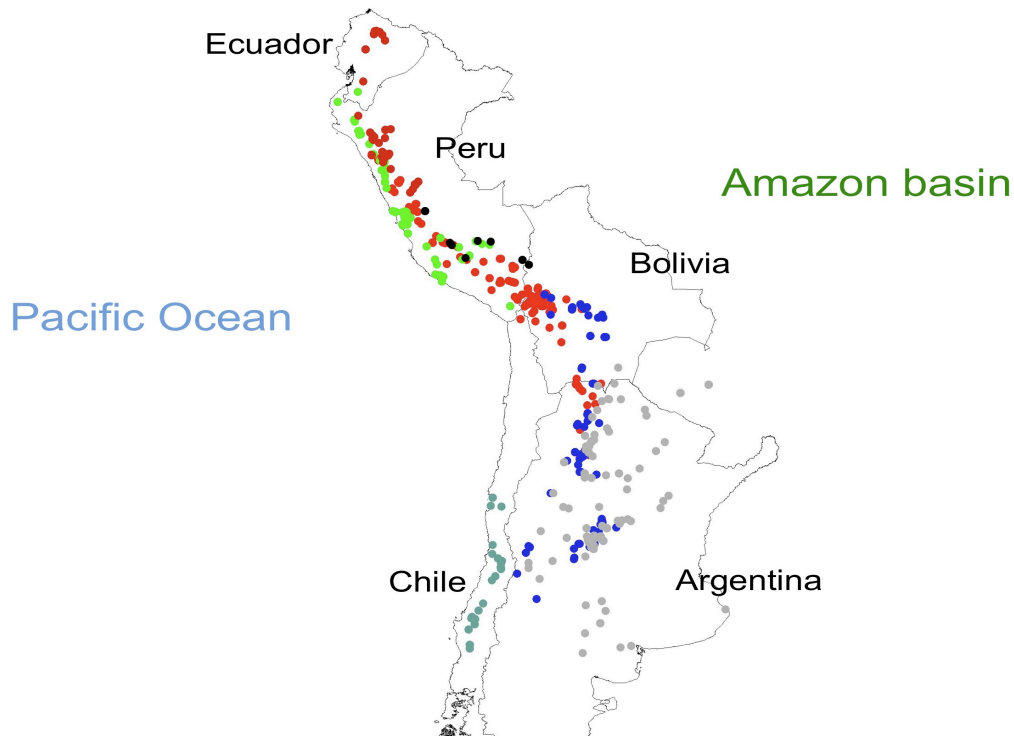


Figure 7. *Nothoprocta* species records used for this study. From north to south: brown=*curvirostris*, green=*oustaleti*, red=*ornata*, black=*taczanowskii*, blue=*pentlandii*, gray=*cinerascens*, blue-green=*perdicaria*.

another species' distribution, but in every case where two species come very close, they differ in elevation or habitat. The steepness of slopes in much of the Andes means that localities closer than 1 km may differ by more than 500 m in altitude. In dpto. La Libertad, for example, up to three species (*N. oustaleti*, *N. curvirostris*, and *N. ornata*) show stratified distributions along a single slope without syntopy. Therefore, as shown in fig. 8, with the exception of *N. perdicaria*, there are no barriers or habitat gaps between species. (Gaps in the case of some subspecies will be discussed below.)



Figure 8. Stratified parapatric distribution pattern of *Nothoprocta tinamous* in western South America. Dark green in the north=*curvirostris*, blue=*oustaleti*, red=*ornata*, black (very thin in eastern edge of Peru-Bolivia)=*taczanowskii*, green in the south=*pentlandii*, gray=*cinerascens*, brown=*perdicaria*.

The distribution pattern of six of the seven species of *Nothoprocta tinamous* form what could be called “parapatric stratified distributions,” i.e., patterns in which two or more species abruptly replace each other elevationally or by habitat, without physical barriers. Whether the separation is strictly habitat-driven or if other mechanisms such as interference competition are involved would need to be tested. The pattern of elevational stratification among congeners is frequent in birds of the humid cloud-forest of the Andes (Terborgh 1971; Terborgh 1977; Terborgh 1978; Terborgh 1985), but the involvement of several species in multiparapatry at their entire distributions has seldom been documented (Remsen and Cardiff 1990; Remsen and Graves 1995a; Remsen and Graves 1995b). Conceivably, better mapping of more species will find it to be much more common in the Andean setting.

This degree of parapatry additionally poses a challenge for niche modeling, particularly at the resolution of 1 km pixel size. Two major problems arise. First, the closeness of training points makes it difficult for the model to discern the difference in environmental variables, particularly with expected variation in the variable and extrapolations between points with climate data. Two parapatric species could potentially fall into the same pixel, in which case models for each species would be fed with the same information. Second, small errors in the georeferenced information for the training points can be very misleading and easily feed the model with information that should belong to another species.

Nevertheless distribution maps in general had high significance levels. All AUC values were over 0.95, which reflects good discrimination between suitable and unsuitable areas for the species. Models that did not work well were always cases with a small number of records. A table (not shown) was constructed with the type I and type II errors and the general performance of the models for each taxa. General performance was the criterion used for choosing the final model for each taxon. Those chosen models are shown next.

3.3.2. Distribution of *Nothoprocta cinerascens*

The model was run with all available data ($n = 75$) for the species including the three points for *N. c. parvimaculata*. At a threshold of 30%, 10 records fell outside the predicted area. The AUC value calculated by Maxent with randomly chosen absence data is 0.951. The variables that contributed most to the model were Bio4 and Bio19, both climatic variables. Given the semi-open, dry Chaco habitat of this species, it makes sense that the model is driven by seasonality (Bio4) and precipitation (Bio19) rather than by any of the topographic variables important in other species' models.

The predicted area is a rather large oval area delimited to the west by the Andes and to the east by denser and wetter Chaco habitat. The predicted area is continuous along the base of the Andes north towards the distribution of other *Nothoprocta* and becomes sparse to the east and south, where it actually fails to predict the presence of some occurrence data. The most distant outliers to the east are both from Paraguay and both had low (10) confidence scores. Eight points to the south, fall in a large area predicted as patchy. Whether these small, scattered patches are real also need to be tested with fieldwork.

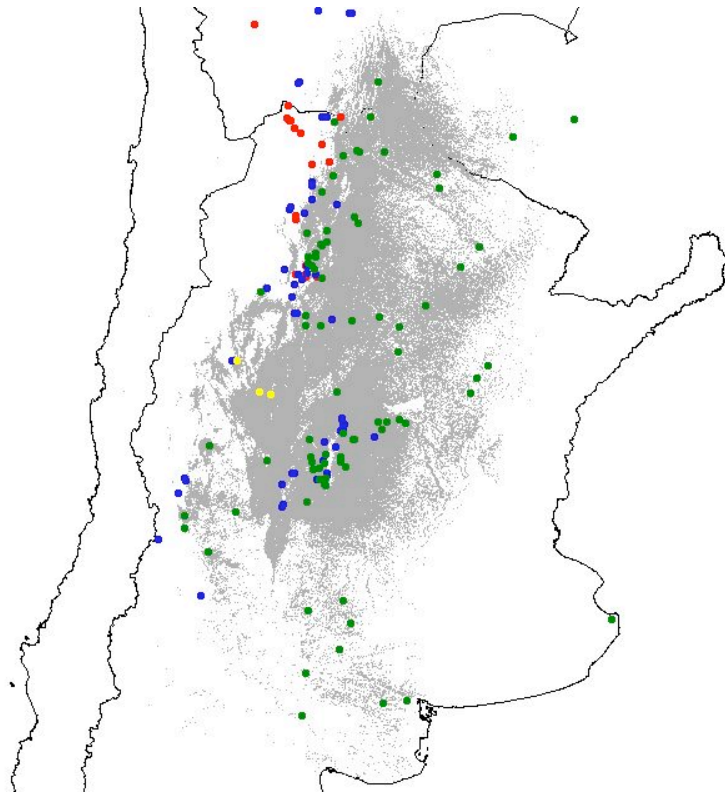


Figure 9. Predicted distribution of *Nothoprocta cinerascens*. Gray area is the predicted area at a threshold of 30%. Green dots are *N. c. cinerascens*, yellow are *N. c. parvimaculata* localities. Red dots are neighboring *N. ornata*, and blue, *N. pentlandii*.

Neighboring *Nothoprocta ornata* (red on fig. 9) to the northwest occurs at higher elevations and might not come into direct contact with this species. *Nothoprocta pentlandii*, however, is in direct contact but segregates by elevation. During my fieldwork, I noted that in the mountains of San Luis, Córdoba, and Mendoza *N. cinerascens* occurs in low, rather flat Chaco, such as areas at the base of the mountains, whereas *N. pentlandii* occurs higher up in nearby Andean brush, where topography becomes steep.

3.3.3. Distribution of *Nothoprocta oustaleti*

Traditionally this taxon is treated as a subspecies of *N. pentlandii* group, but it is treated separate here because of the results in chapter 2, which show that it is evolutionary well-distinguished from nominate *pentlandii* of Bolivia and Argentina, and they are not members of the same clade. This is a tricky species to model because it is the one with the richest taxonomic structure with at least four subspecies, and subspecies boundaries are partially associated with habitat types. Assuming the nominate form is the oldest

because it has the central, larger distribution with habitat more similar to that of other *Nothoprocta* species, we have two subspecies that have moved into new habitat. In the north, *N. o. ambigua* uses dry forest and scrub, and occurs in lower elevations. The subspecies *N. o. niethammeri*, as well as other coastal populations of uncertain subspecific assignment (Koeppke 1968), have also moved to lower elevations, into the “lomas” formations. The fourth subspecies, *N. o. fulvescens*, is not in a different habitat but is known only from the Eastern Andes in dpto. Cuzco.

All three populations, *niethammeri* (including other lomas populations), *ambigua*, and *fulvescens*, modeled independently did extremely poorly, probably due to the few training points available. In contrast, the model for nominate *oustaleti* matched fairly tightly its distribution; the model predicted some occurrences within the range of *fulvescens* and *ambigua*, but not in the lomas. However, when all subspecies were pooled, the predicted distribution included all subspecies fairly well. Of the 64 records in the model (35% threshold), only nine fell outside predicted area. Of these, five were within 1 km of predicted area, and three belonged to the “lomas” populations in the Arequipa area. The AUC value calculated by Maxent with randomly chosen absence data is 0.988. The variables that contributed most to the model were Bio19, Slope, and Bio4.

The overall predicted distribution for *N. oustaleti* is a long, thin band on the western side of the Andes that is patchy in central Ecuador but becomes continuous all along the western slope of Peru, then becoming patchy again in Chile (where there are some hearsay reports of the species but no actual records), and stops abruptly thereafter. Another thinner strip parallels the main distribution farther west, to include the lomas populations; it is fuzzy in dpto. Lima and continues with large gaps all the way to dpto. Arequipa. It seems connected to the Andean habitat by the rivers that transect the Andes, but there are no actual records from these river habitats. Besides the fuzziness at the north and the connecting valleys, the correspondence to lomas vegetation seems fairly good. The eastern spur of the predicted area into the Eastern Andes marks the distribution of *N. o. fulvescens*; however, this predicted area also continues north on the eastern side of the Andes parallel to the predicted area of nominate *oustaleti*, where known to be absent, and *N. curvirostris* is rather found. The predicted area also includes some of the area occupied not by *N. oustaleti* but by *N. pentlandii* in Bolivia.

The switch from nominate *oustaleti* to *ambigua* does not coincide with any apparent gap or barrier, and the predicted area is also continuous. In the field, the switch from Andean scrub where nominate *oustaleti* occurs to lowland dry forest where *ambigua* occurs is in a region of transition between the two habitats. These two subspecies are morphologically diagnosable, but what happens as the contact zone is currently unknown. Unfortunately, genetic material is not available, nor are there study skins from the contact area, but the apparent habitat continuity and possible contact zones call for more attention. They could potentially be proven to be two distinct species.

The lomas scenario differs. These highly seasonal mist-dependent oases are isolated by harsh desert and have a very marked dry season. They bear little resemblance to the Andes, and no niche model prediction without training points from this habitat predicted any suitable conditions here. The populations there are separated from Andean nominate *oustaleti* by at least 30 km of inhospitable desert and at least 2000 m of elevation. Perhaps this is sufficient to prevent gene flow and could explain the differentiation of the subspecies *niethammeri*. The lomas themselves are islands of habitat separated from each other by large gaps; whether the tinamou populations in these islands form a monophyletic group or whether each colonized independently from the Andean populations will not be known without genetic analysis.

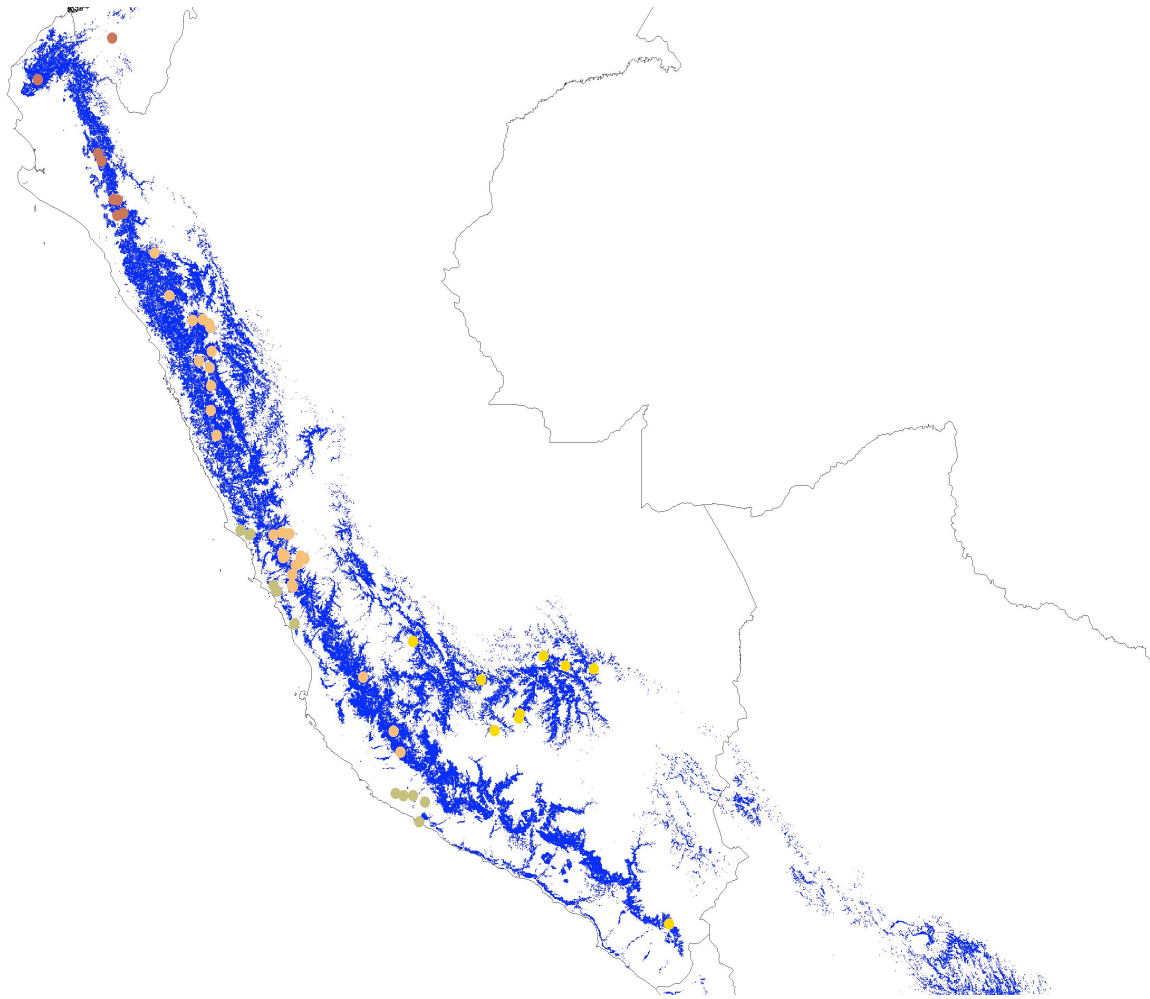


Figure 10. Predicted distribution of the *Nothoprocta oustaleti* in blue. Subspecies: brown is *ambigua*, pink *oustaleti*, yellow *fulvescens*, and gray *niethammeri* and other lomas populations.

As for the subspecies *fulvescens*, the niche models predict isolated habitat conditions on the east slope of the Andes, with a gap between it and nominate *oustaleti*. That gap predicted habitat and records of *N. ornata*. The predicted area for *fulvescens* includes dpto. Huancavelica specimens, identified as *fulvescens*, but it excludes the dpto. Tacna specimen (a young individual in undetermined plumage, with genetic affinity to dpto. Huancavelica specimens). The dpto. Tacna specimen seems to be clearly inside the continuous habitat along the western coast of Peru, and thus inside typical *oustaleti* distribution. Noteworthy is that the predicted continuity of *oustaleti* distribution all along the western slopes of Peru is not backed up by specimens, for the large gaps need to be studied more carefully to confirm the continuity or revise the models.

Regarding neighboring species, *N. oustaleti* comes in contact with *N. curvirostris* in the north, but the latter occurs at higher elevations in wetter, more open habitats. Almost along its entire range, the distribution of *N. oustaleti* parallels that of *N. ornata*, always at lower elevations in scrub rather than in open grasslands. Interspecific competition with *N. ornata* might pose a barrier for *N. oustaleti* to the east, because the model distributions overlap in areas where only *N. ornata* is present.

3.3.4. Distribution of *Nothoprocta curvirostris*

For *N. curvirostris* (n=38) the best model was obtained when each subspecies was run separately and the two then combined. The threshold for both was chosen at 45%. The AUC value calculated by Maxent was 0.997 for *curvirostris* and 0.996 for *peruviana*. All but two records in Ecuador fall within the predicted distribution. Both outliers are old records (confidence value 10) that fall close to the predicted area. The two variables that contributed more than 99% to the nominate *curvirostris* model were Bio4 and Bio11, whereas the variables that contributed most to the *peruviana* model were Elev and Bio4. The predicted area for the species is a relatively even band that seems to start north of Ecuador, where there is no environmental variable information, and extends to central Peru. In the south, the distribution extends beyond the southernmost specimen records by 300 km.

The nominate subspecies, which occurs in paramo and puna habitat, shows a continuous predicted distribution in Ecuador and extends to the Huancabamba depression in northern Peru. That the species is considered to have a patchy distribution in Ecuador (Restall et al. 2006; Ridgely and Greenfield 2001; Vogt 2007) is not consistent with the predicted solid continuous habitat. If the predictions are accurate, then the lack of records might be due to poor sampling in those inaccessible areas or to habitat degradation. The model for nominate *curvirostris* does not predict any of the *peruviana* habitat and ends rather abruptly in northern Peru. There is a clear but narrow gap in the predicted areas, between two subspecies north of the Marañon and in the Huancabamba depression, which is consistent with geographic isolation of both subspecies.

The model for the subspecies *peruviana* also predicts a gap in the Huancabamba depression, but with some predicted area to the north. Some of the over-predicted area for *peruviana* includes two large areas in Ecuador that are not predicted for, nor seem to be occupied by, nominate *curvirostris*.

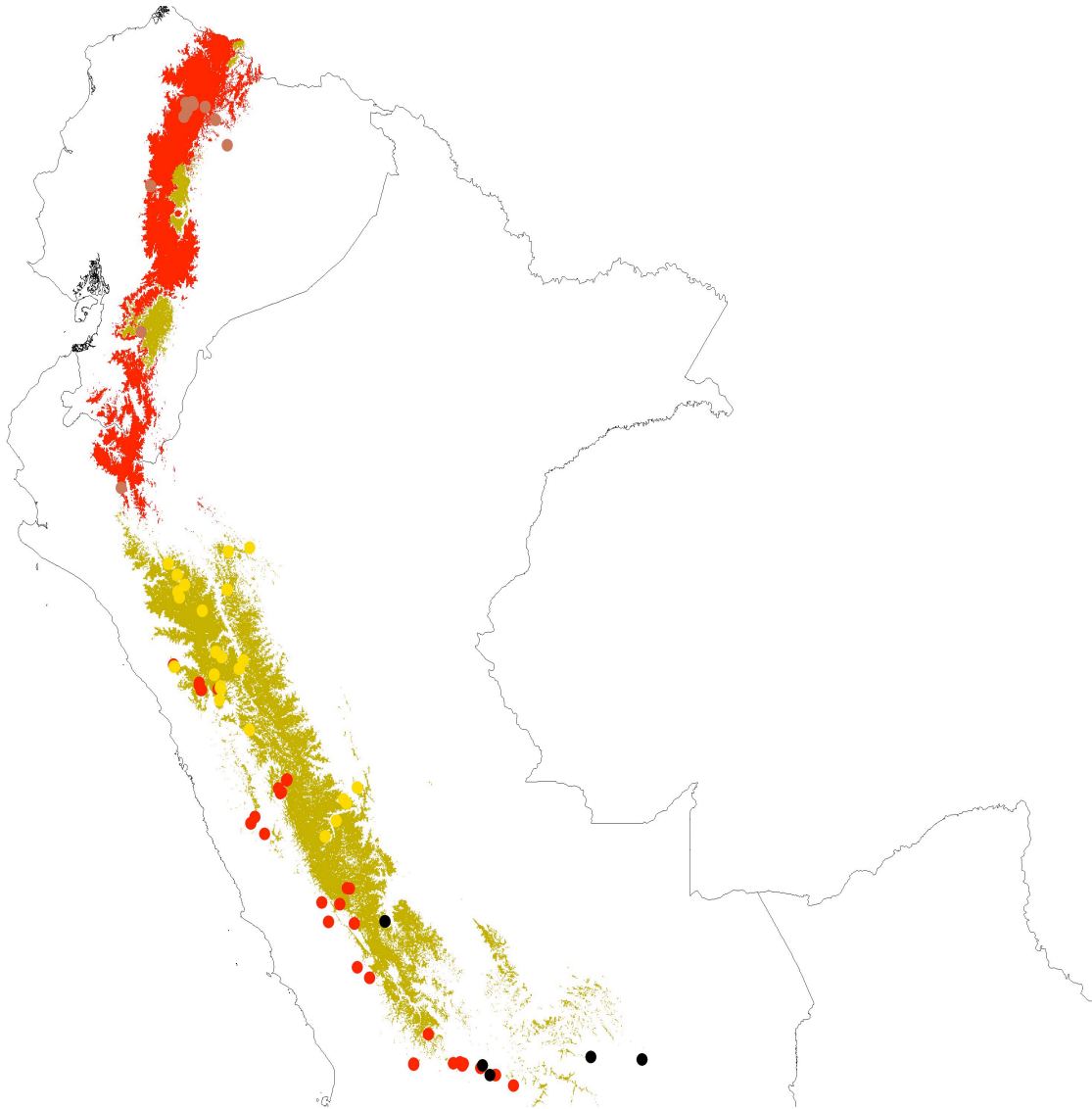


Figure 11. Predicted distribution of *Nothoprocta curvirostris curvirostris* (red) and *N. c. peruviana* (mustard) and their occurrence records (pink and yellow respectively). Red dots are occurrence records for *N. ornata*, black for *N. taczanowskii*.

To the south, the suitable area predicted for *peruviana* seems continuous, but the Marañón separates populations of the Eastern Andes from those in the Western Andes.

The former is in wetter, more paramo-like habitat, and the latter is in drier, generally degraded grassland at higher elevations (above 3500 m). On the east side they predicted areas seem to overlap with *N. ornata* habitat. The continuous 300-km-long, over-predicted area east of the Marañon, south of the known distribution of *N. curvirostris* in central Peru, seems to be at least partly occupied by *N. ornata*, suggesting possible interspecific interaction.

3.3.5. Distribution of *Nothoprocta ornata*

The model run (n=136) for this species performed strongly at a threshold of 30%, with only seven points falling outside the predicted area. However, as many as 42 records of neighboring species fell inside the predicted area. The AUC value calculated by Maxent with randomly chosen absence data is 0.985. The variables that contributed most to the model were Elev and Herb. The model using only *N. o. branickii* (n=32) also performed strongly at a threshold of 30%, with only one point (an old record with confidence score of 10) falling outside the predicted distribution. However, 22 records of neighboring species did fall into the projected distribution. The model also predicted the presence of the new subspecies in La Libertad. The AUC calculated by Maxent was 0.995. The variables that contributed most to the model were Elev and Bio4. The model run with just the southern subspecies (*ornata* and *rostrata*, n=96) also did very well with only five records falling outside the predicted area and 11 records of neighbor species falling inside its projected distribution. The variables that contributed most were Elev, Bio19, and Herb. Because *N. ornata* always occurs at higher elevations than its congeners, it makes sense that elevation is a good predictor of its occurrence.

As previously noted, the overall distribution of this species is central to all other taxa of the genus *Nothoprocta*. It forms a nearly continuous band starting in northern Peru in dpto. La Libertad and extending all the way to the Mendoza area in Argentina. Its general distribution is the Andes wherever there are continuous areas above 4000 m.

Some isolated predicted areas are of interest. To the north the largest terminal patch is partially occupied by the undescribed subspecies. It seems to be somewhat isolated by gaps in the predicted suitable habitat, but not completely so. Some of these areas were visited to see where the break or transition area was, but in areas of seemingly appropriate habitat, either no *Nothoprocta* was found or the species found was *N. curvirostris*. As seen on fig. 12 and 13, the new subspecies is isolated from *branickii* by poor or patchy habitat used by *N. curvirostris*. Also noted in fieldwork was that predicted patches for *N. ornata* to the north of dpto. La Libertad in dpto. Cajamarca were occupied by *N. curvirostris*, another example of possible interspecific competition.

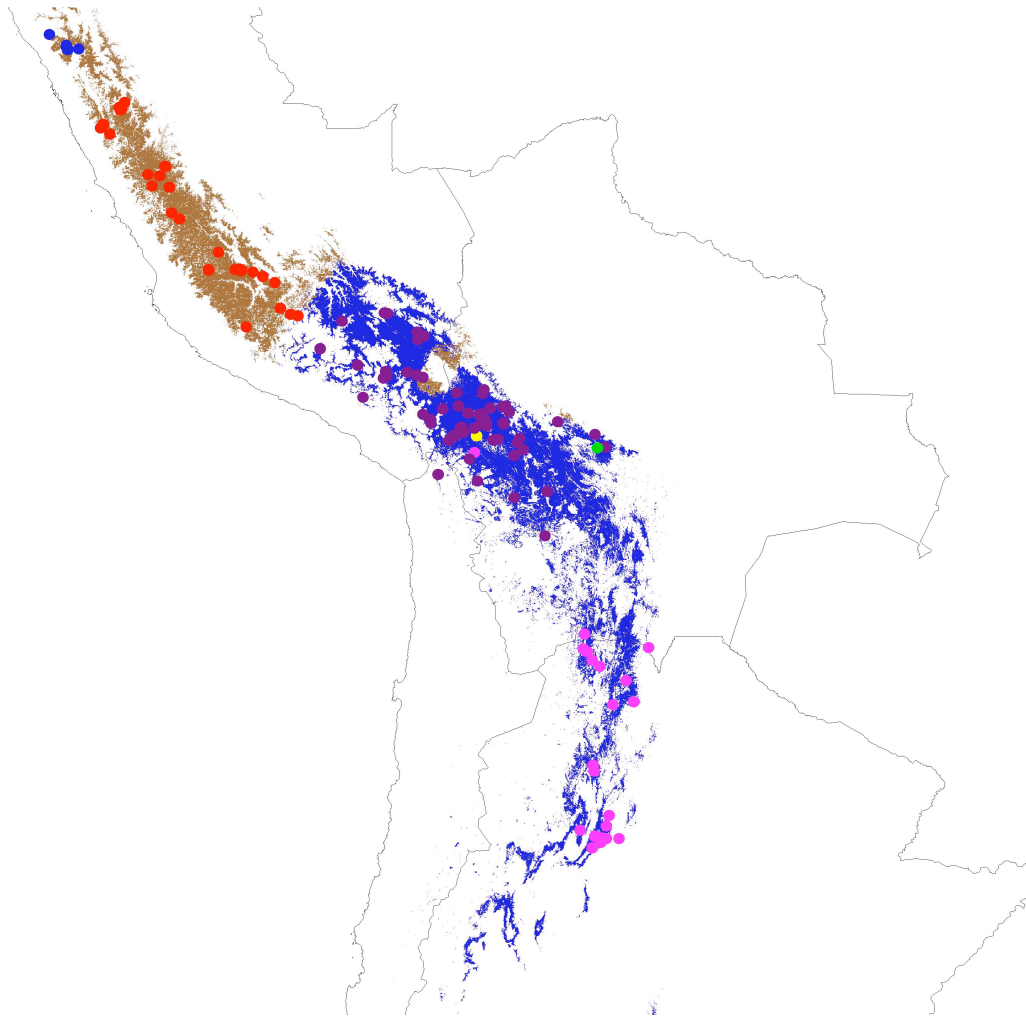


Figure 12. Predicted area of *Nothoprocta ornata*, *N. o. branickii*, and ssp. nov. (brown) and *N. o. ornata* and *N. o. rostrata* (blue). From north to south, blue is ssp. nov., red is *branickii*, violet is *ornata*, yellow is *jimenezi*, green is *labradori*, and pink is *rostrata*.

Farther south, the distribution of *N. o. branickii* seems continuous and rather solid, with some areas of thinning that divide west slope and east slope areas (fig. 14). It ends rather abruptly in dptos. Arequipa and Cuzco, where nominate *ornata* starts. This transition will need further study. Traditional classifications (Blake 1977) state that *ornata* ends in dpto. Puno, or in Cuzco (Fjelds  and Krabbe 1990), followed by a gap before the southernmost limit of *branickii* in dpto. Apurimac. My fieldwork closed that gap with specimens from dpto. Arequipa southern dpto. Cuzco assignable by plumage to *ornata*. Genetically, the split also seems clear-cut (see chapter 2), but morphologically some of the specimens in the area of contact had some intermediate plumage characters, as one would predict where two subspecies are in contact. There is no physical barrier separating the subspecies, so perhaps segregation is driven by subtle climatic change, such as the variables that manage to distinguish the two areas in the Maxent models.

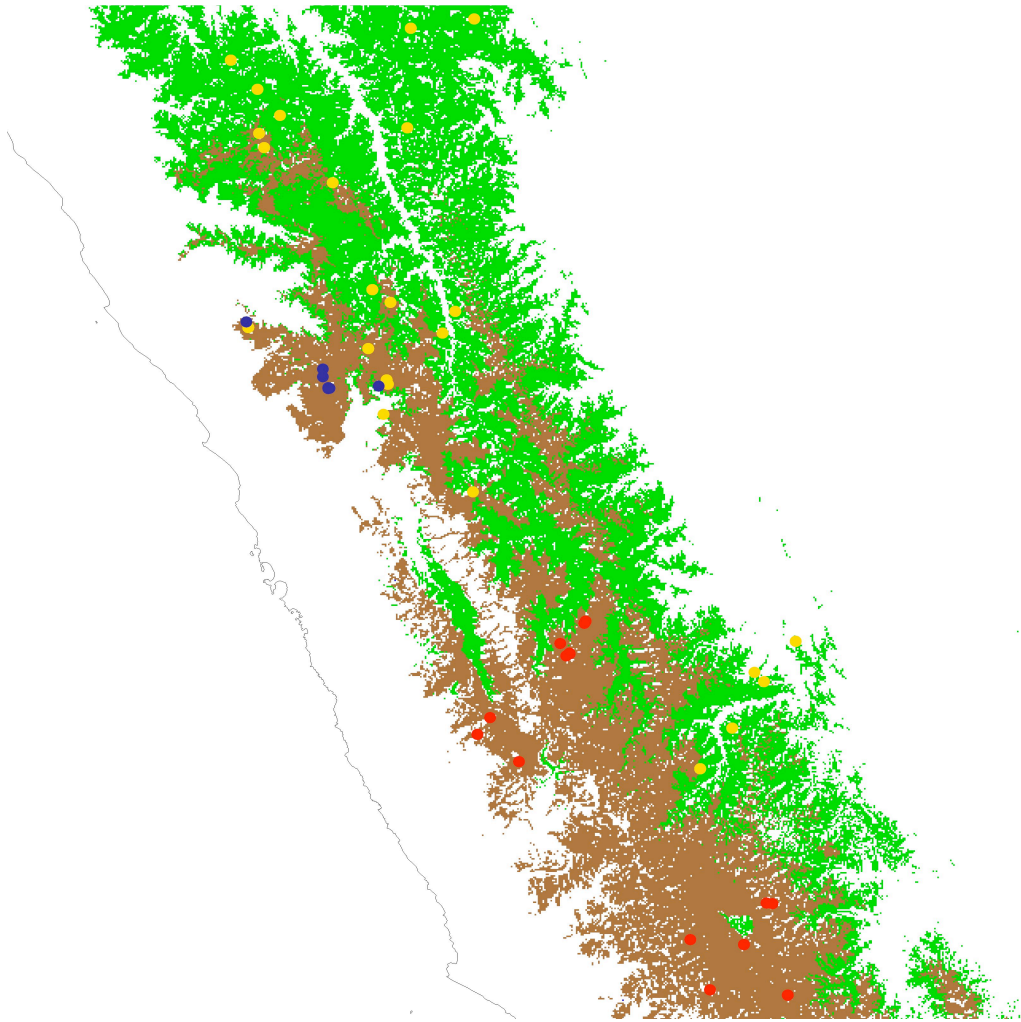


Figure 13. Predicted distribution for *Nothoprocta ornata* (brown) and *N. curvirostris* (green), and new subspecies of *N. ornata* (blue dots). Other occurrence points are red for *N. o. branickii* and yellow for *N. curvirostris*.

Nothoprocta o. ornata continues southward with fairly continuous areas of predicted occurrence to central Bolivia, where the predicted suitable habitat seems to become patchy. The solid area is occupied mainly by the nominate subspecies *ornata*. Within that area, however, two subspecies have been described recently (Cabot 1997). The subspecies *jimenezi* is supposed to occur at Chalacoto, dpto. La Paz, but this makes little sense biogeographically because it is embedded in the range of nominate *ornata*. I was unable to examine study skins or obtain genetic samples from *jimenezi* to ascertain its diagnosability. The subspecies *labradori* was described from three localities in dpto. Cochabamba; the models predicted its distribution to be restricted to a relatively isolated

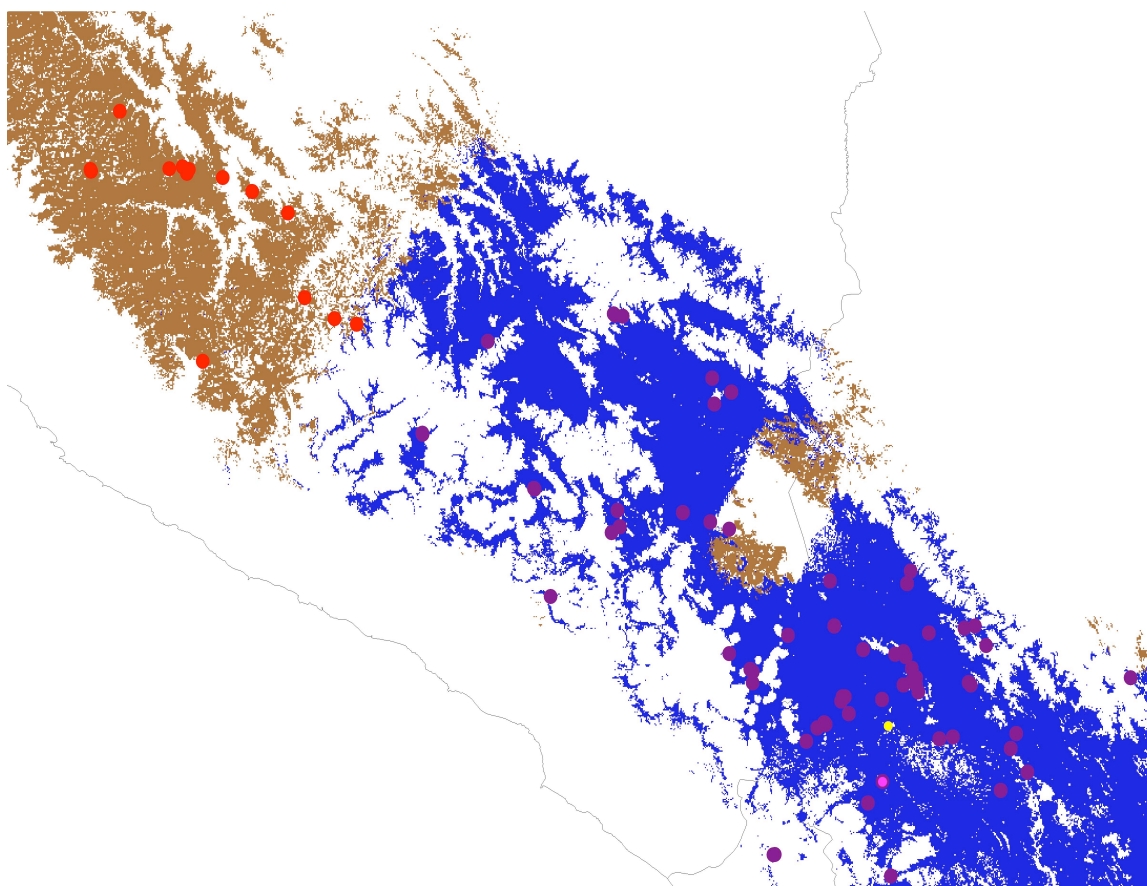


Figure 14. Transition from *Nothoprocta ornata branickii* (brown, red dots) to *N. o. ornata* (blue, black dots).

ridge in the Cochabamba region. I was unable to examine study skins or obtain genetic samples from *labradori* for further analysis; whether other specimens from that area, previously identified as or assumed to be nominate *ornata*, are actually *labradori* is also not known.

The model that combines nominate *ornata* and *N. o. rostrata* (fig. 15) predicts patchiness at the boundary between the two, starting at the Bolivia-Argentina border. Although the diagnosability of *rostrata* has been questioned (Porzecanski 2003), when both subspecies are modeled separately, the predicted areas have a good fit and do not overlap, leaving a large gap, in south-central Bolivia, followed by a solid area in northern Argentina.

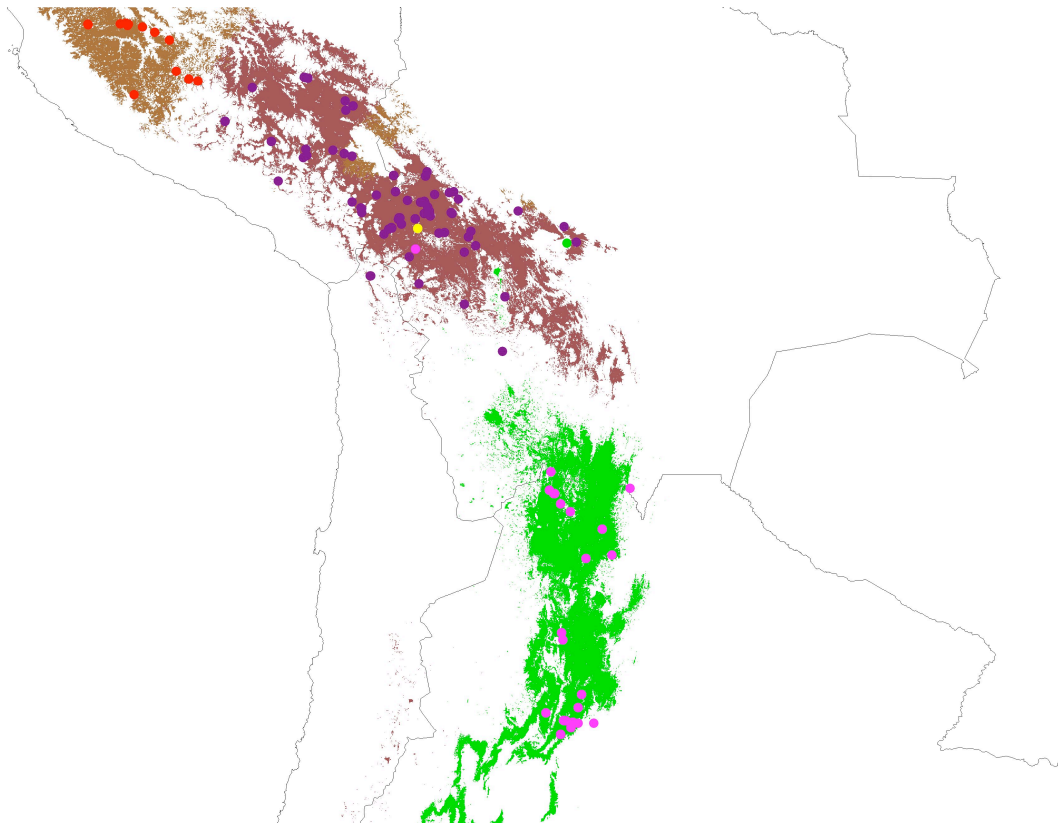


Figure 15. Transition between subspecies *ornata* (brown, blue spots) and *rostrata* (green), when modeled separately. Within records dots, *jimenezi* (yellow) and *labradori* (green), and *rostrata* (pink).

3.3.6. Distribution of *Nothoprocta perdicaria*

The model was run with all available data for *N. perdicaria* (n =22), and a threshold of 35% was chosen. The AUC value calculated by Maxent with randomly chosen absence data is 0.994. For models run by individual subspecies, the model for the nominate subspecies performed poorly, over-predicting large areas, including areas on the opposite side of the Andes. The model run solely on *N. p. sanborni* did much better and was used with a threshold of 45%. The AUC value calculated by Maxent with randomly chosen absence data is 0.995. The variables that contributed more to the species model were Bio11, Bio19, and Herb, and for the *sanborni* model, Bio19, Slope, and elevation.

The species' distribution is a continuous strip on the western coast at the base of the Andes of southern Chile (fig. 16). Gaps are scattered throughout the distribution, and some predicted area oddly occurs in eastern Argentina in Buenos Aires and Misiones, where no member of the genus occurs.

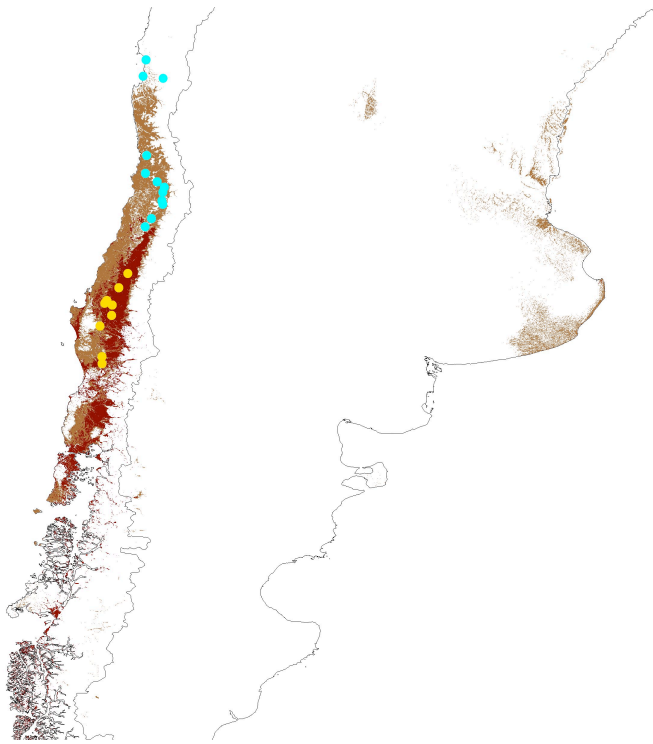


Figure 16. Predicted distribution of *Nothoprocta p. perdicaria* (light brown) and *N. p. sanborni* (dark brown) above. Records light blue and yellow respectively.

The predicted area for the *sanborni* model extended north to include one of the records *perdicaria*. It also predicts a more inland distribution than that of nominate *perdicaria*, only reaching the coast in a few places. To the south both models predicted a relatively large disjoint area where there are no known records. The poor prediction of *perdicaria* by itself could be the result of small sample size; habitat alteration or reintroductions (for hunting) may also have contaminated the occurrence data. There seems to be no evident break between the subspecies in the distribution. The tight fit of the *sanborni* model suggests that the difference could be driven by habitat differences.

3.3.7. Distribution of *Nothoprocta pentlandii*

This species, after the removal of *oustaleti* (chapter 2), occurs only in Bolivia and Argentina. The best model was the one that used all subspecies together ($n = 127$) at a threshold of 35%; only five records fell outside the predicted area, none of which were records with high confidence values. The AUC value calculated by Maxent was 0.973. The variables that contributed most to the model were Elev, Herb, Bio19, and Bio4. The overall predicted area consists of a strip of uneven width entirely along the eastern side of the Andes of Bolivia south to Mendoza, Argentina, attenuating at both ends. A large isolated area is predicted for the San Luis Mountains of Córdoba.

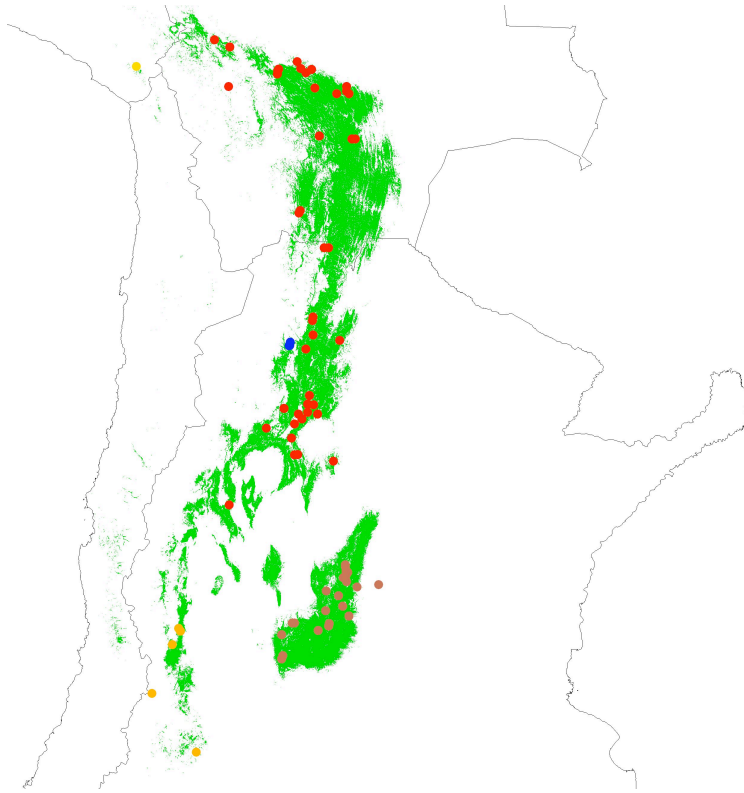


Figure 17. Predicted distribution of *Nothoprocta pentlandii*. Records are: red for nominate *pentlandii*, blue for *N. p. patriciae*, yellow for *N. p. mendozae*, brown for *N. p. doeringi*, and the single yellow spot at the top belongs to *N. oustaleti*, in Tacna, west of the Andes.

The bulk of the distribution corresponds to nominate *pentlandii*. The subspecies *patriciae*, described from Salta, is potentially somewhat isolated according to the predicted area. However, neither morphological (obs. pers.) nor genetic analysis (chapter 2) seems to support its recognition. At the southern end of the distribution, the population in the mountains of Mendoza are somewhat isolated, particularly by the absence of records between the southernmost *pentlandii* in La Rioja and this population. The subspecies *doeringi* is isolated in the mountains of San Luis and Córdoba. The validity of *doeringi* is corroborated morphologically with subtle but diagnosable differences (pers. obs.). No genetic material was available.

As mentioned above, *Nothoprocta oustaleti* west of the Andes, in Peru, is traditionally treated as a subspecies of *N. pentlandii*. According to the models used for each species independently, they predict some of each other's distribution. For example the dpto. Tacna specimen of *oustaleti* shown in Fig. 17 in yellow falls within a patch of predicted also by *N. pentlandii* habitat. Field observations confirm that both species use similar habitat, which might explain their similarity (by convergence or parallel evolution), which is why they are traditionally merged.

3.3.8. Distribution of *Nothoprocta taczanowskii*

Few data points are available for this rare species (n=10), but the model performed well. A threshold of 35% was chosen, which did not leave any records outside the predicted distribution. The AUC value calculated by Maxent with randomly chosen absence data was 0.971. The variables that contributed most to the model were Elev, Slope, and Bio4. The predicted area is a relatively thin and patchy strip that follows the easternmost edge of the Andes. It continues far beyond known records for the species both south and north. Too little is known about the species as to be sure these are indeed over-predictions and not unsurveyed localities. For example, the only record from Bolivia was not discovered until 1999 (Vogel et al. 2001). The patchiness of the overall thin, marginal-looking distribution might be an explanation on why it is rare throughout its occurrence sites.

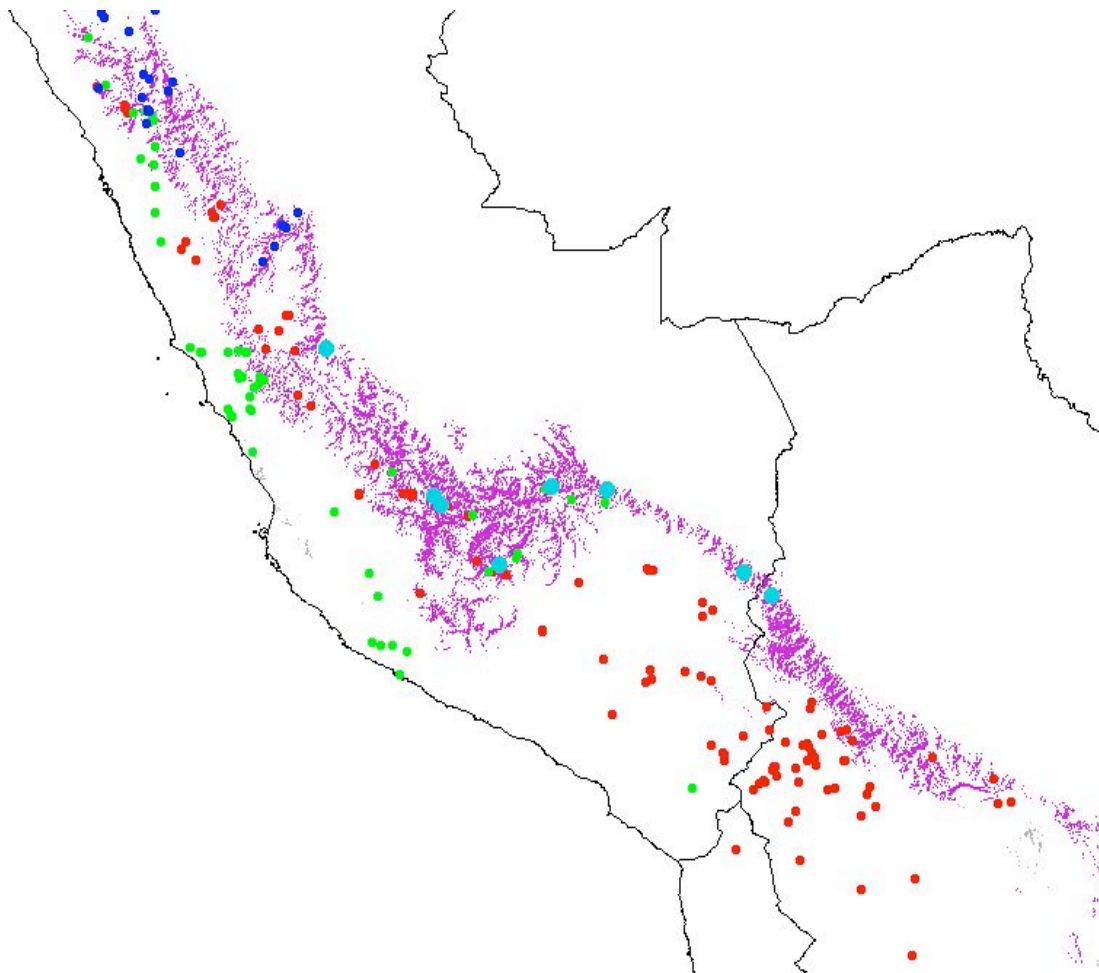


Figure 18. Predicted distribution for *Nothoprocta taczanowskii* in violet, with light blue dots representing the 8 available records. Red dots are *N. ornata*, green are *N. oustaleti* and brown are *N. curvirostris*, its three neighboring species.

The overall distribution seems to be limited to the east by forest and to the west by neighboring species, principally *N. ornata* and *N. oustaleti*. Note that from the records it seems isolated from *ornata* in southern Peru and Bolivia.

3.4. Conclusions

As a primarily Andean genus, with apparent relative low dispersal capability compared to other birds, the distribution of the *Nothoprocta* populations in the complex Andean topography might be expected to show a high incidence of isolation, particularly in the latitudinal axis. However, the pattern seems quite different. At the species level, there are no barriers or gaps among species (except *N. perdicaria*), and all adjacent species are extensively parapatric, with longitudinally oriented boundaries of substantial length. They are not known to be syntopic, but rather segregate by elevation or habitat in what can be called parapatric stratified pattern. At the subspecific level, the pattern is similar. For half of the described taxa, the predicted range shows no geographic isolation. This pattern suggests that speciation, assumed to be allopatric, is driven in *Nothoprocta* by geological or climatic changes in the Andes that are not reflected by current climatological or ecological conditions. In other words, the distribution pattern suggests that populations have gone through extensive expansion phases after the allopatric speciation events. Whether the population genetics of *Nothoprocta* populations show the signal of recent expansion would be feasible to test.

A scenario of extensive secondary contact with interspecific competition is supported by the niche model predictions. In all cases, predicted distributions overlap. Some overlap might be expected from model imprecision, but in many cases relatively large areas might suggest unused suitable habitat. Almost always such areas are occupied by a different species, with a rather predictable “dominance” of one over the other. For example, *Nothoprocta taczanowskii* is overpredicted in all directions but less so to the east of its occurrence where no other *Nothoprocta* occur. Its overpredicted area to the north is occupied by *N. curvirostris* and *N. ornata*, to the west by *N. ornata* and *N. oustaleti*, and to the south by *N. ornata*. Thus, *N. taczanowskii* appears to occupy a narrow sliver of suitable habitat at the eastern margin of areas suitable for members of the genus.

The pattern of overlap of predicted distributions suggests that *Nothoprocta ornata* is the “dominant” species in its central range. When overlaying its range map over those of the neighbor species, the predicted areas correspond well to the records of each species. In other words, the area of overlap is mostly used by *N. ornata*. This seems not to be the case in its latitudinal extremes. At its northern limit in La Libertad, the predicted area for *N. o.* subsp. nov. is actually partially occupied by *N. curvirostris*, and in the south the *N. pentlandii* seems to be occupying its “overpredicted” range.

Some over-predicted areas occur far from the known distribution, such as the case of the predicted range in Buenos Aires and Misiones for *N. perdicaria*. Without translocation experiments, it is hard to determine if these are really suitable regions for the species that the species cannot colonize or if they are model flaws.

Currently, three taxa represent differentiated populations at lower elevations: *N. perdicaria* at the species level and *N. oustaleti ambigua* and *N. oustaleti niethammeri* at the subspecies level. In all three cases, these populations are allopatric not parapatric to their sister taxa. This type of isolation may be an important speciation mechanism in the evolutionary history of *Nothoprocta*.

CHAPTER 4. BIOGEOGRAPHY OF *NOTHOPROCTA* IN A PHYLOGENETIC FRAMEWORK

4.1. Introduction

4.1.1. Theoretical Framework

A central question in ecology has been how diversity is attained (Mittelbach et al. 2007) and maintained (e.g. MacArthur and Horn 1969). This question has proven particularly challenging in the Neotropics, where diversity and diversity patterns seem to be particularly rich and of mixed origin. Most studies of diversity patterns in the Neotropics have concentrated on the more striking alpha diversity. However, beta diversity is not only (considerably) higher in this region than in temperate zones, but also the mechanisms producing beta diversity are an important or necessary step to understand alpha diversity. The most accepted -- often the only accepted (Futuyma and Mayer 1980) mechanism of speciation is that of allopatric speciation. For species groups that share a common ancestor, this means that the development of beta diversity is a necessary step for increasing alpha diversity, thus increasing diversity in general. As seen in chapter 3, *Nothoprocta* tinamous provide an excellent model for the study of beta diversity: alpha diversity is never more than one species throughout the range of the genus. In this chapter, I explore patterns of *Nothoprocta* distributions to see what they tell us about the origin and maintenance of diversity.

4.1.2. Tropical Diversity Patterns

One of the earliest noticed trends of diversity is that of increased diversity towards the tropics. Although still not clearly explained, it seems to be the result of multiple conditions met in the tropics: climatic stability, old age, large area, higher productivity, etc. Such a gradient could be important in a group of species that spans from the equator to 40° S.

Mechanisms of increased diversification have also been attributed directly to the Andes. They represent a strong barrier to dispersal, as shown of the many sister taxa divided into eastern and western taxonomic units. Many deep valleys also create structure, assumed to be a basic mechanism for dispersal and founder effect. Graves (1985) proposed that the Andean setting with long and narrow geographic distributions, such as those of Andean birds, are easier to “break” on the narrow axis. Such breaks, and the subsequent genetic isolation of the populations between the breaks, are the ultimate cause of differentiation and higher speciation rates in the Andes.

Parallel to the reasons of higher diversity, the ability to “pack” species has been postulated to be important for maintaining diversity. Even with same speciation rates, a

region that can pack more species will have more species. From an ecological perspective, tropical habitat complexity has been postulated as the reason for a higher accumulation of species (of birds) than in less complex habitats in temperate zones (MacArthur and MacArthur 1961; Pianka 1971). In species that do not achieve sympatry, tighter packing is only possible by expanding the overall distribution or by reducing the range of one or more of its members. This would produce narrower distributions, which according to Graves (1985) would be more likely to break and promote speciation.

4.1.3. The Phylogenetic Framework

In recent years, the ability to sequence genes has added a new perspective to the analysis of diversity, particularly in two aspects: a) making it possible to incorporate genetic structure in current patterns, and b) strengthening significantly the historical component by use of phylogenetic hypotheses based on genetic information. In chapter 2, the phylogeny of the *Nothoprocta* was analyzed in detail to clarify the taxonomy of the group. For example, analyses that use the traditional classifications, which treat *N. pentlandii* as one species, would produce fundamentally different results than those that use the findings in chapter 2, namely that the *oustaleti* group of subspecies is a separate species that is actually a basal split in the *Nothoprocta* phylogeny. With the phylogenetic framework established in chapter 2, here I analyze the distribution patterns found in chapter 3 to elucidate the evolutionary processes that produced the diversity and current distribution patterns of *Nothoprocta* tinamous.

4.1.4. Mechanisms Leading to Parapatry

The predominant theme of *Nothoprocta* distribution is parapatry among the species. What is the mechanism that produces such a pattern? Two hypotheses for the origin of parapatric patterns of distribution have been proposed. The traditional explanation is that parapatry is a consequence of secondary contact following allopatric differentiation (Mayr 1942). When the barrier between the two differentiated populations disappears, the populations come together to produce a parapatric pattern. If they attained reproductive isolation during allopatry, then the competitive exclusion principle predicts that, after secondary contact, either one species will replace the other geographically or a sharp boundary will be maintained. The latter is predicted to be stable only if their niches differ. Therefore, the allopatric speciation model predicts that sister taxa will be allopatric or, if parapatric, the contact zone will be where two formerly separated geographic regions meet.

A second hypothesis is the parapatric speciation model, which proposes that a continuously distributed population becomes divided by gradual specialization at two resource peaks along a gradient (such as elevation) and that selection against intermediate individuals causes a cessation of gene flow even though the two populations are never

separated (Endler 1977). This hypothesis predicts that sister species will be parapatrically distributed along a gradient. With *Nothoprocta* species showing the stratified parapatric pattern documented in Chapter 3, the genus is ideal for testing the parapatric speciation model, which predicts that adjacent species along an elevational gradient are sisters.

4.2. Methods

4.2.1. Data Sources

4.2.1.1. *Nothoprocta* Samples

Specimen localities were taken initially from specimen labels. The mapping of those points in combination with preliminary niche modeling generated overall distributions that were then used to plan further field sampling. Given the extent of the distributions, this could not be done for all species or for all geographic areas that needed confirmation of presence.

Of 964 specimens, 724 provided useful locality data for 407 unique localities, which were then used for niche modeling. Georeferenced locations for 307 localities were taken directly from museum specimens, or georeferenced by using gazetteers (Paynter 1988; Paynter 1989; Paynter 1992; Paynter 1993; Paynter 1995; Stephens and Traylor 1983), 1/100 000 maps, or Google Earth. I collected specimens and sight records at an additional 100 localities, all with relatively precise (± 20 m) geographic positions. These were the points where the bird was detected by a pointing dog before flushing or where an undisturbed bird was seen by me or other experienced observers.

Table 8. Number of locality data per species.

Species of <i>Nothoprocta</i>	Total localities	Museum specimen localities	New localities from this study
<i>ornata</i>	136	90	46
<i>curvirostris</i>	38	19	14
<i>cinerascens</i>	77	76	2
<i>oustaleti</i>	61	29	32
<i>pentlandii</i>	65	62	3
<i>perdicaria</i>	22	20	2
<i>taczanowskii</i>	8	7	1
TOTAL	407	307	100

4.2.1.3. Data Reliability

Each georeferenced position was assigned an arbitrary confidence value of 10, 50, 80, or 100, depending on the expected accuracy of the position. The scale of 10, 50, 80, and 100 has no particular meaning and should be seen as discrete variables. It started as a subjective % confidence in a coordinate and is a reduction of a once broader range of values. Localities that referred only to a major city only were discarded, but for towns, proximity to the town was assumed, but a low confidence value (10) was assigned. The same value (10) was given to localities found in the gazetteers but for which variation in the names left some doubt about the correct interpretation of the locality. A value of 50 was given for good matches between label data and gazetteers or maps, but the specific site was uncertain. A value of 80 was given to recently collected specimens for which the coordinates were taken by the collector; these coordinates typically refer to a specific locality from which specimens may have been collected as far away as 1 km. A confidence value of 100 was given to specimen localities gathered during this study, for which GPS readings were taken within 20 m of where the bird was seen.

4.2.2 Environmental Variables

4.2.2.1 Variable Definition

In niche modeling, variables are raster layers that need to be standardized so that they all cover the exact same area and have the same resolution (pixel size).

Climatic variables available at the WORLDCLIM website were used (table 9). These have been processed from analyses of climatic data from the 1950 to 2000. Most are based on temperature (maximum, minimum, and mean) and monthly precipitation. As a result of various combinations of those, 19 variables are available (table 10). Four topographic variables, also available at WORLDCLIM, were obtained from calculations from the Digital Elevation Model (Bates and Demos 2001). Using the MODIS GLCF images, a percent coverage for each of the following vegetation types was initially calculated: herbs, bare ground, and trees in three individual layers.

Because most of these variables have been constructed from other variables, autocorrelation is expected. To minimize autocorrelation, my final selection included variables of all three types. I also tried to use those that have biological meaning to facilitate interpretation.

Table 9. Source for the variables before standardization.

Variable	Source	Resolution
Climatic	WORLDCLIM http://www.worldclim.org/current.htm	1 km
Topographic	WORLDCLIM http://www.worldclim.org/current.htm	1 km
Vegetation	Global Land Cover Facilities MODIS http://glcf.umiacs.umd.edu/data/modis/vcf/data.shtml	500 m

4.2.2.3 Final Selection of Variables

After 28 variables had been standardized for the area and to the same resolution (1 km² pixel size), I decided to use the three topographic variables (given their relative accuracy and assumed importance in Andean topography), the vegetation layer on herbs, and three climatic variables. I used the following criteria to select those three climatic variables:

(a) Low autocorrelation. A correlation matrix using Pearson's index was constructed to exclude climatic variables that were highly autocorrelated (i.e., Pearson coefficient > 0.05) with other variables, including the topographic and vegetation variables. This first selection left 12 variables.

(b) For the final selection, I discarded an additional 5 climatic variables, with similar correlation patterns, by using an "ecological relevance" criterion that gave priority to presumably more-relevant variables. Knowing which variables are ecologically relevant to *Nothoprocta* tinamous can only be weakly inferred from the meager data available on the biology of the genus. The final seven variables were not used to draw conclusions concerning their individual effects on tinamous, so the subjective nature of this last step had no impact on the results of the modeling, but was designed to make the climatic layers as interpretable as possible.

Table 10. Seven variables used for the environmental envelope.

Type = type of variable: Clim=climatic, Topo= topographic, Veg=vegetation.

Type	Name of variable	File name	Units	Source
Clim	Seasonality of T (standard deviation x 100)	BIO4	-	Worldclim
Clim	Mean T ^o of the coldest trimester	BIO11	°C x 10	Worldclim
Clim	Precipitation of the coldest trimester	BIO19	mm	Worldclim
Topo	Elevation above sea level	alt	m	Worldclim
Topo	Slope	Slope	degrees	derived from elevation
Topo	Aspect (orientation)	Aspect	degrees	derived from elevation
Veg	Percentage of herbs covering the ground	herb.	%	MODIS

4.2.2.4 Determining the Threshold Probability of Occurrence

As a first step the Receiver Operating Curve (ROC) and Area Under the Curve (AUC) output from Maxent were checked for each model for problems with the models, such as the behavior of their precision errors. A ROC curve without a curvature would represent poor discrimination of true positives (predicted area with records) and true negatives (unpredicted area with known absence). An AUC of 0.5 or less indicates random discrimination. The better the model discriminates the predictions of presence and absence, the larger the AUC, hypothetically up to 1 in a perfect model. The use of pseudo-negatives, given the lack of negatives in the Maxent models, means that values of 1 cannot be achieved. To evaluate the importance of each variable, jackknifing was performed by deleting one variable at a time and rerunning the model to monitor the impact of the missing variable. If the model was considered to be acceptable given its ROC and AUC curves and jackknife results, the selection of a threshold probability of occurrence was the next step.

I followed the procedure used by (Young 2007) for choosing the threshold by increasing the threshold progressively to the highest possible value that minimizes the number of presence records and minimizes the areas of known overprediction. However, rather than setting a fixed number of unwanted false negatives, the decision to accept the threshold depended on the precision of that point. If the false negative had a confidence value of 10 or 50 (see section 2.1.3), then it was ignored for a decision, particularly if close to the predicted area. Points with a confidence of 80 or 100, however, were never left out without considering a problem in the threshold. These models were run for each species and its subspecies independently, as well as with some combination of taxa that were known to be closely related. The model representing the final species could be chosen

from the model of the species as a whole, or as an aggregate of its subspecies (or of a combination of these).

To choose which model (species or subspecies models) was the best, the criteria was to minimize “interspecific false positives”. These false positives were defined as those points where a different species (or subspecies) occurred in the predicted modeled distribution (see table in appendix). Because the model could be correctly predicting the distribution range in an area of another species (as unused fundamental niche), this is a somewhat biased way to look at error. However, if the area “over-predicted” is correct, then a reduction in the threshold should not eliminate that area without creating false positives. Because the false positives are the main criteria to choose a threshold, such overprediction, if real, could never be avoided, as expected, for example, under condition of interspecific competition.

All models performed well, with all AUC curves above 0.95. Jackknifing of variables showed that some contributed little to the model. Models rerun without those variables resulted in very similar distributions, but for consistency all seven variables were retained in each model. The variables identified as not important varied among models without an apparent pattern (Appendix), so I decided to run all models with all seven environmental variables for consistency.

4.2.2.5. Map Processing

As a proposed representation of the distribution of the ancestral species of a clade, the distributions of all species in the clade were combined. For geographic distances with respect to predicted area, the ruler of the ArcView main menu was used. To calculate the number of species in the latitudinal axis, the pointer of the ArcView program was positioned at what was considered the extreme of a distribution and the latitude then read from the output screen.

4.2.3. Building the Phylogenies

4.2.3.1 Taxon Sampling

Locality information was obtained for 168 individuals sampled for this study. Twenty-five tissues were borrowed from the Louisiana State University Museum of Natural Science Collection of Genetic Resources, 27 were borrowed from other North American collections and 103 were collected specifically for this study and are deposited in the LSU MNS tissue collection. Thirteen sequences were downloaded from GenBank.

4.2.3.2. Laboratory Methods

Total genomic DNA was extracted with a DNeasy Kit (Qiagen, Inc.). The final extraction product was stored at -20°C until further analyses. PCRs were performed in $25\ \mu\text{l}$ volumes and contained $16.4\ \mu\text{l}$ dH_2O , $2.5\ \mu\text{l}$ 10X buffer, $1.5\ \mu\text{l}$ dNTPs (10 mM), $1\ \mu\text{l}$ of each primer (10 μM), $0.1\ \mu\text{l}$ *Taq* polymerase, and $2.5\ \mu\text{l}$ template ($\sim 50\ \text{ng}$). For cytochrome *b* (Cyt-B), the primers used were L14990 and H16065. For ND2, the primers used were L5215 and H6313. (see table X). Thermal amplification profiles for both mitochondrial genes were 35 cycles of 94° (30 sec), 50°C (30 sec) and 72°C (1 min). For CLTC, the primers used were CLTC_f and CLTC_r (see table of primers for origin). The thermal profile of amplification used 35 cycles of 94° (30 sec) denaturation, 53°C (30 sec) annealing and 72° extension (30 sec). PCR products were cleaned using a PEG purification protocol. Cycle sequencing was performed in $7\ \mu\text{l}$ volumes containing $1.75\ \mu\text{l}$ dH_2O , $1.5\ \mu\text{l}$ buffer 5X, $1\ \mu\text{l}$ primer (10 μM), $0.25\ \mu\text{l}$ Big Dye 3.1 (Applied Biosystems, Inc), and $2.5\ \mu\text{l}$ purified PCR product. The amount of template PCR product was varied slightly in some cases. Cycle sequencing reactions were cleaned with Sephadex and visualized on an ABI Prism 3100 Genetic Analyzer.

Sequences were imported into Sequencher 4.7 (Genecodes, Inc) and aligned visually. In some cases, alignments were performed visually using a text editor (TextWrangler). All cytochrome-*b* sequences in this analyses start at position 13,737 of the gene (compared to *Eudromia elegans* AF338710 from GenBank) The sequence length used in the analysis is 1048 base pairs. ND2 sequences start at position 3933 of the mitochondrial genome (compared with *Eudromia elegans* AF338710 from GenBank). The sequence length used in the analysis is 1098 base pairs. The aligned sequence length of the CLTC gene used in the analysis was 740 base pairs. A 6 base pair long region of sequence that was difficult to align was excluded prior to all phylogenetic analyses. Not all individuals amplified with the same ease for each gene. As a result some genes were not obtained for some of the individuals. The table in the appendix shows the individuals for which sequences of all genes were available. Protein-coding mitochondrial sequences were translated into amino acids to verify the absence of stop codons or other anomalous residues. All phylogenetic analyses were performed using a portable UNIX version of PAUP*4.0b10 on Macintosh G5 computers with two parallel processors (Swofford 2003).

Maximum-likelihood (ML) and Bayesian methods were the primary methods of phylogenetic analysis. To determine the optimal ML model for each data set (each locus plus combined), I used the Akaike Information Criterion implemented in the program ModelTest 3.5 (Posada and Buckley 2004; Posada and Crandall 1998). Using PAUP*, likelihood scores for input into ModelTest were estimated on neighbor-joining trees inferred for each data set from an uncorrected “*p*” distance matrix. The best-fit ML model (Table 11) for CLTC was TVM + Γ and for Cyt-B, ND2 and the combined data set was GTR + Γ + INV (Swofford et al. 1996). A PAUP* search was first performed under the “minimum evolution” criterion of Rzhetsky and Nei (1992) (originally described as “LS-length” by Kidd and Sgaramella-Zonta 1971) using maximum-likelihood genetic

distances. Using the optimal ML model inferred from the AIC tests, Bayesian analyses were performed on each data set using the program MrBayes (version 3.0b4, Huelsenbeck and Ronquist 2001). Because the TVM + Γ substitution model is not implemented in MrBayes, I replaced it with GTR for the analysis of CLTC. On the combined data set, the data were partitioned by gene and analyzed under the best-fit ML model for each gene. Uniform interval priors were assumed for the parameters, except for base frequencies, which were assigned a Dirichlet prior (Huelsenbeck and Ronquist 2001). Four heated chains were run for 2.0×10^6 generations, and sampled every 1000. After visually examining burn-in plots from each run using Tracer (Rambaut and Drummond 2003) to insure the chain had reached stationarity, trees from the first 100,000 generations were discarded, with the remaining trees used to estimate posterior probabilities of tree topology and other ML parameters. Three independent runs with different random seeds were performed to ensure the posterior probabilities were stable.

Table 11. Parameters for maximum-likelihood finite-sites DNA substitution model.

	Maximum-likelihood			
	ND2	Cyt- <i>b</i>	CLTC	Combined
# bp	1098	1048	735	2881
r_{AC}	0.185	0.273	1.109	0.823
r_{AG}	9.194	9.468	5.622	7.069
r_{AT}	0.596	1.089	0.785	1.806
r_{CG}	0.539	0.499	1.938	0.611
r_{CT}	4.219	6.709	5.622	10.784
α	0.784	0.795	1.348	0.593
p_{iv}	0.0313	0.368	-	0.270
freq(A)	0.335	0.323	0.296	0.309
freq(C)	0.374	0.391	0.186	0.289
freq(G)	0.053	0.058	0.201	0.140
freq(T)	0.238	0.228	0.317	0.263

4.2.4. Co-phylogeny of *Lamprocorpus* and *Nothoprocta*

Parallel line to this study, we (J. Weckstein & Valqui in prep.) analyzed the co-phylogenetic history between *Nothoprocta* and one of its ectoparasites, the lice of the genus (*Lamprocorpus*).

Lice extraction, sequencing and database construction, was done in the Field Museum of Chicago by Jason Weckstein. Even though more than four genera of lice were collected, for this analysis only lice from the genus *Lamprocorpus* were included in the analysis so far.

The louse tree consisted of 38 in-group taxa (*Lamprocorpus* sp.) and two outgroup taxa (*Cuclotocephalus* sp. and *Heptapsogaster* sp.). Two genes were sequenced: 379 base pairs of COI and 347 of the nuclear protein coding EF1alpha gene. A Bayesian tree was constructed using a partitioned analysis with the two genes set as unlinked partitions and applied the GTR+I+G model to both. This analysis estimates all parameters separately for each partition. Two separate runs were performed with four chains (default setting) for 5 million generations and saved a sample every 500 generations. Tracer was used to determine when the chains reached stationarity and conservatively, the first 500 sampled trees were discarded as burnin.

For the cophylogenetic analysis, Treemap 1.0b was used to construct a tanglegram of associations between host and parasite terminal taxa. We used reconciliation analysis, as implemented in Treemap (Page 1995) to assess whether there was a strong pattern of co-speciation between *Lamprocorpus* and its *Nothoprocta* hosts. 10,000 randomizations of the parasite tree with respect to the host tree were run.

4.3. Results

4.3.1 General Pattern of Diversity

As seen in chapter 2, *Nothoprocta* diversity in the Andes is entirely beta-diversity. The species show what I term a parapatric stratified distribution pattern, with little empty space (few gaps) between them. Despite possible variations in the width of suitable distributional area and habitats over such a large latitudinal range, mapping latitudinal patterns of richness (fig. 20) indicates that there is no region of peak diversity that might suggest a “center of diversification”, nor a latitudinal diversity pattern. A plot of number of species by latitude shows a pattern similar to that for subspecies. Thus, in contrast to many patterns of species richness, *Nothoprocta* shows no peak near the equator (or anywhere else).

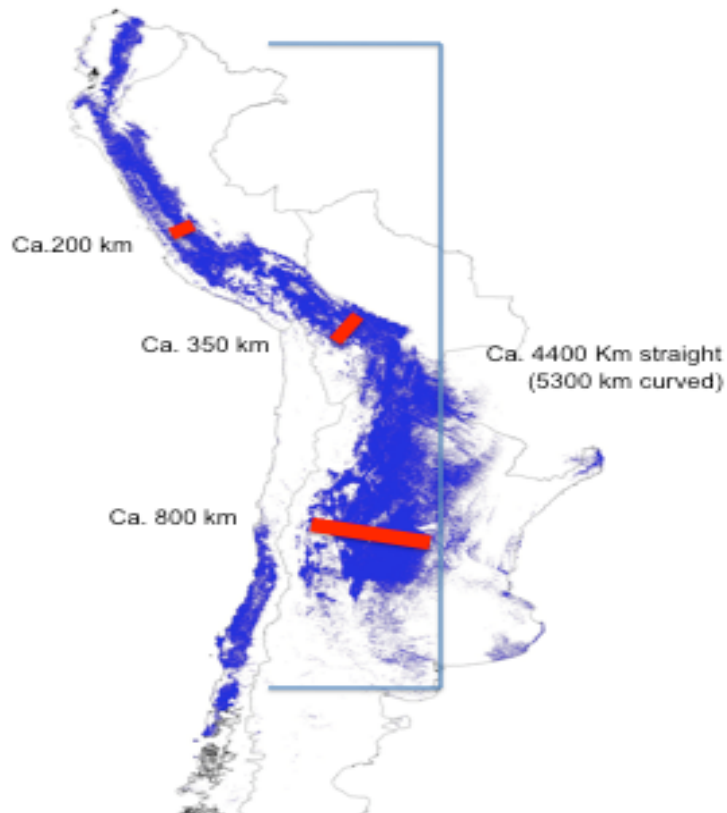


Figure 19. Overall shape of *Nothoprocta* distribution and approximate width of suitable habitat.

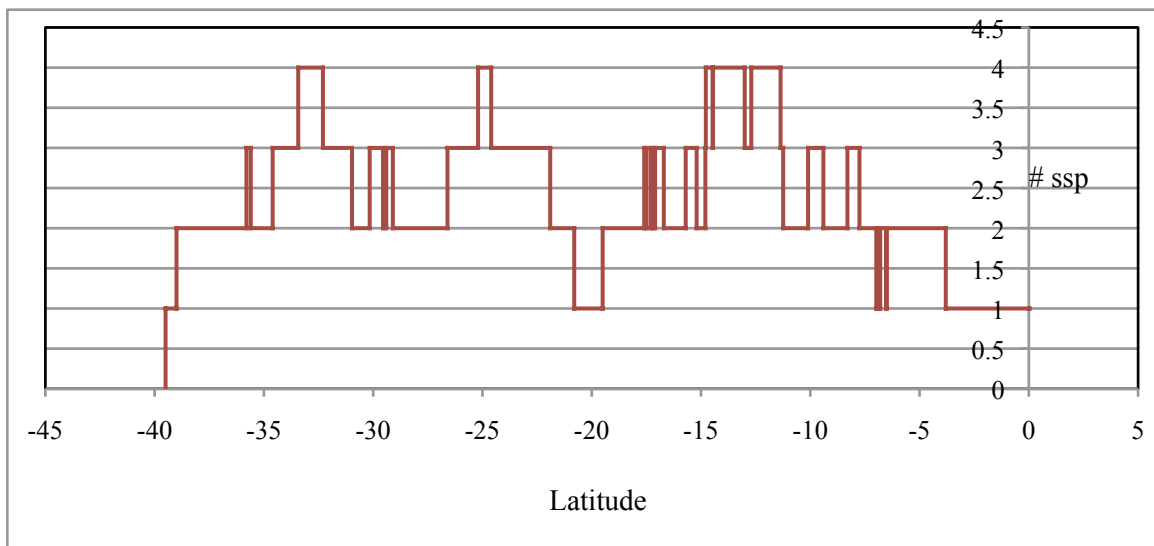


Figure 20. Number of subspecies taxa for *Nothoprocta* vs. latitude.

4.3.2. Are *Nothoprocta* of Andean or Lowland Origin?

Most taxa of *Nothoprocta* occur in high elevations, and even the lowland forms always have distributions contiguous with the base of the Andes. Therefore, the group is considered “Andean”. Because the Andean setting is considered an important condition in the diversification and current distribution patterns of Andean birds, it is important to determine whether the Andean “character” is ancestral or not. This requires the resolved phylogeny of the group. Two most-parsimonious explanations exist (fig.21), which imply four character changes. One is an early-acquired Andean character after the split of *N. cinerascens*, followed by three independent lowland derived characters. Alternatively, the Andean character could have been acquired later, after the split of *N. oustaleti* and the remaining *Nothoprocta* species. This would imply one or two character changes to higher elevations (subspecies *fulvescens* and *oustaleti*), and one by the rest of the species, with one reversal, i.e., lowland *N. perdicaria*. The latter would seem less likely given the central distribution of the Andean subspecies of *oustaleti*, but until the relationships among the subspecies of *N. oustaleti*, currently a four-way polytomy, are better resolved, we cannot be certain.

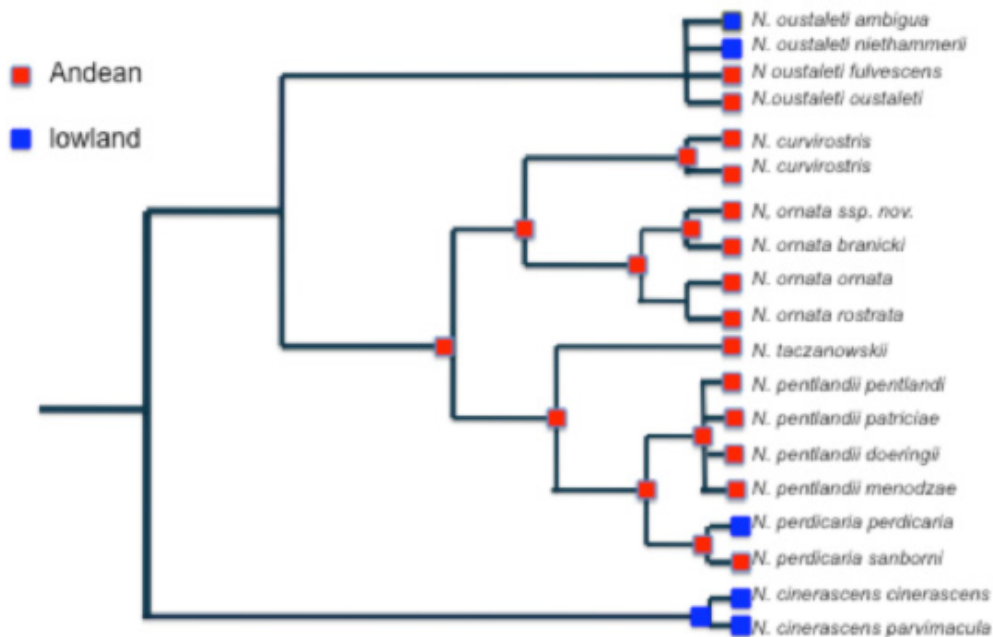


Figure 21. *Nothoprocta* phylogeny with Andean and lowland character states.

4.3.3 Distribution Patterns and Phylogeny

The basal split in the genus is the one between *N. cinerascens* and the ancestor to the rest of all *Nothoprocta*. Geographically, *N. cinerascens* is at a southeastern edge of the overall distribution of *Nothoprocta*. The next split is that between *N. oustaleti* and the ancestor of the remaining *Nothoprocta*. *Nothoprocta oustaleti* has a rather central distribution latitudinally, but is at the western edge of the overall distribution of *Nothoprocta* (fig. 22). *Nothoprocta oustaleti* and *N. cinerascens* are allopatric, separated by at least 1000 km and the Andean cordillera.

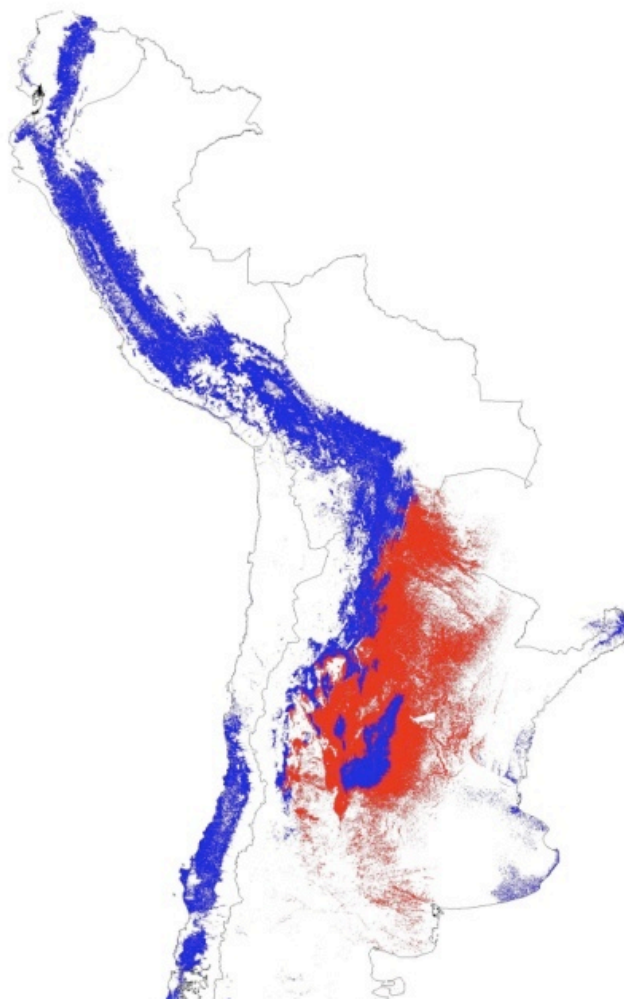


Figure 22. Map of *Nothoprocta cinerascens* (red) and all other species combined (blue).

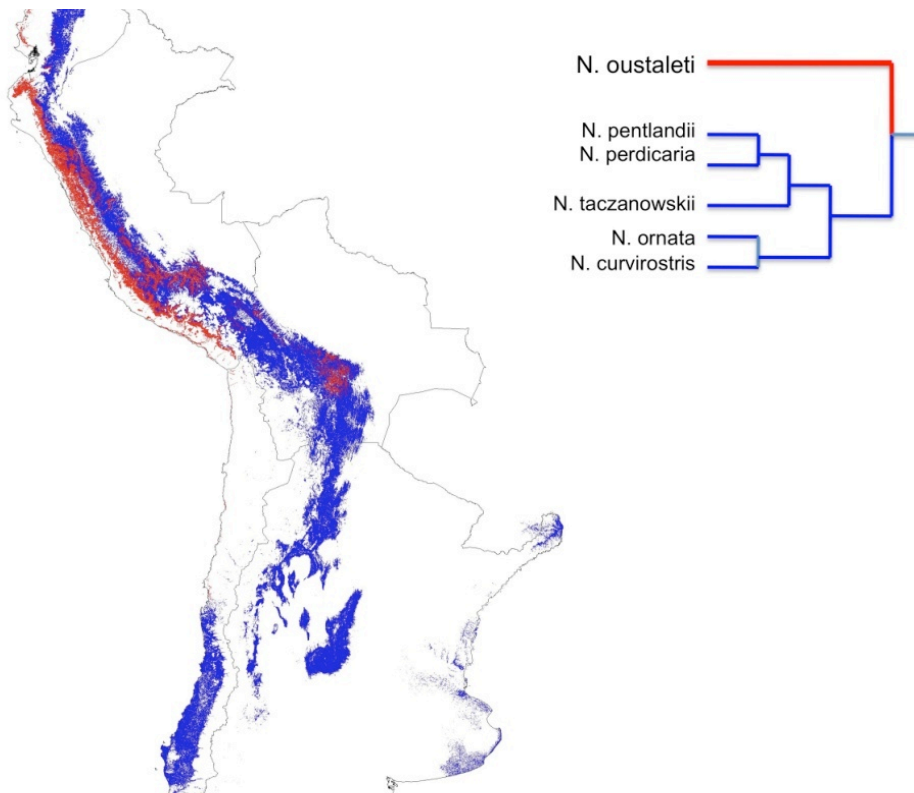


Figure 23. Predicted distribution of *Nothoprocta oustaleti* (red) and all other species (minus *N. cinerascens*) combined.

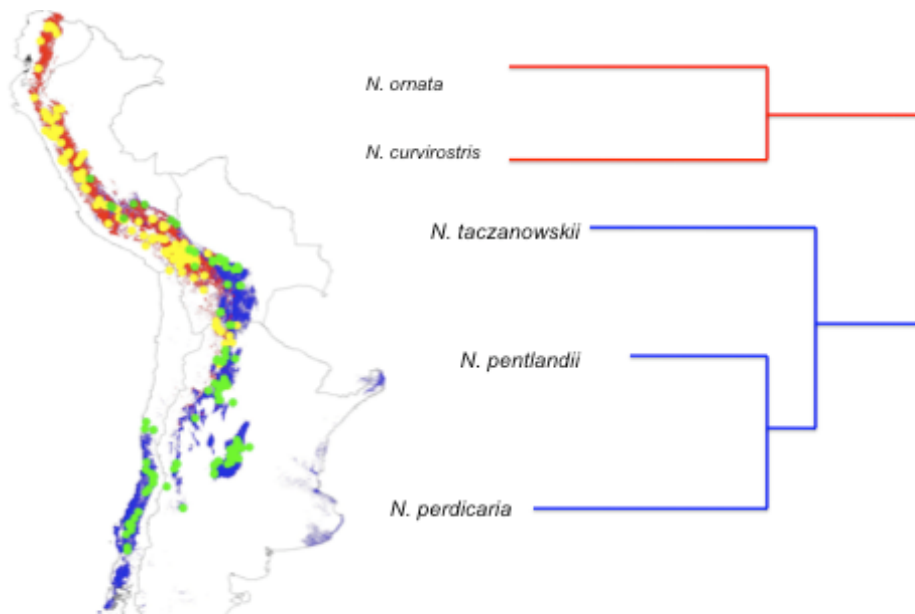


Figure 24. Predicted area and actual records for combined *Nothoprocta curvirostris*-*N. ornata* (red) and yellow (dots), and combined *N. pentlandii*-*N. perdicaria*-*N. taczanowskii* (blue) and green dots).

The remaining species form two distinct clades that divide two mostly-northern species from three mostly-southern species (fig. 24), and where they overlap latitudinally, the separation is in the east-west axis. In the remaining clade, the three species (*N. pentlandii*, *N. perdicaria*, and *N. taczanowskii*) are all allopatric, although the niche models suggest that there could be an area of contact between *N. taczanowskii* and *N. pentlandii* in the east.

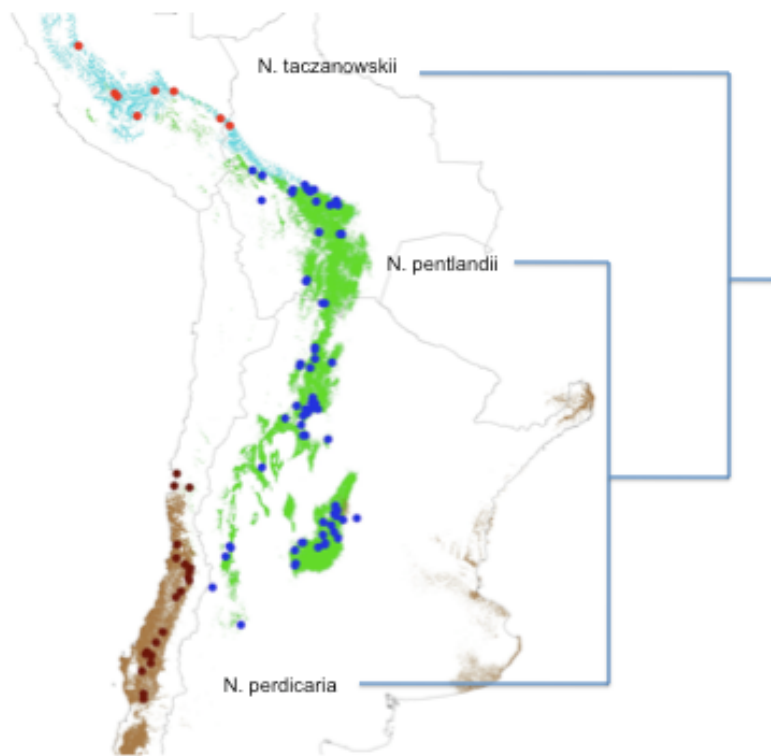


Figure 25. Distribution pattern of *Nothoprocta taczanowskii*, *N. pentlandii* and *N. perdicaria*.

The sister taxa in this clade are *N. pentlandii* and *N. perdicaria*, which are divided by the Andean cordillera. Given the Andean distributions of *N. curvirostris* and *N. pentlandii*, the most likely speciation scenario in this case would be a dispersal event from the eastern Andes to the western lowlands. The remaining clade consists *N. ornata* and *N. curvirostris*. Their combined distribution spans almost 4000 km of latitude but with a maximum width of only 280 km; the zone of parapatry is less than 400 km in length. Where parapatric, they segregate by elevation, and the niche models predict that they experience interspecific competition. Toward the northern distributional limit of *N. ornata*, the patches of suitable habitat predicted by the niche models are occupied by *N. curvirostris*, not *N. ornata*. Likewise, towards the southern distributional limit of *N. curvirostris*, large areas predicted to be occupied by the species are occupied by *N. ornata*, with *N. curvirostris* displaced to lower elevations.



Figure 26. Distribution of sister clade *Nothoprocta ornata* and *N. curvirostris*. Shades of colors represent different subspecies.

4.3.4. Distribution Patterns at the Subspecies Level

Subspecies potentially show different distribution patterns than species, because their patterns are by definition of more recent origin. Table 12 summarizes some of the patterns considered relevant at the subspecies level.

Table 12. Patterns of distribution in geographically adjacent subspecies according to predicted niche models.

Subspecies pairs	Distribution	Latitudinal distribution break	Habitat differentiation
<i>ambigua- oustaleti</i>	Continuous	Yes	Yes
<i>branickii-ornata</i>	Continuous	Yes	Weak
<i>rostrata-ornata</i>	Gap	Yes	Weak
<i>curvirostris-peruviana</i>	Gap	Yes	Weak
<i>sanborni-perdicaria</i>	Gap	Yes	Weak
ssp. nov. – <i>branickii</i>	Gap	Yes	No
<i>mendozae-pentlandii</i>	Gap	Yes	No
<i>niethammeri-oustaleti</i>	Gap	No	Yes
<i>fulvescens-oustaleti</i>	Gap	No	Weak
<i>doeringi-pentlandii</i>	Gap	No	Weak

Eight of ten adjacent pairs of subspecies are allopatric, and two are parapatric. As in the pattern among species, there is a strong latitudinal component in the taxonomic breaks, with seven of ten boundaries along the latitudinal axis. Clear habitat differentiation seems only to play an important role in the case of *N. o. oustaleti*- *N. o. ambigua*; in the other nine cases, habitat differences are nonexistent or weak, thus implying allopatric differentiation.

4.3.5. Can Chewing Lice Tell Us Something about *Nothoprocta* Biogeography?

10,000 randomizations of the parasite tree with respect to the host tree (fig. 27) indicate that the three co-speciation events reconstructed do not differ more than would be expected by chance alone; in other words, there is no strong evidence ($P = 0.17$) of co-speciation between *Nothoprocta* and its *Lamprocorpus* chewing lice (fig 28).

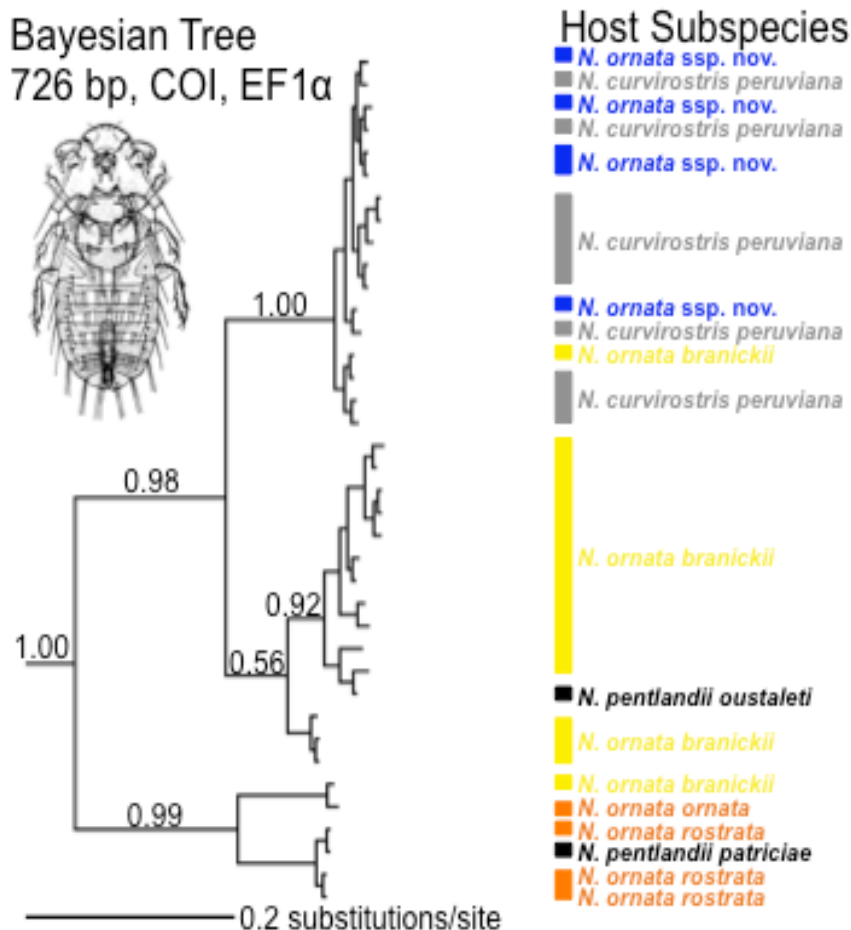


Figure 27. Host subspecies mapped to the *Lamprocorpus* phylogeny. From Weckstein & Valqui in prep.

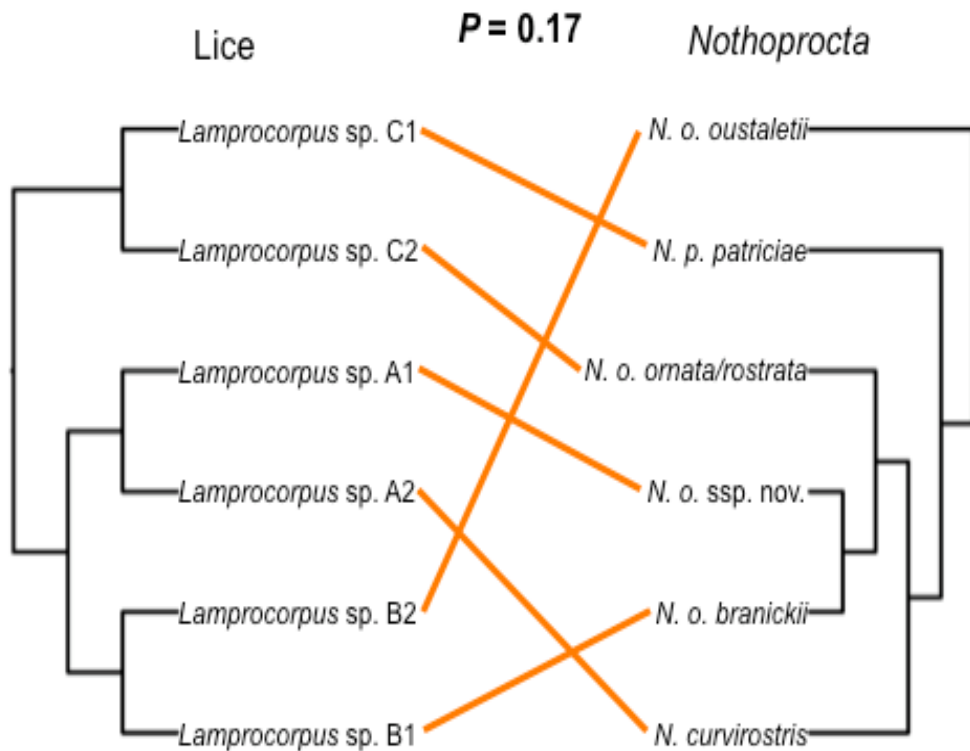


Figure 28. Tanglegram of phylogenies of *Lamprocorpus* lice and *Nothoprocta* tinamous. Orange lines indicate host-parasite associations. The P -value of 0.17 (>0.1) indicates that the three co-speciation events reconstructed via reconciliation analysis do not differ significantly from random. From Weckstein & Valqui in prep.

We mapped host species and host subspecies onto the louse tree to understand patterns of host specificity. Host species fall out all over the louse tree, without a clear taxonomic pattern, and different subspecies of the same tinamou species host different louse species. The species-level taxonomic mismatch between louse and host, as well as the lack of co-speciation, can be explained by lateral transfer of parasites within three major biogeographic units. A strong pattern of phylogenetic signal within a geographic region is revealed when one maps them onto the *Lamprocorpus* louse phylogeny (fig.29). Clade A occurs in the north, B in the center, and C in the south. The only exception is of central-clade-lice intruding into the north by means of a host species (*N. oustaletii*) that occurs in both north and central regions, but on which additional samples ($n=12$), no *Lamprocorpus* lice were found.

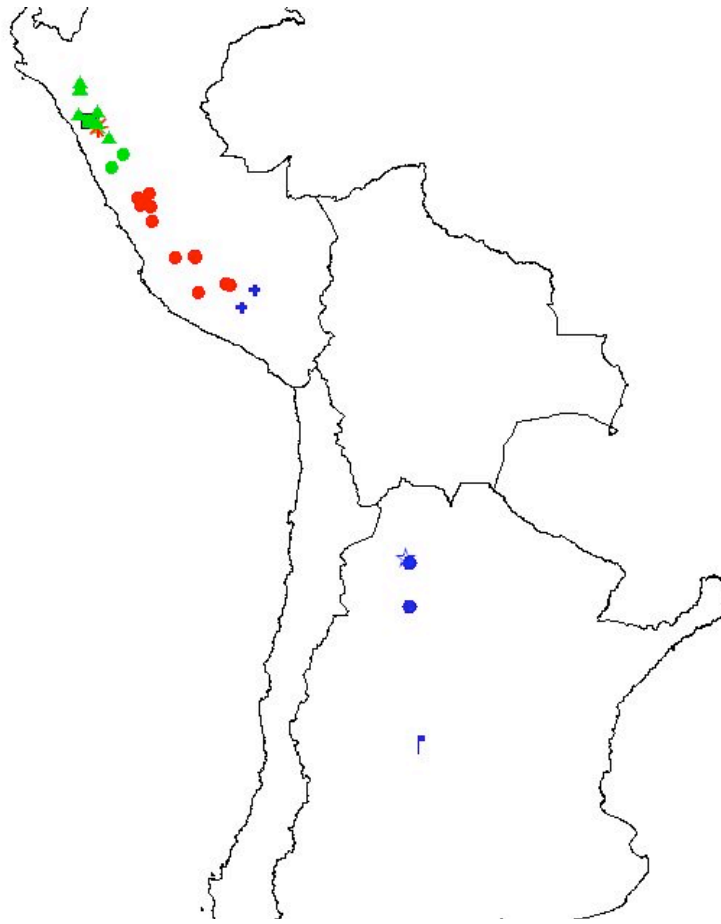


Figure 29. Lice of the genus *Lamprocorpus* mapped in the localities where tinamou hosts were collected. Colors correspond to lice from clades A (green), B (red), and C (blue). Symbols correspond to host species: flag (blue)= *N. cinerascens*, star (blue)= *N. pentlandii*, hexagon (blue)=*N. o. rostrata*, cross=*N. o. ornata*, circles=*N. o. branickii*, square=*N. ornata* ssp. , triangle=*N. curvirostris*, and asterisk (red)= *N. oustaleti*.

It is also noteworthy that northern (clade A) lice parasitize both *N. ornata* ssp. nov. and the most northern populations of *N. ornata branickii*, despite isolation of these two subspecies (Chapter 3). More southerly populations of *N. o. branickii* are parasitized by *Lamprocorpus* lice from clade C. Thus, louse-host co-speciation at the subspecies level seems not to have happened here either, despite apparent host isolation. This might be readily explainable by the other host for that louse clade, *N. curvirostris*, acting as a means for lice in clade A to travel between *N. ornata* ssp. nov. and *N. o. branickii*. Is the southern limit of this louse clade determined by *N. curvirostris*? The potential of a deep phylogeographic split between lice found on one host subspecies (*N. o. branickii*) is intriguing, but requires additional samples. The central vs. south boundary of louse clades seems to fall neatly at the *N. ornata- N. branickii* boundary in southern Peru. Here, it is noteworthy that, despite proximity, continuity, and a possible hybridization zone between the host subspecies, the louse clades B and C exhibit a clean break. Again, better sampling is needed to confirm this pattern.

4.3.6. A Northern, Central, and Southern Partitioning of *Nothoprocta*

I used the same three-way partition found in the *Lamprocorpus* lice with the *Nothoprocta* phylogeny to see if the mechanism dividing the louse clades produces the same signal among their hosts. With regards to the central-southern partition, the pattern is straight forward: *N. pentlandii*, *N. perdicaria*, and *N. cinerascens* clearly belong in the southern section, whereas *N. ornata* is split, with subspecies *ornata* and *rostrata* falling in the southern region and *branickii* in the central region. The rest of the taxa fall in the central + northern region. Fig. 30 shows the predicted distributions, thus explaining some of the overlap (not reflected by real distributions).

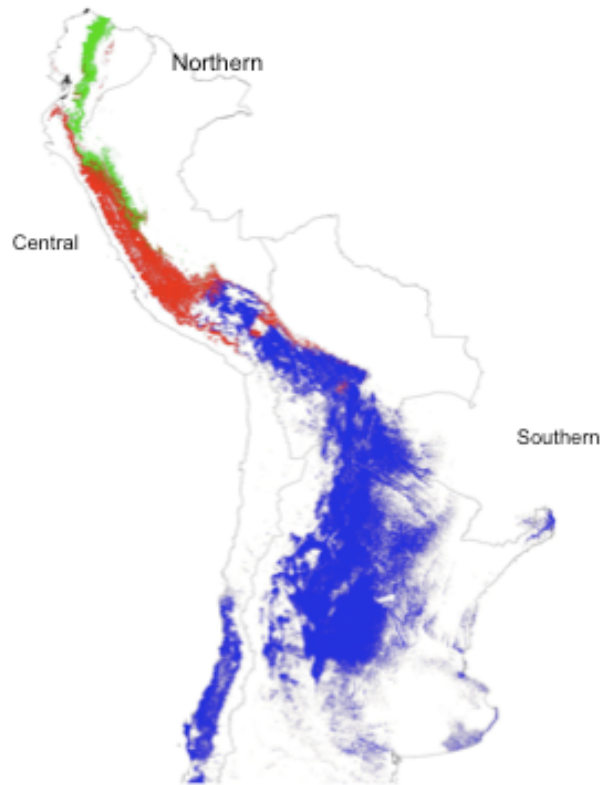


Figure 30. Three-way partitioning of *Nothoprocta* taxa according to the zonation of the three *Lamprocorpus* lice clades.

The northern-central split is less clear, and assigning taxa to each area is not so clear cut. In fig. 31, the southern, central and northern “character” states are imposed onto the phylogeny of *Nothoprocta*. Any of these regions, rather than being of ancestral origin (as in the lice), seem to have been derived repeatedly for each major clade. The only exception is a clade with two members, *N. perdicaria* and *N. pentlandii*, in the same region. At the subspecies level, the taxa are mostly confined to one of the three regions. Exceptions are shown in the Fig. 31 as terminal branches.

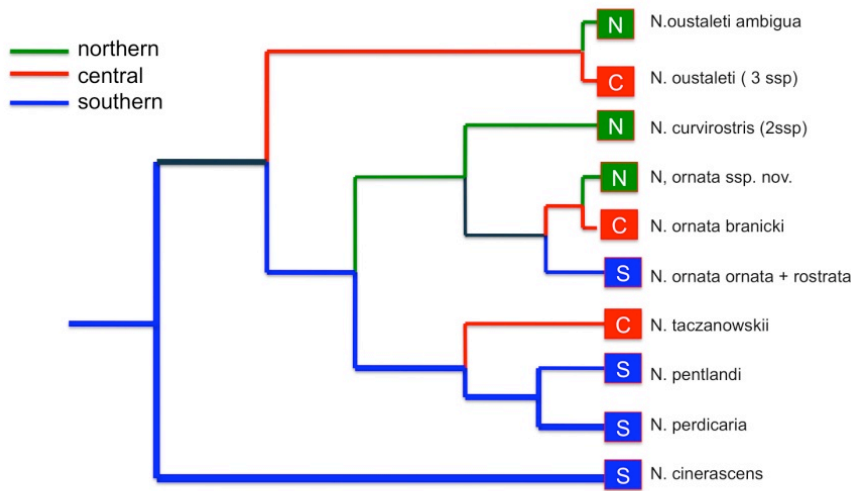


Figure 31. Northern, Central, and South character states in the phylogeny of *Nothoprocta*.

4.4 Conclusions

Seven species and 17 subspecies of *Nothoprocta* are packed into a large section of the high Andean massif without geographic overlap and few gaps among taxa. The high density of parapatric and barely allopatric distributions naturally provokes questions concerning the mechanism of *Nothoprocta* diversification. Despite the extensive parapatry, none of the analyzed distributions show a pattern that would support parapatric speciation. The only sister species with a large, altitudinally stratified contact zone, are *N. ornata* and *N. curvirostris*. However, the contact area is less than 10% of their overall distribution, which would more likely be explained by latitudinal allopatric speciation, followed by secondary contact. The other examples of sister species occurring parapatrically do so in contact zones at the latitudinal boundaries of their distributions, typically where two ecoregions meet. Allopatric distribution of sister taxa is the norm. Parapatric species sharing long altitudinal boundaries along an elevational gradient and stratifying by elevation are not sister taxa.

Table 13. Summary of the geographic pattern among sister subspecies, species or major clades.

	cis Andean break		trans-Andean break (allopatric)	no defined pattern
	parapatric	allopatric		
major sister clades or sister species	2	1	1	2
Subspecies	2	5	3	2+

However current examples of allopatric speciation by isolation are also uncommon. At the species level, one case of isolation might best be explained by dispersal and a founding population: *Nothoprocta perdicaria* is isolated from its sister species and all other members of the genus. At the subspecies level, another two examples of this pattern of isolation exist: *N. oustaleti niethammeri*, isolated in the west-Peruvian lomas formations, and *N. pentlandii doeringi* isolated in the Córdoba-San Luis mountain range. Other, less clear-cut cases of isolation, such as *Nothoprocta oustaleti fulvescens*, in the eastern inter-Andean valleys of Peru may further support the pattern. The mechanisms that produce these patterns are considered most likely, but we cannot discard, that even allopatry can be attained after parapatric speciation (such as after climate change).

As noted by Graves (1985), long and narrow geographic distributions, such as those of Andean birds, are more easily fractured on the narrow axis. Such breaks, and the subsequent genetic isolation of the populations between the breaks, are necessary for allopatric differentiation. In most cases, *Nothoprocta* taxa fit this pattern. Three clear examples of latitudinal breaks between subspecies exist. Only one is based on an actual geographic barrier: *N. c. curvirostris* - *N. c. peruviana* on opposite sides of the Huancabamba valley. Another case of allopatry may be the consequence of an interaction with another species: *N. ornata* ssp. nov. and would likely be parapatric, but the intervening area is occupied by *N. curvirostris*. A third case of latitudinal allopatry *N. p. perdicaria* and *N. p. sanborni*, does not correspond to any known barrier or habitat discontinuity, but may be a sampling artifact.

For the remainder, the overall continuity of the distributions, and suitable habitat predicted by the niche models, indicates secondary contact. The lack of a consistent pattern where such breaks occur suggests that such breaks either occur (a) randomly (regarding their geographic position), (b) at places different than current distributions could suggest, or (c) at sites that were breaks historically, but are no longer true barriers to distribution.

The study of the geographic distribution of the parasitic lice (*Lamprocorpus*) suggests that their three main clades are tied to three geographic regions: northern, central, and southern. Of these, the southern-central break seems concordant with the distribution patterns of their tinamou hosts. This break separates *Nothoprocta* into northern (three species) and southern (three species) groups and with the seventh species evenly split into two southern and two northern subspecies. Whether this split is significant to the overall underlying speciation mechanism requires further analysis, such as the modeling of historic niche conditions for the species.

Elevation has shown to be an important variable in *Nothoprocta* distribution, because they largely occur in the Andes and stratify by altitude. However elevation does not seem to play a direct role in the speciation process. Two of the examples of possible isolation by dispersal are accompanied by major shifts in elevation. However, at least in the case of *N. perdicaria*, a major barrier was the source of isolation. The case of *N. o.*

niethammeri could be considered a case of elevational isolation, but it is based on a very unusual ecological phenomenon in the western Peruvian Andes: the lomas formations isolated by desert.

Elevational stratification, however, is important in species packing, with up to three species dividing up a single slope by elevation. Thus, it plays an important role in maintaining diversity. The natural history of tinamous seems to prevent them from occurring syntopically. These terrestrial birds inhabit relatively simple vegetation such as grassland and scrub, with no opportunity to segregate by vegetational strata. An interpretation of the lack of syntopy is that their habitat is insufficiently complex or heterogeneous to allow horizontal segregation. The homogeneity in the genus in terms of body size and bill shape also suggests that either (a) morphological differentiation is phylogenetically constrained or that (b) limited resource diversity constrains segregation by the morphological features typically associated with niche differences in birds. How their elevational stratification is maintained would require investigation of resource availability and testing physiological responses to environmental conditions at different elevations.

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APPENDIX . SAMPLES FOR WHICH TISSUE WAS AVAILABLE AND GENES FOR WHICH SEQUENCES COULD BE OBTAINED

TAXA with tissue	Species code	ND2	CytB	CLTC	origin & storage
<i>Nothoprocta perdicaria</i>	NprCLCTeu302730			x	GenBank
<i>Nothoprocta perdicaria</i>	NprGB_U76053		x		GenBank
<i>Nothoprocta p. perdicaria</i>	NprpTV960	x	x		This project/LSU
<i>Nothoprocta p. perdicaria</i>	NprpTV961	x	x	x	This project/LSU
<i>Nothoprocta p. sanborni</i>	NprsTV962	x	x		This project/LSU
<i>Nothoprocta p. sanborni</i>	NprsTV963	x	x	x	This project/LSU
<i>Nothoprocta p. sanborni</i>	NprsTV964	x	x		This project/LSU
<i>Nothoprocta p. sanborni</i>	NrsTV965	x		x	This project/LSU
<i>Nothoprocta p. sanborni</i>	NprsTV966	x	x	x	This project/LSU
<i>Nothoprocta p. sanborni</i>	NprsTV967	x	x		This project/LSU
<i>Nothoprocta perdicaria</i>	NprxNK35279	x	x	x	UNM
<i>Nothoprocta c. cinerascens</i>	NcicTV934	x	x	x	This project/LSU
<i>Nothoprocta c. cinerascens</i>	NcicTV935	x	x	x	This project/LSU
<i>Nothoprocta c. cinerascens</i>	NcicTV936	x	x	x	This project/LSU
<i>Nothoprocta taczanowskii</i>	NtaNK159818	x	x	x	UNM
<i>Nothoprocta curvirostris peruviana</i>	NcupTV615	x	x		This project/LSU
<i>Nothoprocta curvirostris peruviana</i>	NcupTV660	x	x		This project/LSU
<i>Nothoprocta curvirostris peruviana</i>	NcupTV863		x		This project/LSU
<i>Nothoprocta curvirostris peruviana</i>	NcupTV917	x	x	x	This project/LSU
<i>Nothoprocta curvirostris peruviana</i>	NcupTV924	x	x	x	This project/LSU
<i>Nothoprocta curvirostris peruviana</i>	NcupKGM1352		x	x	UAF
<i>Nothoprocta curvirostris peruviana</i>	NcupKGM1354	x	x		UAF
<i>Nothoprocta curvirostris peruviana</i>	NcupKGM1355	x	x	x	UAF
<i>Nothoprocta curvirostris peruviana</i>	NcupKGM1356	x	x		UAF
<i>Nothoprocta ornata ornata</i>	NoroTV887	x	x	x	This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroTV888	x	x	x	This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroTV889	x	x		This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroTV890	x	x	x	This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroTV891	x	x		This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroTV892	x	x	x	This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroTV893		x	x	This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroB61421	x	x	x	This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroB61422	x	x	x	This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroB61426	x	x		This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroB61451	x	x	x	This project/LSU

<i>Nothoprocta ornata ornata</i>	NoroB61459	x	x	x	This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroB61463	x	x		This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroB103894	x	x	x	This project/LSU
<i>Nothoprocta ornata ornata</i>	NoroYPM136961	x	x		YPM
<i>Nothoprocta ornata ornata</i>	NoroYPM136962	x	x		YPM
<i>Nothoprocta ornata ornata</i>	NoroYPM136963	x	x		YPM
<i>Nothoprocta ornata ornata</i>	NoroYPM136964	x	x		YPM
<i>Nothoprocta ornata ornata</i>	NoroYPM136965	x	x	x	YPM
<i>Nothoprocta ornata ornata</i>	NoroYPM136966	x	x	x	YPM
<i>Nothoprocta ornata ornata</i>	NoroYPM136967	x	x		YPM
<i>Nothoprocta ornata ornata</i>	NoroYPM136968	x	x		YPM
<i>Nothoprocta ornata rostrata</i>	NorrTV943	x	x		This project/LSU
<i>Nothoprocta ornata rostrata</i>	NorrTV944	x	x	x	This project/LSU
<i>Nothoprocta ornata rostrata</i>	NorrTV945	x	x	x	This project/LSU
<i>Nothoprocta ornata rostrata</i>	NorrTV946	x	x	x	This project/LSU
<i>Nothoprocta ornata rostrata</i>	NorrUSNM609491	x	x	x	USNM
<i>Nothoprocta ornata rostrata</i>	NorrUSNM620750	x	x	x	USNM
<i>Nothoprocta ornata rostrata</i>	NorrUSNM620751	x	x	x	USNM
<i>Nothoprocta ornata branickii</i>	NorbTV617	x	x	x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV618	x		x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV619	x		x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV684	x	x	x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV744	x	x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV745	x	x	x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV746		x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV747	x	x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV805	x	x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV806	x	x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV807	x	x	x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV808	x	x	x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV809	x	x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV814	x	x	x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV817	x	x	x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV822	x	x	x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV825	x	x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV862	x	x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV871			x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV873	x	x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV877	x	x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV878	x	x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV968	x	x		This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbTV969	x	x	x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbB61359	x	x	x	This project/LSU
<i>Nothoprocta ornata branickii</i>	NorbB61361	x	x	x	This project/LSU
<i>Nothoprocta ornata ssp. nov.</i>	NornTV911	x	x	x	This project/LSU

<i>Nothoprocta ornata ssp. nov.</i>	NornTV912	x	x		This project/LSU
<i>Nothoprocta ornata ssp. nov.</i>	NornTV913	x	x	x	This project/LSU
<i>Nothoprocta ornata ssp. nov.</i>	NornTV915	x	x	x	This project/LSU
<i>Nothoprocta ornata ssp. nov.</i>	NornTV916	x	x		This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV612	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV613	x	x		This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV614	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV616	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV651	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV652	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV653	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV654	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV734	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpepTV753	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV811	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV812		x		This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV813	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV864	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV865	x	x		This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV867	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV868	x			This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV894	x	x		This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV910	x	x	x	This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoTV994BND2_7	x			This project/LSU
<i>Nothoprocta oustaleti oustaleti</i>	NpeoNK162918	x	x	x	UNM
<i>Nothoprocta oustaleti oustaleti</i>	NpeoPE6035	x	x		UNM
<i>Nothoprocta p. pentlandii</i>	NpepTV942	x	x	x	This project/LSU
<i>Nothoprocta p. pentlandii</i>	NpepB6601	x	x	x	LSU
<i>Nothoprocta p. pentlandii</i>	NpepYPM136997	x	x		YPM
<i>Nothoprocta p. pentlandii</i>	NpepYPM136998	x	x		YPM
<i>Nothoprocta p. patriciae</i>	NpetTV947	x	x	x	This project/LSU
<i>Nothoprocta p. patriciae</i>	NpetTV948	x	x	x	This project/LSU
<i>Nothoprocta p. patriciae</i>	NpetTV949	x	x	x	This project/LSU
<i>Nothoprocta p. patriciae</i>	NpetTV950	x	x	x	This project/LSU
<i>Nothoprocta p. patriciae</i>	NpetTV951	x	x	x	This project/LSU
<i>Nothoprocta p. patriciae</i>	NpetTV952	x	x	x	This project/LSU
<i>Nothoprocta p. patriciae</i>	NpetTV953	x	x	x	This project/LSU
<i>Nothoprocta p. patriciae</i>	NpetTV954	x	x	x	This project/LSU
<i>Nothoprocta p. patriciae</i>	NpetTV955	x	x	x	This project/LSU
<i>Nothoprocta p. patriciae</i>	NpetTV956	x	x	x	This project/LSU
<i>Rhynchotus rufescens</i>	RhynrufB113855		x	x	LSU
<i>Rhynchotus rufescens</i>	RhynrufB13971	x	x		LSU
<i>Rhynchotus rufescens</i>	RhynrufYPM100922	x	x		YPM
<i>Rhynchotus rufescens</i>	RhynrufYPM100995	x	x		YPM
<i>Rhynchotus rufescens</i>	RhynrufYPM136984	x	x		YPM

<i>Rhynchotus rufescens</i>	RhynrufYPM136985	x	x		YPM
<i>Eudromia elegans</i>	EuelB37357	x	x	x	LSU
<i>Eudromia elegans</i>	EudeleGB_AF338710	x	x		GenBank
<i>Eudromia elegans</i>	Eudele_eu302722			x	GenBank
<i>Nothura boraquira</i>	NotborB6622	x	x		LSU
<i>Nothura darwinii</i>	NotdarTV819	x	x	x	This project/LSU
<i>Nothura darwinii</i>	NotdarTV820	x	x	x	This project/LSU
<i>Nothura darwinii</i>	NotdarTV821	x	x	x	This project/LSU
<i>Nothura darwinii</i>	NotdarB103903	x	x	x	LSU
<i>Nothura maculosa</i>	NotmacUSNM630474	x	x		USNM
<i>Tinamotis pentlandii</i>	TinpendTV756	x	x	x	This project/LSU
<i>Tinamotis pentlandii</i>	TinpendB7597	x	x	x	LSU
<i>Nothocercus nigrocapillus</i>	NotnigrB43542	x	x	x	LSU
<i>Nothocercus nigrocapillus</i>	NotnigrB44076	x	x	x	LSU
<i>Nothocercus bonapartei</i>	NotbonB33178	x	x	x	LSU
<i>Nothocercus julius</i>	NotjulB380	x	x	x	LSU
<i>Nothocercus julius</i>	NotjulB32810	x		x	LSU
<i>Tinamous major</i>	TinmajGB_AF338707	x	x		GenBank
<i>Tinamous major</i>	TinmajB28055	x		x	LSU
<i>Tinamous guttatus</i>	TingutB27649	x	x		LSU
<i>Tinamous guttatus</i>	TingutB42614	x	x	x	LSU
<i>Tinamous guttatus</i>	Tingut_eu302745			x	GenBank
<i>Tinamous solitarius</i>	TinsolitB25977	x	x	x	LSU
<i>Tinamous tao</i>	TintaoB10860	x	x	x	LSU
<i>Crypturellus undulatus</i>	CrypunGB_AY139629		x		GenBank
<i>Crypturellus undulatus</i>	CrypunduB3594	x	x	x	LSU
<i>Crypturellus parvirostris</i>	CrypvarB13927	x	x	x	LSU
<i>Crypturellus parvirostris</i>	CrypvarB40657	x	x		LSU
<i>Crypturellus obsoletus</i>	CryptobsoB18248	x	x	x	LSU
<i>Crypturellus obsoletus</i>	CryptobsB36824	x	x	x	LSU
<i>Crypturellus tataupa</i>	CrytataGB_AY16012	x	x		GenBank
<i>Crypturellus tataupa</i>	CrypttatauN46004	x	x	x	GenBank
<i>Crypturellus cinereus</i>	CryptcinB40430	x	x		LSU
<i>Crypturellus atrocapillus</i>	CryatroTV857	x		x	This project/LSU
<i>Crypturellus bartletti</i>	CrybartTV321	x		x	This project/LSU
<i>Crypturellus duidae</i>	Cryduid3199	x			LSU
<i>Crypturellus soui</i>	CrysouUSNM586295	x	x	x	USNM
<i>Crypturellus strigilosus</i>	CrystriGB_U76056		x		GenBank
<i>Crypturellus soui</i>	Crysou_eu738107			x	GenBank
<i>Crypturellus sp.</i>	CryspB10756	x		x	LSU
<i>Pterocnemia pennata</i>	PterpecnAF338709	x	x		GenBank
<i>Pterocnemia pennata</i>	PtepecnEU805778			x	GenBank

YPM=Yale Peabody Museum, UNM=University of New Mexico, LSU=Museum of Natural Science, Louisiana State University, USNM=Smithsonian, United States Museum of Natural History, UAF=University of Alaska Fairbanks.

VITA

Thomas Holger Valqui Haase, was born in Lima, Peru, in May, 1966, to Holger Gustavo Valqui Casas and Ana Maria Haase Goldkuhle. He attended elementary, high and Abitur in the Humboldt school, graduating from Abitur in 1986. He got a bachelor's and an engineer's degree in forestry sciences in the Universidad Nacional Agraria, la Molina in Peru. In 1995 he attended Princeton University and got a Master in Arts degree in October of 1998. In the year 2000 he started doctoral studies in Louisiana State University where he expects to earn a degree of Doctor in Philosophy in the spring of 2009 with a dissertation on the biogeography and phylogeny of *Nothoprocta tinamous*. He plans to return and conduct research in Peru in the Center for Ornithology and Biodiversity, where he has been president since 2007.