WHY DO BIRDS MIGRATE? THE ROLE OF FOOD, HABITAT, PREDATION AND COMPETITION

by

W. Alice Boyle

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

2006

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

As members of the Dissertation Committee, we certify that we have read the dissertation prepared by W. Alice Boyle entitled “Why do Birds Migrate? The Role of Food, Habitat, Predation, and Competition” and recommend that it be accepted as fulfilling the dissertation requirement for the degree of Doctor of Philosophy.

____Date: 11/17/06
Judith Bronstein

____Date: 11/17/06
Courtney Conway

____Date: 11/17/06
Brian Enquist

____Date: 11/17/06
Daniel Papaj

____Date: 11/17/06
Robert Steidl

Final approval and acceptance of this dissertation is contingent upon the candidate’s submission of the final copies of the dissertation to the Graduate College. I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

____Date: 11/17/06
Dissertation Director: Judith Bronstein

____Date: 11/17/06
Dissertation Director: Courtney Conway

STATEMENT BY AUTHOR

SIGNED: Alice Boyle .

ACKNOWLEDGMENTS

I am indebted to my two advisors, Judie Bronstein and Courtney Conway, for having the confidence in me to take me on as their student. They have provided me with abundant support and advice. Above all, they have taught me how to think about science, do science, and teach science to others. The rest of my committee—Brian Enquist, Dan Papaj, and Bob Steidl—have been there for me whenever needed, and have provided excellent feedback at all stages of this project.

I have been exceptionally lucky in number and quality of those people who volunteered days, weeks, or months of their time to help me in the field: B. Boyle, J. Brokaw, M. Burke, R. Cabezas, L. Cholodenko, C. Clews, S. Cullen, D. Erikson, W. Goulding, , M. Hill, V. Johnson, N. Kahn, C. Leumas, M. Lord, I. Manley, J. Montoya-Morera, K. Meyers, P. Sanchez, H. Reider, R. Repasky, C. Romagosa, J. Sun, A. Torres, A. Wargon, A. Weldon, M. Williams, J. Wolfe, A. Zambrano, and J. Zook. In Tucson, E. Dreyer, S. Hemmings, B. Horvath, B. Ruppell helped with the data entry, S. White spent a summer sorting fecal samples, and M. Ali and G. Bieber gleaned flycatcher data.

Many fellow graduate students, post-docs, and staff at the University of Arizona have provided advice, help, and support. In particular, I thank P. Abbot, E. Arnold, G. Binford, K. Bonine, K. Borgmann, M. Brewer, S. Forsyth, V. Garcia, H. Harvey, E. Hebets, N. Holland, K. Hughes, J. Mason, M. Mayfield, J. Ness, K. Prudic, J. Oliver, K. Riley, J. Weeks, S. Whitworth, J. Schondube, L. Schwartz, M. Smith and W. Turner.

Permission to work in Costa Rica was granted by J. Guevara (Ministerio del Ambiente y Energía), R. Tenorio (ACCVC, Parque Nacional Braulio Carrillo), A. Bien (Rara Avis), R. Matlock and L. D. Gómez (La Selva Biological Station), Selva Tica, and the U. Arizona IACUC committee. The staff of Rara Avis, La Selva, the LS-Barva TEAM project (D. Clark), and the ALAS project (J. Longino, D. Brenes) greatly facilitated field logistics. M. Snyder helped with GIS matters. C. Valldeperas kindly donated canary eggs. The curators and staff of the herbarium at INBio processed my plants, and B. Boyle, B. Hammel, J. Gonzalez, R. Kriebel, F. Morales, C. Taylor, O. Vargas, and N. Zamora greatly assisted with plant identification.

My dissertation work was supported financially by the National Science Foundation (DDIG No. 0410531), the Natural Sciences and Engineering Research Council of Canada (PGS-B fellowship), the Research Training Group in Biological Diversification at the University of Arizona (NSF-DIR-9113362, BIR-9602246), the Silliman Memorial Research Award, the Center for Insect Science, the International Arid Lands Consortium, the American Ornithologists' Union, the Explorer's Club, the Tinker Foundation, the Women in Science and Engineering, the Dept. of Ecology and Evolutionary Biology, and the University of Arizona Graduate College.

Among the many talented people who have worked on migration, frugivory, and tropical ornithology, four exceptional scientists provided perennial inspiration over the past six years. I am indebted to Doug Levey, Bette Loiselle, Alexander Skutch and Gary Stiles for providing so much of the foundation I have built this dissertation upon.

Finally, my thanks go to Brad who got me hooked on birds in the first place, who has taught me so much, and loved me throughout.

DEDICATION

To my mom who didn’t live to see me succeed and my dad who didn’t doubt that I would.

TABLE OF CONTENTS

ABSTRACT

The ultimate causes of bird migration are largely unknown despite more than a century of research. By studying partially migratory short-distance tropical migrants and by employing comparative methods, some difficulties in testing hypotheses for evolution of migration can be overcome. Using comparative methods I tested a major hypothesis for why migration evolved in some lineages and not in others. The results of this study conflicted with many assumptions and predictions of the evolutionary precursor hypothesis. Most importantly, migratory behavior was not related to diet and habitat in simple ways. The interaction between diet and habitat as well as consistent associations between flocking behavior and migration suggested that food variability is poorly captured by the surrogates embodied in the evolutionary precursor hypothesis. I then employed comparative methods to studying tropical altitudinal migration. Comparisons of diets and fruit preferences between species pairs showed that migrants are more frugivorous, eat a broader diversity of fruits, and have diets that more strongly resemble their preferences than do residents. Although providing evidence that food limitation plays a role in altitudinal migration, these results do not support the hypothesis that interspecific competition explains variation in migratory behavior. Next, I provided the first test of a predation-based hypothesis to explain altitudinal migration. Migrants breed at higher elevations than where they spend their non-breeding season. Thus, birds may migrate uphill to escape high nest predation risk at lower elevations. Results from this experimental study are largely consistent with this hypothesis, but anomalies between predicted and observed patterns suggest that either the migration of lowland

birds occurs in response to other factors, or that anthropogenic change has altered the tradeoffs involved in deciding whether or not to migrate. Finally, I focus on a single migrant species and evaluate (a) two food-based hypotheses to explain the destination of migration movements, and (b) mechanisms underlying intra-specific differences in migratory strategy. Food can explain why *Corapipo altera* migrate uphill, but not why they migrate downhill. My data on sex bias and body condition leads to a new hypothesis explaining the complete annual cycle of this tropical migrant bird.

INTRODUCTION

An explanation of the problem and review of literature

Animal migration is among the most conspicuous of animal behaviors. The best-known examples involve large numbers of individuals that synchronously migrate long distances over inhospitable terrain, and make the return journey only a few months later. In no other group is annual, cyclical migration as well-studied as in birds. A great deal of research has been devoted to elucidating the patterns of migration exhibited by different taxa (Dingle 1996, Gauthreaux 1996), and more recently, to explain how such migrations operate at physiological and genetic levels (e.g., Alerstam 1991, Berthold 1991). In addition to these proximate questions, the ecological (Keast and Morton 1980, Greenberg and Marra 2005) and conservation (Hagan and Johnston 1992, Martin and Finch 1995) implications of bird migration have also been the focus of considerable research. However, a major gap in my understanding of migration lies in identifying which ecological factors have been the most important in promoting the evolution of migration. Hypotheses explaining how (Berthold 1999, Joseph et al. 1999, Bell 2000, Kokko and Lundberg 2001, Zink 2002, Joseph et al. 2003) and why (Cox 1968, Fretwell 1980, Greenberg 1980, Ketterson and Nolan 1983, Cox 1985, Fretwell 1985, Levey and Stiles 1992, Holmgren and Lundberg 1993, Lloyd et al. 2001, Lank et al. 2003, Sol et al. 2005) bird migration evolved abound, but tests of these hypotheses are rare. My dissertation addresses this important gap in our knowledge by providing specific tests of both established and new hypotheses to explain why bird migrate, focusing attention on those mechanistic hypotheses why only *some* birds migrate.

The major ecological processes proposed to explain the evolution migration in birds are of food limitation (e.g., Cox 1968, Levey and Stiles 1992), predation (e.g., Fretwell 1980, Greenberg 1980), and intolerance of climatic conditions (e.g., Ketterson and Nolan 1976). Spatial and/or temporal variation in one or more of these three factors underlies all explanations for bird migration. Yet each hypothesis relies on a different combination of factors acting through various potential mechanisms to produce observed patterns of migratory behavior. Part of the complexity lies in the fact that different parts of the migratory cycle may best be explained by different sets of selective pressures. For instance, birds may migrate to their breeding grounds because the risk of nest predation is lower on breeding grounds than on non-breeding grounds. However, they may migrate away from the breeding grounds because they cannot find enough food there to survive during the non-breeding season (Greenberg 1980). Often, climatic extremes, food availability, and density of potential predators covary in such a way that isolating which factor has been the most important in the evolution of migration is extremely difficult.

The standard approach to dealing with such a problem—through manipulative experiments—is simply not feasible in the majority of bird migration systems. For example, we cannot manipulate predation risk (or food availability) and expect a change in migratory behavior (even if that factor is responsible for the evolution of migration) for at least two reasons. First, in many species migratory behavior is an evolutionary response to a set of ecological conditions, and that response no longer varies among individuals. Second, even if it were reasonable to expect a response on ecological time scales, the act of migrating itself makes the response difficult to detect. Until recently, determining the non-breeding locations of breeding birds has relied upon the inefficient method of banding millions of birds and subsequently recapturing a tiny fraction of those individuals thousands of kilometers away (Alerstam 1990). Even with the advent of more sophisticated techniques for tracking individuals, the spatial and temporal resolution possible is generally poor (Webster et al. 2002).

Two main approaches can be employed to circumvent the difficulties of testing hypotheses for migration. First, comparative methods provide excellent means of testing evolutionary hypotheses. This approach is especially powerful when the trait of interest is highly labile, being repeatedly gained and lost over evolutionary history within families or genera as is true for bird migration (Joseph et al. 2003, Outlaw et al. 2003). All hypotheses explaining bird migration make predictions regarding the suite of traits that would be expected to differ between migrant and non-migrant birds. When comparisons among species account for similarities due to shared evolutionary history, the correlated evolution of traits across taxa provides strong evidence for similar selective pressures having acted in the same way in the evolution of a trait (Harvey and Pagel 1991). Second, one can focus on migration systems in which (a) migratory behavior varies among ecologically similar species and among individuals within a species, (b) the distances migrated are short, and (c) the breeding and non-breeding areas are similar. Such conditions greatly reduce the number of hypotheses that could explain migration, facilitate linking breeding and non-breeding areas, allow an examination of the correlates of migratory behavior both among and within species, and also permit landscape-level studies that encompass the entire environmental gradient over which a species migrates.

I utilized both of these approaches in my dissertation. Much of my work focused on the altitudinal migration of frugivorous birds in Central America. These migrations involve uphill movements of birds to breeding grounds followed by downhill movements during the non-breeding season (Stiles 1983). Increasing evidence is revealing that such migrations are important in both tropical forests (Pearson 1980, Ramos-Olmos 1983, Loiselle and Blake 1991, Cardoso da Silva 1993, Johnson and Maclean 1994, Ornelas and Arizmendi 1995, Burgess and Mlingwa 2000, Solórzano et al. 2000, Galetti 2001, Symes et al. 2001, Chaves-Campos et al. 2003, Hobson et al. 2003) and temperate forests (Rabenold and Rabenold 1985, Laymon 1989, Gutiérrez and Delehanty 1999) around the world. Previous work has focused exclusively on the role that spatial and temporal variation in food resources play in the evolution of tropical altitudinal migration (Loiselle and Blake 1991, Rosselli 1994, Solórzano et al. 2000, Chaves-Campos 2004). However, these studies provide inconclusive evidence for the role of food-limitation, and have not tested any alternative hypotheses based on factors such as predation or weather. Thus, although we know a great deal more regarding the ecology and migration patterns of tropical frugivorous birds, the ultimate causes for those migrations, and the ways in which the evolution of altitudinal migration and long-distance migration might be related, are still not known.

My dissertation work has substantially contributed to these gaps in our knowledge of bird migration. First, my work provides a large body of empirical data that greatly expands our understanding of the correlates of bird migration at both macro- and micro scales. The results of the large-scale comparative work (Appendix A) challenge many important features of one of the most widely-cited hypotheses for variation among lineages in migratory behavior, and advance the field by reformulating that hypothesis to be consistent with the new data. The results of the local-scale comparative work (Appendix B) rule out competition for food as a mechanism to explain the differences among closely related species in migratory tendency, also demonstrating for the first time that a previously-noted pattern of increased frugivory among lineages of altitudinal migrant birds is reflected even at the species level even among ecologically similar species pairs. The results of the nest predation study (Appendix C) present the first data on patterns of nest predation risk along a contiguous elevational gradient risk from any region in the world. The detailed studies of food resources and variation in migratory behavior within a single species (Appendix D) contribute demonstrate that food availability must only be part of a full explanation for altitudinal migration. Appendices B and D contribute both conceptual arguments and empirical data suggesting that the methods currently used to estimate fruit availability to tropical frugivores is inadequate to test the hypotheses they are frequently called upon to support or reject. Additionally, Appendix D provides the first tests of hypotheses explaining partial migration in a tropical species which differs in important life-history traits from the temperate species in the context of which these hypotheses were formulated.

In addition to the these conceptual contributions to the field of bird migration and avian ecology, the large quantity of empirical data from a relatively understudied region of the world will likely be of use to a variety of tropical biologists in fields ranging from plant-animal interactions, life-history evolution, and foraging ecology. Finally, this dissertation provides an example of the utility of tackling broad research questions using a variety of approaches and working at several levels—from the level of the hemisphere down to the level of the individual bird. The conclusions drawn at each level can inform our understanding of the results of studies at different levels. Appendices A and B point toward variability in food resources being the most important factor in the evolution of bird migration, but appendix C shows that we can’t rule out predation as an alternative, at least to explain part of the migratory cycle. Appendix D suggests that variability in food resources affects migratory tendency via weather-related and metabolic mechanisms, potentially explaining some of the causes for the dietary differences observed among short- and long-distance migrants (Appendix A) and between altitudinal migrant and resident species (Appendix B).

Explanation of dissertation format

The research included in this dissertation investigates the causes of migration from a macroevolutionary scale down to the level of the individual bird. I evaluate hypotheses relying on variation in foraging guild, habitat-related differences in food and climate, dietary constraints, gradients of nest predation risk, and in within- and among-species competition. Four manuscripts are included as appendices.

Appendix A, “Why migrate? A test of the evolutionary precursor hypothesis,” takes a broad-scale comparative approach to evaluate a widely-cited hypothesis relying upon habitat- and diet-related differences in resource availability to explain why some lineages of birds contain species that migrate both short and long distances, whereas many lineages contain only sedentary species. Appendix B, “Why do some, but not all, tropical birds migrate altitudinally?” evaluates two mechanistic hypotheses based on differences among species in competitive abilities and dietary preferences to explain why some tropical frugivores migrate altitudinally whereas other do not. Appendix C, “Can variation in risk of nest predation explain altitudinal migration in tropical birds?” tests an alternative to food-based hypotheses to explain the movements of birds uphill to their breeding grounds by examining the spatial patterns of relative nest predation risk along a tropical mountain slope. Appendix D, “Extrinsic and intrinsic factors explaining altitudinal migration in a tropical bird” examines seasonal and spatial patterns of resource abundance and the migration patterns of a single migrant species (*Corapipo altera*) to evaluate the role of food limitation in explaining altitudinal migration, both among and within species.

PRESENT STUDY

The methods, results, and conclusions of this study are presented in the manuscripts appended to this dissertation. The following is a summary of the most important findings in this document.

Appendix A provides the first rigorous empirical test of one of the major hypotheses proposed to explain the evolution of avian migration. Levey and Stiles (1992) suggested that use of open habitats and a frugivorous diet are both precursors to the evolution of migration in birds, and Chesser and Levey (1998) later argued that habitat preference is *more* important than diet in determining whether a particular species evolved migratory behavior. I tested the evolutionary precursor hypothesis by examining the nature and extent to which habitat and diet are associated with migratory behaviour in a large New World group of birds. I also examined the influence of foraging group size, membership in mixed-species flocks, elevational range, and body mass. In addition to using raw species means, I constructed supertrees for all 556 species in the Tyranni and repeated the analyses using phylogenetically independent contrasts. Raw species analyses corroborated some results from the previous two studies that put forth the evolutionary precursor hypothesis, but results derived from phylogenetically independent contrasts highlighted an important (yet previously ignored) interaction between habitat and diet and shed some doubt on their roles as “precursors” to migration. Habitat was an important correlate of migratory behaviour for insectivores but not frugivores, and contrary to the predictions of the evolutionary precursor hypothesis, migrants were more insectivorous than were residents. Foraging group size was negatively associated with migratory behaviour in both raw species and independent contrast analyses. Furthermore, the ecological traits associated with sedentary vs. migratory behaviour differed from the traits associated with migratory distance, suggesting that short- and long-distance migratory strategies may represent different responses to different sets of selective pressures.

Appendix B makes two conceptual contributions to the study of short-distance migration and the foraging ecology of frugivorous animals by empirically testing two alternative hypotheses to explain migration. Because tropical altitudinal migrant birds are drawn disproportionately from frugivorous foraging guilds, hypotheses explaining variation in migratory behavior have focused on how spatial and temporal patterns of fruit availability might favor migratory behavior. However, these hypotheses fail to explain species-specific patterns of migration, and cannot explain why many sympatric frugivorous birds do not migrate. I developed two mechanistic hypotheses that potentially explain how variation in fruit resources could explain variation in migratory behavior among coexisting species. The second conceptual contribution was to clarify the predictions and methods appropriate when testing hypotheses that rely on measuring fruit resources. Previous studies have estimated the standing crop of fruits among elevations and seasons. I argue that standing crop is not the measure of fruit availability relevant to testing hypotheses explaining the evolution of altitudinal migration. Optimal foraging theory predicts that fruit standing crop should not differ among sites within a season if birds migrate in response to those resources because consumption rates should equilibrate at levels where the per capita net energetic intake is the same. Thus, measuring the relative production of fruit biomass for the relevant subset of the fruiting plant community is critical to testing such hypotheses.

The empirical portion of Appendix B involves testing the two mechanistic hypotheses. The competitive exclusion hypothesis casts migrants as competitively inferior fruit foragers compared to residents, whereas the dietary specialization hypothesis casts migrants as dietary specialists compared to residents. I tested five predictions of these two hypotheses by comparing species-level differences in diet breadth, fruit preferences, and the relationship between diet and preference among related pairs of migrant and resident species. I found that migrants and residents differed in all aspects of diet and preference I evaluated. Migrant species consumed a greater diversity of fruits and proportionally fewer arthropods than their resident counterparts. The fruit preferences of migrants were stronger than their resident counterparts, and despite sharing preferences for fruits of the same plant species (within a species pair), the diets of migrants more closely reflected those preferences than did the diets of their resident counterparts. My results suggest that migrants may be competitively superior foragers for fruit than residents. This finding allows us to eliminate the competitive exclusion hypothesis.

Appendix C reformulates and tests a previously-ignored hypothesis that could potentially explain why many tropical species migrate uphill to breed. Fretwell (1980) proposed an hypothesis that predicts (when adapted to altitudinal migration systems) that if nest predation explains why many tropical birds migrate uphill to breed, then predation risk must be negatively correlated with elevation. Using data from 385 artificial nests at eight sites spanning 2740 m of elevation, I showed that predation risk declines with increasing elevation. However, nest predation risk was not highest at the lowest elevations sampled (30–120 m), but rather was lowest in premontane forest at 500–650 m. My results suggest that for many altitudinal migrant birds, higher elevation breeding areas are safer nesting areas than their lower elevation non-breeding areas. However, elevational patterns of predation risk cannot explain why some lowland birds migrate to mid-elevations to breed. Lower nest predation risk in lowland vs. premontane forest implies that either (a) other ecological processes influence the migrations of lowland birds, or (b) that anthropogenic disturbance and fragmentation in the lowlands has caused changes in the predator communities, such that the risk of nest predation at lowland sites has been reduced.

In Appendix D, I used a focal manakin species (*Corapipo altera*) to test food-based hypotheses for migration. I tested two alternative hypotheses based on arthropod availability and fruit production rates to explain the migration patterns of *C. altera*. I also tested three hypotheses proposed to explain why some *C. altera* individuals migrate but other individuals do not. I examined dietary data, and estimates of arthropod abundance and fruit production rates of 18 plant species consumed by *C. altera* over 12 months at three elevations spanning this species' migratory range. I also quantified the relative abundance of different age- and sex-classes of *C. altera* at different elevations, and assessed individual body condition. Results based on arthropod sweep samples suggest that manakins do not migrate uphill to breed to exploit abundant arthropod prey. In contrast, results based on fruit production rates suggest that C. altera might migrate uphill to breed to exploit an abundance of preferred fruits for fledglings. However, differences in fruit availability can not explain downhill migration; breeding elevations consistently produce more fruit than lower elevations. Migratory behavior appears to be male-biased in this species, and the consequences of migration differ between sexes. Females that do migrate have lower body mass for their body size than do females that remain on breeding grounds, whereas males that migrate have higher body mass for their body size than do males that remain on breeding grounds. Rejection of the fruit availability hypothesis to explain downhill movements and the variation within *C. altera* in both migratory strategy and the consequences of migration lead me to propose a new hypothesis to explain altitudinal migration in *C. altera*. This new hypothesis relies upon both food abundance and physiological constraints imposed by the interactions between a highly frugivorous diet, physiology, and climatic differences among elevations to explain why many (but not all) *C. altera* spend the non-breeding season in the lowlands, but return to mid-elevations to breed.

REFERENCES

Alerstam, T. 1990. Bird Migration, English edition. Cambridge University Press, Cambridge, UK.

Alerstam, T. 1991. Bird flight and optimal migration. Trends in Ecology & Evolution **6**:210-215.

Bell, C. P. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. Journal of Avian Biology **31**:258-265.

Berthold, P. 1991. Genetic control of migratory behavior in birds. Trends in Ecology & Evolution **6**:254-257.

Berthold, P. 1999. A comprehensive theory for the evolution, control and adaptability of avian migration. Ostrich **70**:1-11.

Burgess, N. D., and C. O. F. Mlingwa. 2000. Evidence for altitudinal migration of forest birds between montane Eastern Arc and lowland forests in East Africa. Ostrich **71**:184-190.

Cardoso da Silva, J. M. 1993. The Sharpbill in the Serra dos Carajás, Para, Brazil, with comments on altitudinal migration in the Amazon Region. Journal of Field Ornithology **64**:310-315.

Chaves-Campos, J. 2004. Elevational movements of large frugivorous birds and temporal variation in abundance of fruits along an elevational gradient. Ornitología Neotropical **15**:433-445.

Chaves-Campos, J., J. E. Arévalo, and M. Araya. 2003. Altitudinal movements and conservation of Bare-necked Umbrellabird *Cephalopteris glabricollis* of the Tilarán Mountains, Costa Rica. Bird Conservation International **13**:45-58.

Chesser, R. T., and D. J. Levey. 1998. Austral migrants and the evolution of migration in New World birds: diet, habitat and migration revisited. American Naturalist **152**:311-319.

Cox, G. W. 1968. The role of competition in the evolution of migration. Evolution **22**:180-192.

Cox, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. American Naturalist **126**:451-474.

Dingle, H. 1996. Migration: the Biology of Life on the Move. Oxford University Press, NY.

Fretwell, S. D. 1980. Evolution of migration in relation to factors regulating bird numbers. Pages 517-527 *in* A. Keast and E. S. Morton, editors. Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC.

Fretwell, S. D. 1985. Why do birds migrate? Inter and intraspecific competition in the evolution of bird migration: contributions from population ecology. Pages 630-637 *in* Proceedings of the 18th International Ornithological Congress.

Galetti, M. 2001. Seasonal movements and diet of the Plumbeous Pigeon (*Columba plumbea*) in a Brazilian Atlantic Forest. Melopsittacus **4**:39-43.

Gauthreaux, S. A. 1996. Bird migration: methodologies and major research trajectories (1945-1995). Condor **98**:442-453.

Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493-504 *in* A. Keast and E. S. Morton, editors. Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC.

Greenberg, R., and P. P. Marra, editors. 2005. Birds of Two Worlds: The Ecology and Evolution of Migration. Johns Hopkins University Press, Baltimore, MD.

Gutiérrez, R. J., and D. J. Delehanty. 1999. Mountain Quail (*Oreortyx pictus*). Pages 1-28 *in* A. Poole and F. Gill, editors. The Birds of North America. The Birds of North America, Inc., Philadelphia, PA.

Hagan, J. M., and D. W. Johnston, editors. 1992. Ecology and Conservation of Neotropical Migrant Landbirds. Smithsonian Institution Press, Washington, DC.

Harvey, P. H., and M. D. Pagel. 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford, UK.

Hobson, K. A., L. I. Wassenaar, B. Mila, I. Lovette, C. Dingle, and T. B. Smith. 2003. Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. Oecologia **136**:302-308.

Holmgren, N., and S. Lundberg. 1993. Despotic behavior and the evolution of migration patterns in birds. Ornis Scandinavica **24**:103-109.

Johnson, D. N., and G. L. Maclean. 1994. Altitudinal migration in Natal. Ostrich **65**:86-94.

Joseph, L., E. P. Lessa, and L. Christidis. 1999. Phylogeny and biogeography in the evolution of migration: shorebirds of the *Charadrius* complex. Journal of Biogeography **26**:329-342.

Joseph, L., T. Wilke, and D. Alpers. 2003. Independent evolution of migration on the South American landscape in a long-distance temperate-tropical migratory bird, Swainson's flycatcher (*Myiarchus swainsoni*). Journal of Biogeography **30**:925-937.

Keast, A., and E. S. Morton, editors. 1980. Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC.

Ketterson, E. D., and V. Nolan Jr. 1976. Geographic variation and its climatic correlates in sex-ratio of eastern wintering Dark-eyed Juncos (*Junco hyemalis hyemalis).* Ecology **57**:679-693.

Ketterson, E. D., and V. Nolan Jr. 1983. The evolution of differential bird migration. Current Ornithology **1**:357-402.

Kokko, H., and P. Lundberg. 2001. Dispersal, migration, and offspring retention in saturated habitats. American Naturalist **157**:188-202.

Lank, D. B., R. W. Butler, J. Ireland, and R. C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. Oikos **103**:303-319.

Laymon, S. A. 1989. Altitudinal migration movements of Spotted Owls in the Sierra Nevada, California. Condor **91**:837-841.

Levey, D. J., and F. G. Stiles. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. American Naturalist **140**:447-476.

Lloyd, P., R. M. Little, T. M. Crowe, and R. E. Simmons. 2001. Rainfall and food availability as factors influencing the migration and breeding activity of Namaqua Sandgrouse, *Pterocles namaqua*. Ostrich **72**:50-62.

Loiselle, B. A., and J. G. Blake. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology **72**:180-193.

Martin, T. E., and D. M. Finch, editors. 1995. Ecology and Management of Neotropical Migratory Birds. Oxford University Press, New York, NY.

Ornelas, J. F., and M. d. C. Arizmendi. 1995. Altitudinal migration: implications for the conservation of the Neotropical migrant avifauna of western Mexico. Pages 98-

109 *in* M. H. Wilson and A. Sader, editors. Conservation of Neotropical Migratory Birds in Mexico. Maine Agricultural and Forest Experiment Station. Miscellaneous Publications 727.

Outlaw, D. C., G. Voelker, B. Mila, and D. J. Girman. 2003. Evolution of long-distance migration in and historical biogeography of Catharus thrushes: A molecular phylogenetic approach. Auk **120**:299-310.

Pearson, D. L. 1980. Bird migration in amazonian Ecuador, Peru, and Bolivia. Pages 273-283 *in* A. Keast and E. S. Morton, editors. Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC.

Rabenold, K. N., and P. P. Rabenold. 1985. Variation in altitudinal migration, winter segregation, and site-tenacity in two subspecies of Dark-eyed Juncos in the southern Appalachians. Auk **102**:805-819.

Ramos-Olmos, M. A. 1983. Seasonal movements of bird populations at a Neotropical study site in southern Veracruz, Mexico. Ph.D. dissertation. University of Minnesota, Minneapolis, MN.

Rosselli, L. 1994. The annual cycle of the White-ruffed Manakin, *Corapipo leucorrhoa*, a tropical frugivorous altitudinal migrant, and its food plants. Bird Conservation International **4**:143-160.

Sol, D., L. Lefebvre, and J. D. Rodriguez-Teijeiro. 2005. Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. Proceedings of the Royal Society of London Series B **272**:1433-1441.

Solórzano, S., S. Castillo, T. Valverde, and L. Avila. 2000. Quetzal abundance in relation to fruit availability in a cloud forest of southeastern Mexico. Biotropica **32**:523-532.

Stiles, F. G. 1983. Birds. Pages 502-530 *in* D. H. Janzen, editor. Costa Rican Natural History. University of Chicago Press, Chicago, IL.

Symes, C. T., C. T. Downs, and S. McLean. 2001. Seasonal occurrence of the Malachite Sunbird, *Nectarinia famosa*, and Gurney's Sugarbird, *Promerops gurneyi*, in KwaZulu-Natal, South Africa. Ostrich **72**:45-49.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology & Evolution **17**:76-83.

Zink, R. M. 2002. Towards a framework for understanding the evolution of avian migration. Journal of Avian Biology **33**:433-436.

APPENDIX A

WHY MIGRATE? A TEST OF THE EVOLUTIONARY PRECURSOR HYPOTHESIS

Why migrate? A test of the evolutionary precursor hypothesis

W. Alice Boyle, Dept. of Ecology and Evolutionary Biology, University of Arizona,
alboyle@email.arizona.edu

Courtney J. Conway, USGS Arizona Cooperative Fish and Wildlife Research Unit,
School of Natural Resources, University of Arizona, cconway@ag.arizona.edu

Keywords: diet, evolution of migration, foraging flock, habitat, phylogenetically independent contrasts, resource variability, Tyranni

Short title: Precursors to the evolution of migration

Supplementary online materials: online appendix A and online appendix B (phylogeny figures 1 and 2)

Abstract

The question of why birds migrate is still poorly understood despite decades of debate. Previous studies suggested that use of edge habitats and a frugivorous diet are precursors to the evolution of migration in neotropical birds. However, these studies do not explore other ecological correlates of migration and do not control for phylogeny at the species level. We tested the evolutionary precursor hypothesis by examining the extent to which habitat and diet are associated with migratory behavior using a species-level comparative analysis of the Tyranni. We used both sedentary vs. migratory behavior and migratory distance as response variables. We also examined the influence of foraging group size, membership in mixed-species flocks, elevational range, and body mass on migratory behavior. Raw species analyses corroborated some results from studies that put forth the evolutionary precursor hypothesis, but phylogenetically independent contrast results highlighted an important interaction between habitat and diet and their roles as precursors to migration. Foraging group size was consistently associated with migratory behavior in both raw species and independent contrast analyses. Our results lead to a resource variability hypothesis that refines the evolutionary precursor hypothesis and reconciles the results of several studies examining precursors to migration in birds.

Introduction

Migration of birds has attracted much attention from biologists, especially those interested in the physiological and navigational challenges posed by long-distance movements (Gauthreaux 1996; Alerstam and Hedenstrom 1998). Despite this interest, many ecological and evolutionary aspects of migration remain unknown and the ultimate causes of migration are still debated (Rappole et al. 2003; Greenberg and Marra 2005). Many alternative hypotheses have been proposed to explain why some sedentary birds became migratory (Cox 1985; Alerstam 1990; Berthold 2001), but few studies have tested these alternatives. One impediment to testing hypotheses related to the evolution of bird migration is the inability to conduct manipulative experiments. However, comparative analyses that identify ecological correlates associated with variation in migratory behavior across species can contribute to our understanding of why migration evolves, why it is maintained, and what factors are associated with further evolutionary changes in migratory behavior (Zink 2002).

Most hypotheses proposed to explain ultimate factors influencing the evolution of bird migration have invoked one or more of the following three ecological processes: food limitation, direct climatic effects on physiological function, or risk of nest predation (e.g., Fretwell 1980; Cox 1985; Alerstam 1990; Berthold 2001). Variation in food resources may favor annual migration by forcing individuals out of unproductive areas during lean seasons, by enabling exploitation of seasonal peaks in local food availability for breeding, or via both mechanisms. Climate could lead to migratory movements if seasonality in temperature or humidity results in conditions exceeding the range in which an individual can survive or reproduce. Latitudinal (or altitudinal) gradients in predation risk may favor migratory movements if geographic differences in nest predation enable migrants to increase clutch sizes and reduce the probability of nest failure than non-migrants. These processes are not mutually exclusive, but few studies have attempted to elucidate their relative importance to the evolution of migration in birds.

Hypotheses explaining migration based on food-resource variability assume that with increasing seasonal variation in food abundance, there will be increasing likelihood that food availability will fall below threshold levels which should increase the likelihood that a bird will migrate. The degree of climatic seasonality varies among habitats, and climatic seasonality probably influences the degree of seasonality of food resources. However, the link between climatic seasonality and differential seasonality of food resources (e.g., fruit, insects, or nectar) is not clear. Some authors have assumed that, in the Neotropics, the magnitude of temporal fluctuation in fruit resources is greater than in insect resources (Levey and Stiles 1992). Janzen (1973) provided some evidence for strong seasonality in abundance of neotropical insects across seasons and among sites. Currently, no convincing evidence exists showing fruit resources to be any more seasonally variable than insect resources within a single tropical site. Nevertheless, many short-distance tropical migratory species are frugivores or nectarivores; a fact that suggests either that fruit and nectar resources are indeed more seasonal than insect resources, or that some other factor associated with diet is important in promoting migration. If either of these associations is real, then diet should explain a significant proportion of the variation in migratory behavior independent of an association between habitat and migration.

Two previous papers that attempted to identify traits associated with the evolution of bird migration focused on the role of resource fluctuation in promoting the evolution of migration. Levey and Stiles (1992) noted that many short-distance neotropical migrants are primarily frugivorous and inhabit what they termed “open habitats” (forest canopy, edge, or non-forested areas). They suggested that these open habitats are subject to large fluctuations in temperature and humidity relative to “buffered” forest interiors. They went on to note that many long-distance Neotropical migrants are drawn from the same families as these short-distance migrants. These observations led Levey and Stiles (1992) to propose the “evolutionary precursor hypothesis” to explain why some birds evolved migration whereas others did not. The evolutionary precursor hypothesis states that lineages dependent upon certain habitats (“unbuffered” areas) or resources (fruits) were pre-adapted to evolve long-distance migration.

Chesser and Levey (1998) tested the evolutionary precursor hypothesis by examining the association between habitat, diet, and migration in South American austral migratory birds, controlling for the effects of phylogeny at the family-level. They concluded that habitat type (“unbuffered” open areas vs. “buffered” forest interior) was more closely associated with migration than was diet type (fruits vs. insects) among families and subfamilies of South American birds. The association between unbuffered open areas and migration could reflect either direct physiological intolerance to climatic conditions in those habitats (i.e., fluctuations in temperature and humidity), response to climate-driven seasonality (or absolute scarcity) of food resources in those habitats, or predictable differences in predator densities between habitats. Hence, the association between habitat and migration could reflect a number of ecological processes through a variety of mechanisms.

The papers by Levey and Stiles (1992) and Chesser and Levey (1998) differ in important ways (table 1). Although Levey and Stiles (1992) contrasted sedentary species with short-distance intra-tropical migrants, Chesser and Levey (1998) compared lineages of entirely sedentary species with lineages in which ≥1 species has evolved long-distance migration between tropical and temperate regions. This difference is important because selective pressures imposed by longer migratory flights and decreasing similarity of resources and habitats available during breeding and non-breeding seasons may change the strength or nature of the associations between habitat, diet, and migration. The evolutionary precursor hypothesis does not explicitly predict that traits associated with short-distance migration are the same as traits associated with long-distance migration, although lineages are presumed to pass through an intermediate stage of short-distance migration during this evolutionary pathway toward long-distance migration. A second major difference between these two papers is the taxonomic level of the data analyzed. Levey and Stiles (1992) conducted a species-level study without the use of phylogenetically independent contrasts, whereas Chesser and Levey (1998) conducted a family-level study. Because habitat, diet, and migration can vary greatly among species within a family (del Hoyo et al. 2004), and because relatively few families or sub-families (12) were considered, Chesser and Levey's (1998) results were likely influenced by how habitat, diet, and migration categories were assigned to families. For example, using Chesser and Levey's (1998) diet classification rules, an entire family could be categorized as frugivorous if it contained

≥1 frugivorous species that may not belong to a sub-familial lineage in which migration arose. Finally, neither study included both habitat and diet in the same analysis. A thorough understanding of how these traits affect migration requires an analytical approach that reveals whether both habitat and diet explain similar portions of the variation in migratory behavior, act independently, or interact in their association with migration. Furthermore, the importance of habitat and diet should be evaluated relative to other ecologically-relevant traits not considered by either previous study (especially those potentially correlated with habitat and diet).

Chesser and Levey (1998) recognized many of these limitations and made three recommendations for future tests of the evolutionary precursor hypothesis: (1) a species-level analysis using phylogenetically independent contrasts, (2) consideration of other potential ecological correlates of migration, and (3) a more detailed coding of migratory behavior that begins to capture the diversity of movement patterns called "migration." In this paper, we test the evolutionary precursor hypothesis using an approach that incorporates all three recommendations. We use both raw species data and phylogenetically independent contrasts from the Tyranni to address the following questions. First, are habitat and diet independently associated with sedentary versus migratory behavior across species? Second, are traits other than habitat and diet more strongly associated with migratory behavior? Third, are the traits associated with increases in migratory distance the same as the traits associated with transitions from sedentary to migratory behavior?

Methods

The Tyranni is a clade of New World suboscine birds made up of 556 species in 143 genera that are grouped by different authors into one to several families. The Tyranni includes all mionectine and tyrant flycatchers, manakins, cotingas, tityras, becards, and their allies. As such, the Tyranni is one of the largest radiations of New World birds and includes the largest family of birds in the world. It is an excellent group in which to test the evolutionary precursor hypothesis because species exhibit a range of migratory behaviors, habitat associations, and diets typical of other migratory passerine species. Additionally, this clade includes both austral and nearctic migrants.

Raw Species Data

We searched for published information on non-breeding habitat, diet, foraging flock behavior, elevation, body mass, and migratory movements for all species in the Tyranni. We began with field guides and reference volumes on birds of the World and of North, Central, and South America (Snow 1982; Belton 1985; Hilty and Brown 1986; Stiles and Skutch 1989; Fjeldså and Krabbe 1990; Bond 1993; Dunning 1993; Sick 1993; Ridgely and Tudor 1994; Howell and Webb 1995; Stotz et al. 1996; National Geographic Society 1999; Poole and Gill 2000; Hilty 2003; Fitzpatrick et al. 2004; Snow 2004; Snow et al. 2004). We then supplemented these sources with many journal articles, book sections, and theses (Morton 1971, 1977; Fitzpatrick 1980; Sherry 1984; Fitzpatrick 1985; Loiselle and Blake 1991; Chesser 1994, 1995; Poulin and Lefebvre 1996; Chesser 1997, 1998; Blake and Loiselle 2002; Chesser 2005; Greenberg and Salewski 2005). We eliminated species from our dataset for which: (1) we failed to located information for any one or more of our explanatory variables, or (2) the appropriate classification for any explanatory variable was ambiguous. Our final dataset consisted of the 379 mainland species of Tyranni for which we found at least one source of information for the six variables of interest. We then sent the dataset to four ornithologists with extensive field experience with South American birds for review and made changes to the classifications of seven species based on comments received. The complete data table and a detailed explanation and rationale of how we compiled information from different sources and assigned species to categories is available online (online appendix A). We followed the taxonomic order and naming of the American Ornithologists' Union check-list of North American birds (American Ornithologists' Union 2005) and the preliminary AOU checklist of the Birds of South America (Remsen et al. 2006).

We collected information for each species based on its behavior during the non-breeding season for three reasons. First, most migrants spend more time on their non-breeding grounds than their breeding grounds (Keast and Morton 1980). Second, migratory species in the Tyranni are believed to be derived from neotropical ancestors (Traylor 1977; Rappole and Jones 2002), so habitat associations and behaviors in the non-breeding range may be more likely to represent ancestral states than breeding-range traits. Third, comparisons of habitat and diet are meaningful only between sedentary tropical species and wintering migrants because many long-distance migrants utilize habitats and resources during the breeding season that are unavailable to sedentary tropical species.

Migration. We used a more detailed classification of migratory behavior than simply sedentary versus migratory categories. Increasing evidence suggests that both temperate-breeding and tropical-breeding birds migrate annually from only a few kilometers to voyages of ≥7000 km (Berthold 2001). By including migration distance as a response variable in analyses, we assessed the implicit assumption of the evolutionary precursor hypothesis that similar selective pressures favor the evolution of all types of migratory behavior.

We considered a species as migratory when at least some populations of the species migrate annually. To estimate migratory distance, we compiled an equal-area projection map of North, Central, and South America from the MacMillan World Atlas (MacMillan 1996). We classified the 140 migratory species into one of seven migratory distance categories (sedentary, <100 km, 100–300 km, 300–700 km, 700–1500 km, 1500–3000 km, >3000 km) using range maps and range descriptions in the sources listed above. We constructed distance categories to be linear on a $\log_2$ scale. We assigned a species to the shortest migratory distance category (<100 km) when at least some populations of that species migrate locally. The number of species in this category undoubtedly underestimates the true number of species undertaking such movements because our understanding of the annual movements of many neotropical species is still growing (e.g., Ramos-Olmos 1983; Winker et al. 1997). For all other migratory species, we measured the shortest distance between the reported northern edge of the non-breeding range and the northern edge of the breeding range (for nearctic migrants) or the shortest distance between the reported southern edge of the non-breeding range and the southern edge of the breeding range (for austral migrants).

These distances correspond to the minimum distance individuals of that species must migrate. We classified partially migratory species as migratory, and when migratory distance varied among populations within a species, we used the population with the longest estimated migratory distance to represent the species as a whole.

Habitat and Diet. We assigned species to one of six general habitats: thickets or ground dwellers, forest understory, forest midstory, forest canopy, disturbed habitats and woodland, and open/arid habitats with few trees. These habitats are similar to (but more detailed than) those used by Levey and Stiles (1992) and Chesser and Levey (1998), and may represent a gradient of buffering from daily (and possibly seasonal) fluctuations in temperature and humidity (Fetcher et al. 1985; Didham and Lawton 1999). Where classifications from different sources conflicted, we chose the habitat designation that was best supported among the various sources, referring to descriptions found in (del Hoyo et al. 2004) to resolve conflicts as this source is the most taxonomically complete and thus probably most consistent among species. We used dummy variables for habitat in all analyses (Zar 1999).

Quantitative information on degree of insectivory or frugivory was unavailable for the majority of species, so we classified diet descriptions from each data source on a discrete scale. Diet categories ranged from 1 (insectivorous, rarely or never eating fruit) to 4 (frugivorous, rarely eating insects). We classified species of *Phytotoma* as frugivores although these species consume much vegetative material (Snow et al. 2004). We examined information on diet from all available sources and eliminated three species whose diet classifications varied by more than two categories among sources.

We took the average score among sources for all other species.

Foraging group size and mixed-species flocking. We included these two measures of foraging behavior because flocking may be an important correlate of resource dispersion and predictability in tropical environments (Beauchamp 2002). For example, birds feeding on locally abundant but spatially unpredictable resources such as mast-fruiting trees may forage in flocks more than other birds (Beauchamp 2002). Such structuring of resources led previous authors to first hypothesize the role of diet in the evolution of migration (Morton 1971; Fretwell 1980). Alternatively, flocking could be negatively associated with migration if annual migratory movements limit the ability of species to form foraging flocks. The foraging-group-size variable refers to the number of conspecifics an individual typically forages with during the non-breeding season. We assigned species to one of three group size categories based on whether individuals were reported to forage alone, in pairs, or in larger groups ($\leq$3 individuals).

We also included information on whether a species was known to join mixed-species foraging flocks during the non-breeding season. Mixed-species flocking may be associated with migratory behavior in many of the same ways as foraging group size. However, because mixed-species flocking may form as a result of different patterns of resource availability or require that a bird possesses different behavioral adaptations than required to form single-species flocks, we chose to treat membership in mixed-species flocks separately in our analyses.

Elevation. We included elevational distribution because many factors relating to migration routes, climatic seasonality, and availability of food types are believed to be constrained by the biogeography of New World mountain ranges (O'Neill and Parker 1978; Bates and Zink 1994; Roy et al. 1999; Chesser 2000). We classified species into three categories based on where they spend their non-breeding season: (1) those found primarily in lowland areas (<700 m), (2) those found over very broad elevational ranges, or (3) those found primarily in montane (>700 m) regions.

Body Mass. We included body mass to account for physiologically-caused variation in migratory behavior unassociated with the ecological factors we considered. Because many species-level attributes are associated with body mass (Brown 1995), we sought to explore the ecological correlates of migration after accounting for any physiological constraints on migration associated with body mass. When we found multiple estimates of body mass, we used the average of all estimates, sexes combined. We *ln*-transformed body mass before analysis.

Phylogeny

We searched the primary literature for published phylogenies at the subfamily, genus, and species level for the Tyranni. This search produced a large number of sources of phylogenetic information: Fitzpatrick (1973); Lanyon (1984b, 1984a); Zink and Johnson (1984); Lanyon (1985a, 1985b, 1986, 1988b, 1988a, 1988c); Lanyon and Lanyon (1989); Prum and Lanyon (1989); Prum (1990); Sibley and Ahlquist (1990); Prum (1992); Bates and Zink (1994); Prum (1994a, 1994b); Mobley and Prum (1995); Prum (1997); García-Moreno et al. (1998); Roy et al. (1999); Bostwick (2000); Chesser (2000); Prum et al. (2000); Brumfield and Braun (2001); Irestedt et al. (2001); Birdsley (2002); Cicero and Johnson (2002); Johansson et al. (2002); Johnson and Cicero (2002);

Fjeldså et al. (2003); Chesser (2004); Höglund and Shorey (2004); Joseph et al. (2004); Cheviron et al. (2005). We gleaned additional sources of phylogenetic information from the preliminary checklist of the Birds of South America (Remsen et al. 2006), incorporating sister taxa relationships among species wherever mentioned in that source.

Because we lacked a species-level phylogeny for the entire Tyranni we constructed composite phylogenies or "supertrees" based on all the phylogenetic sources listed above. The supertree method is an algorithm for combining the topologies of many phylogenies of overlapping sets of taxa (Sanderson et al. 1998). Several variations on supertree construction have been proposed (Bininda-Emonds 2004). We compiled phylogenetic information by entering all source phylogenies into the program Mesquite (Maddison and Maddison 2005), and constructing an MRP matrix (Matrix Representation with Parsimony) with which to run supertree analyses.

We performed two heuristic tree searches in PAUP 4.0b10 (Swofford 2002) to generate supertrees of the Tyranni. During both searches, we constrained all genera to be monophyletic except for those (*Inezia*, *Mecocerculus, Myiophobus, Muscisaxicola,* and *Pipra*) suspected of para- or polyphyly by authors of our phylogenetic sources. The assumption of genus-level monophyly allowed us to incorporate taxa not represented by any of the source phylogenies for which we had complete ecological data by adding those taxa to completed supertrees as basal polytomies within their respective genera. The assumption of genus-level monophyly also overcame the problem of misleading phylogenetic information resulting from taxa being represented in source phylogenies only as outgroups to distantly-related genera. We used *Sapayoa aenigma* as the outgroup taxon in the construction of our trees (Fjeldsä 2003).

In the first search, we used an additional "backbone" constraint in the following seven subclades: Pipridae, Cotingidae, Elaeniinae, Platyrinchinae, Fluvicolinae, Tyranninae, and a group of eight *incertae cedis* genera (*Iodopleura*, *Laniisoma*, *Laniocera*, *Pachyramphus*, *Pachyramphus*, *Schiffornis*, *Tityra*, *Xenopsaris*) believed to be closely related to each other (Johansson et al. 2002; Chesser 2004). We followed the American Ornithologists' Union (American Ornithologists' Union 1998; American Ornithologists' Union 2005; Remsen et al. 2006) for assignment of genera to subclades. The placement of *Onchorhynchus, Lipaugus, Piprites, Calyptura* was too uncertain to constrain to any subclade, and were thus free to be grouped within constrained sub-clades. In this first search, we performed 1000 heuristic search replicates of which two replicates recovered equally parsimonious trees (treelength = 980); we sampled 100,000 trees from each of these two replicates to generate two majority rule consensus trees. Although the consensus trees from these replicates resulted in similar phylogenetic hypotheses, one of the trees recovered some questionable relationships among constrained and unconstrained taxa (e.g., placement of *Calyptura* within the Elaeniinae) and was discarded. We used the remaining consensus tree (hereafter referred to as 'Tree 1'; online appendix B, figure 1) to calculate phylogenetically independent contrasts.

For the second search, we again performed 1000 heuristic search replicates, removing the backbone constraints on the seven subclades, but still constraining genera to be monophyletic. During this search, nine replicates recovered equally parsimonious trees (treelength = 965); we sampled 1,000 trees from each of these nine replicates. The 9,000 resulting trees were then used to generate a single majority rule consensus tree (hereafter referred to as 'Tree 2'; online appendix B, figure 2).

Before calculating phylogenetic independent contrasts, we pruned both trees to include only the 379 taxa for which we had complete ecological data. For analyses in which migratory distance was our response variable, we further pruned trees to include only the 142 migratory taxa.

Analyses

We examined the ecological correlates of migration using two analytical approaches; either treating migration as a dichotomous trait (sedentary vs. migratory), or as a continuous trait (migratory distance). To identify factors associated with sedentary behavior vs. migratory behavior we used all data. To examine whether the same factors were associated with increases in migratory distance, we limited our dataset to migratory species only, using migratory distance as our response variable. To enable a comparison between our results and results of past studies, we first examined the relationships proposed by Levey and Stiles (1992) and Chesser and Levey (1998) between habitat, diet, and migration, except that we also included the habitat*diet interaction term. The habitat, diet, and habitat*diet models are referred to hereafter as "restricted models". We then constructed "complete models" that also included foraging group size, mixed-species flocking, elevation, and body mass. Finally, we conducted each of these analyses once with raw species data and again with phylogenetically independent contrasts.

Phylogenetically Independent Contrasts. We used the Mesquite-module (Maddison and Maddison 2005) version of the program PDAP (Midford et al. 2005) to calculate independent contrasts to examine the association between traits in the absence of phylogenetic effects (Harvey and Pagel 1991). We performed all phylogenetically independent contrast analyses twice using contrasts calculated from each of our supertrees. Because branch lengths were not available for our supertrees, we set all branch lengths equal to one. Arbitrary branch lengths can influence contrast estimates (Garland et al. 1992; Díaz-Uriarte and Garland 1998). Thus, we checked diagnostic plots for evidence of violation of the assumptions of independent contrast analyses. We found no indication of systematic bias associated with branch length so performed all contrast analyses using untransformed branch lengths. All regression analyses on contrast data were forced through the origin (Pagel 1993).

Statistical Analyses. We used multiple linear and logistic regression to model migratory behavior using both raw species data and contrast data. For the analyses of sedentary vs. migratory species based on raw species data, we used a logistic regression framework treating migration as a binary response. For all contrast analyses and for the analyses of migratory distance, we used multiple linear regression, treating migration as a continuous response. When choosing among candidate models, we used Akaike's Information Criterion (AIC; Burnham and Anderson 2002). When more than one model was supported by the data (i.e., ΔAIC <0.5) we chose the model with the most explanatory variables. To examine the association between migration and habitat and habitat*diet, we conducted extra sum-of-square *F*-tests.

For raw species data, we treated foraging group size and elevation as continuous explanatory variables because they vary continuously in nature. However, to ensure that our results were not influenced by treating these ordinally-coded variables in a continuous manner, we repeated our analyses using dummy variables for foraging group size and elevation. Because our results were qualitatively identical, we present only the results obtained treating these variables as continuous.

Results

Results of phylogenetically independent contrast analyses from the two supertrees were qualitatively identical. We report here only the results based on tree 1 (online B, figure 1). Associations among habitat, diet, and migration differed between models using either raw species data or phylogenetically independent contrasts (table 2). Moreover, factors associated with sedentary vs. migratory behavior were not the same as those associated with migratory distance (table 2).

Sedentary vs. Migratory Species—Restricted Model

In the restricted model based on raw species data the association between habitat and migration was strong (table 2), and the nature of this association was consistent with that predicted by earlier studies: forest understory and midstory birds were least likely to migrate, followed by thicket and canopy birds, with birds of open, arid, and disturbed areas most likely to migrate. Overall, increasing frugivory was associated with a slight increase in likelihood of migration. However, the nature of the relationship between diet and migration appears to depend on where a bird lives ($P = 0.071$ for the habitat*diet interaction, table 2). To explore this interaction, we plotted the regression lines for the relationship between diet and percentage of migratory species for each of the six habitat types (figure 1). Increasing frugivory is associated with an increasing incidence of migratory behavior among birds living in thickets, forest understory, and forest canopy. Conversely, increasing frugivory is associated with a decreasing incidence of migratory behavior among birds living in disturbed and arid areas.

PDAP calculated contrasts for 378 nodes in the phylogeny. The restricted model based on independent contrasts revealed a strong positive association between diet and the likelihood of migration. However, like the model based on raw species data, the association between diet and migration depended on habitat ($P < 0.0001$ for the habitat*diet interaction term, table 2, figure 1). To facilitate comparison of these restricted model results with those of Levey and Stiles (1992) and Chesser and Levey (1998), we grouped birds in our six habitats and our range of diet values into four general categories; those living in forested habitat vs. non-forested habitats, and those consuming mainly fruit vs. mainly insects. Although only 19% of insectivores living in forested habitats migrate (compared to 61% of insectivores in non-forested habitats), roughly equal proportions of frugivores living in forested and non-forested habitats are migratory (figure 2). Hence, habitat is associated with migratory behavior in insectivores, but not in frugivores.

Sedentary vs. Migratory Species—Complete Model

In the complete model based on raw species data, habitat was again strongly associated with the likelihood of being migratory, and we found suggestive evidence that the relationship between diet and migration depended upon habitat (*P* = 0.080 for habitat*diet interaction, table 2). As with the restricted model based on raw species data, birds of forest interior were less likely to migrate than birds living away from forests. Foraging group size was negatively associated with the likelihood of migrating although it appears that this relationship is not linear (figure 3); birds that typically forage alone were most likely to be migratory whereas birds that typically forage in pairs were the least likely to be migratory. After accounting for the effect of other variables, each increase in group size was associated with a 39% decrease in the odds of migrating. Body mass was positively associated with migration; the odds of migrating increased by 154% with each increase of 1 *ln* mass.

The complete model based on independent contrasts included habitat, diet, habitat*diet, foraging group size, and body mass (table 2). The strong effect of the habitat*diet interaction in this model indicated that, like the restricted models, the associations between habitat, diet, and migration were interrelated. As in results based on raw species data, foraging group size was negatively associated with the likelihood of migrating, and body mass was positively associated with the likelihood of migrating.

Migratory Distance—Restricted Model

The restricted model of migratory distance based on raw species data was similar to the equivalent model contrasting sedentary and migratory species in that migratory distance was more strongly related to habitat than to diet (table 2). Mean migratory distance was associated with habitats in the same way as the likelihood of migrating was associated with habitats. On average, forest understory birds migrate the shortest distances with mean migratory distance increasing in the following way: forest understory < forest midstory < forest canopy < thickets < disturbed areas < open/arid areas. Unlike the analyses of sedentary vs. migratory behavior, we found no evidence for an effect of diet, nor a habitat*diet interaction in the restricted model.

PDAP calculated contrasts for the 141 nodes in the phylogeny based on the 142 migratory species. The restricted model based on independent contrasts suggested little association between migratory distance and habitat or diet (table 2).

Migratory Distance—Complete Model

The complete model based on raw species data included habitat, diet, foraging group size and elevation (table 2). In contrast to the restricted model, diet was more strongly associated with migratory distance than was habitat. Furthermore, the nature of the relationship between diet and migratory distance was opposite to the relationship between diet and the likelihood of migrating. Insectivorous birds migrate longer distances on average than frugivorous birds. After accounting for the effects of habitat and diet, foraging group size was again negatively associated with migratory distance, and lowland birds migrated further than highland birds.

The complete model based on independent contrasts included only foraging group size and elevation as correlates of migratory distance (table 2). Like the equivalent model based on raw species data, both group size and elevation were negatively associated with migratory distance.

Discussion

Migration is often considered an adaptation to exploit seasonal peaks in food abundance or avoid climatic extremes by dividing time among numerous locations. If variation in food or climate favors migration in some species, however, why has migration not evolved in all species? One possibility is that certain traits make some species more likely to migrate. The evolutionary precursor hypothesis (Levey and Stiles 1992) suggests that both a frugivorous diet and use of “unbuffered” habitats are both precursors to the evolution of migration in birds. Our results show that habitat and diet are indeed related to migration, but in more complex ways than previously proposed. Our comparative analysis of 379 species in the Tyranni provided ambiguous support for the evolutionary precursor hypothesis with results depending on which migratory response variable we used and whether we analyzed raw species or independent contrast data.

The results of our raw species analyses suggest that sedentary species differ on average from migratory species in the habitats they occupy and in the broad types of food they consume. However, our results also suggest that the relationship between diet and migration depends upon where birds live, with most forest and thicket birds being more likely to migrate if they are frugivorous (consistent with the evolutionary precursor hypothesis), and birds of non-forested habitats being less likely to migrate if they are frugivorous (figure 1). Analyses of independent contrast data strengthened the evidence that the association between evolutionary changes in migration and habitat depends upon on the type of foods consumed (support for the habitat*diet interaction term increased after controlling for phylogeny). The proportion of primarily frugivorous species that migrate was very similar regardless of the broad habitat in which a bird lives (figure 2). In contrast, the proportion of primarily insectivorous species that migrate was lower for birds living in the forest interior compared with those living in canopy and open habitats. This suggests that differences in migratory behavior among birds occupying different habitats were attributable to the habitat-specific behavior of insectivores but not frugivores.

Our results differ from those of Levey and Stiles (1992), who concluded (for all birds and specifically for flycatchers) that both living in open habitats and eating fruit were separately associated with being migratory. Differences in the results between studies could perhaps be explained by differences in taxonomic scope. Alternatively, habitat and diet may be confounded, but by analyzing habitat and diet separately, both factors appeared to be associated with migration. However, the most likely explanation lies in the different types of migratory behavior considered among studies. On average, the diets of migrants as a whole may not differ from their sedentary neighbors, but those of short-distance migrants may differ from both long-distance migrants and sedentary species. Indeed, evidence from our analyses of migratory distance supports this explanation: short-distance migrants are more frugivorous than long-distance migrants (although this difference disappears after considering phylogeny).

The most pervasive correlate of migration was foraging group size. In analyses using both raw species data and independent contrast data, of both sedentary vs. migratory behavior and of migratory distance, group size was consistently and negatively associated with migration. Furthermore, in some of our models foraging group size was more strongly associated with migration than habitat or diet. Our data suggest that birds foraging solitarily are more likely to migrate and migrate further than birds foraging either in pairs or in groups (figure 3), suggesting that migration could impede the maintenance of pair and family group foraging bonds. This hypothesis is supported by increasing evidence suggesting that individuals of different age and sex classes often migrate on different timetables and occupy different non-breeding ranges or habitats (Conway et al. 1995; Marra et al. 1998; Lank et al. 2003). A more intriguing possibility is that migration and group foraging represent alternative evolutionary strategies. If migration evolves primarily in response to temporal variation in food resources, and if foraging with conspecifics overcomes some of the same problems of resource scarcity through improved foraging efficiency, then these two types of behavior could represent different evolutionary solutions to the same environmental constraint (i.e., food limitation).

Why Migrate Farther?

Previous reviews of the evolution of bird migration have assumed that short-distance migratory movements were a necessary precursor to the evolution of long-distance migration. Our results do not support this assumption as factors associated with changes in migratory distance differed from those associated with sedentary vs. migratory behavior. Most importantly, the effects of diet and the interaction between habitat and diet helped differentiate sedentary vs. migratory species but were not related to migratory distance after controlling for phylogeny. Increasing frugivory was associated with increasing likelihood of migrating (at least in some habitats), but insectivory, not frugivory, was associated with increases in migratory distance (in models including foraging group size). Consideration of habitat was a critical factor necessary to interpret the association between diet and migration in models of sedentary vs. migratory behavior, whereas foraging group behavior was critical in understanding the association between diet and migration in models of migratory distance.

A primarily frugivorous diet could possibly constrain birds to short migratory distances regardless of whether frugivory predisposes lineages to evolving migration in the first place. Indeed, breeding seasons of long-distance migrants coincide with abundant insect resources and relatively scant fruit resources at northerly latitudes. Although many migrants consume fruit during migratory and non-breeding seasons, the morphological, physiological, cognitive, and behavioral adaptations required to efficiently forage for and digest a frugivorous diet conflict to some degree with adaptations for an insectivorous diet (Lepczyk et al. 2000; Levey and Martínez del Rio 2001, but see Parrish 1997). Because fruit is scare at high latitudes during the breeding season, year-round insectivory may thus be a consequence, not a cause, of long-distance migration. Another possible explanation for the differences in importance of diet in Levey and Stiles (1992), Chesser and Levey (1998), and our study is that short- and long-distance migration may evolve in response to different sets of selective pressures. If true, this would further erode support for the evolutionary precursor hypothesis because an implicit assumption of this hypothesis is that short- and long-distance migration are endpoints of a single behavioral continuum.

The additional variables included in complete models also differed between analyses of sedentary vs. migratory behavior and changes in migratory distance.

Whereas increasing body mass was associated with increasing likelihood of migrating, body mass was not associated with changes in migratory distance. If birds migrate in response to resource scarcity, and if increases in foraging efficiency do not scale 1:1 with increasing energetic requirements of larger body sizes, then as food levels decrease, heavier birds will experience food shortages sooner than lighter birds. In contrast to body mass, the non-breeding elevational range occupied by a species was associated with changes in migratory distance, but not in likelihood of migrating. The longest-distance migrants we studied spend the non-breeding season in lowland Amazonia, migrating to northern Boreal regions to breed whereas many of the shortest distance migrants in our dataset were montane species that migrate altitudinally. This suggests that topographical diversity results in areas of differing patterns of resource availability being located closer to highland birds than to lowland birds.

Raw Species Data vs. Phylogenetically Independent Contrasts

Use of phylogenetically independent contrasts helped clarify the ecological correlates of bird migration. In the analysis of sedentary vs. migratory behavior, the effect of controlling for phylogeny was to strengthen the habitat*diet interaction, reinforcing the argument that the relationship between these two factors and migration ought not to be evaluated separately from each other. In the analyses of migratory distance, raw species analyses suggested effects of habitat and diet but phylogenetically independent contrasts showed no correlation between habitat or diet and migration. Contrast models might fail to identify the same associations as raw species migratory distance models if the evolution of correlated traits occurred deep in the phylogeny and been subsequently conserved. To some extent, this may be true in the Tyranni. For instance, most species in the genus *Empidonax* are characterized by long distance migration and high levels of insectivory. Phylogenetic conservatism of trait associations may well imply that combinations of certain traits are adaptive and have persisted because they are adaptive (Price 1997), but such associations provide poor evidence for correlated trait evolution.

The discrepancies in results between raw species and independent contrast analyses are unlikely to be artifacts of the details of our methodology. Numerous modifications have elaborated on the simple calculation of independent contrasts by incorporating specific models of character evolution, maximum likelihood methods, and Baysian inference. Because many of these methodological advances influence the estimation of branch lengths, understanding the consequences of branch-length error is potentially important (Díaz-Uriarte and Garland 1998). Our results are unlikely to be affected by assigning arbitrary branch lengths for two reasons. First, large phylogenies are fairly robust to branch length errors (Freckleton et al. 2002), and second, branch length errors result in inflated Type I error rates (Díaz-Uriarte and Garland 1998). In our case, model type influenced results by both strengthening and weakening individual variable associations; we found no systematic pattern of increasing *P*-values in independent contrast models as compared to raw species models (table 2).

Habitat and the evolutionary precursor hypothesis

What implications do the associations between habitat and migration have for hypotheses regarding the evolution of migration? Although our results are uninformative in evaluating the role of predation risk, we can speculate on the role of climatic effects and food limitation. It is unlikely that climate promotes the evolution of migration through direct effects limiting physiological efficiency. If so, we would have expected a stronger and more consistent association between elevation and migration; elevational gradients provide the strongest temperature gradients within the non-breeding ranges of Tyranni species. However, we cannot rule out indirect climatic effects and their role in influencing resource variation. The observed relationship between habitat and migration may simply reflect lower temporal variation in micro-climate in forests compared to non-forested habitats. If this is the case, it is not clear how or why insectivores and their insect prey should be more strongly influenced by that variability than frugivores and their fruit resources. The inconsistency in associations between migration and habitat, diet, and foraging group size suggest that some unmeasured parameter related to variation in resource abundance has influenced the evolution of migration. Although resource seasonality, patchiness, or both are likely major factors influencing the evolution of migration, our surrogates of resource seasonality do a poor job at capturing that variation. The logical next step is to measure the magnitude of seasonality in fruit and insect resources within different habitats in tropical environments and assess how solitary vs. pair or group foraging influences the efficiency of resource acquisition.

What can we infer about the evolutionary precursor hypothesis? Our results imply that simple direct associations between either habitat or diet and the evolution of migration do not exist. Not only are the associations of these traits among modern species more complex than previously suggested, but results of our migratory distance analyses imply that different traits are associated with different types of migratory behavior. Short-distance migrant frugivores may not be precursors of long-distance migratory lineages in the sense of representing an evolutionary bridge between sedentary species and long-distance migratory species, but instead represent a distinct evolutionary response to a different set of selective pressures.

Resource variability hypothesis

Results of this study suggest that the evolutionary precursor hypothesis as previously stated must be refined. We hope that by restating this hypothesis explicitly in terms of resource variability instead of presumed surrogates for resource variability, we will stimulate tests of critical predictions of this and other hypotheses explaining the evolution of migration. We propose a resource variability hypothesis that states that species living in areas where fluctuation in food resource availability is large will be more likely to initially evolve migratory behavior than species depending on less seasonal resources, regardless of where those areas are located (i.e., habitat) or what type of food resources they depend on (i.e., diet). Once migration has evolved, factors associated with the extension and modification of this behavior will not necessarily be the same as factors associated with the initial steps toward becoming migratory. Additionally, migration seems to somehow constrain the ability of species to forage with conspecifics; group foraging may in turn be an alternative strategy to migration allowing sedentary species to overcome some of the difficulties associated with variation in resource availability.

The resource variability hypothesis and results of this study make testable predictions regarding the seasonal patterns of resource variation expected between habitats for tropical insectivores and frugivores. If habitat-specific variation in resources promotes migration, then the extent of food limitation should be more temporally variable (or more severe) for insectivores in open areas than for insectivores in forests, but the extent of food limitation for frugivores should be similar across habitats. Furthermore, food should be more limiting for birds of open habitats than for forest-dwelling species. We do not know whether the overall magnitude of temporal variation in resources, a drop in resource abundance below some critical threshold, or an interaction between resource availability and resource quality is the critical factor influencing whether a species embarks upon the evolutionary pathway to migration. We recommend an empirical approach to resolving these questions. Only by carefully quantifying community-level production and consumption rates of fruits and insects in forested and open habitats can we infer that “habitat” is indeed a good surrogate for resource variability.

We believe this to be the first species-level comparative study to address factors associated with the evolution of avian migration in a phylogenetically-explicit context. Although our inferences are limited to the Tyranni, we feel the discrepancies between results of this study and previous studies form a compelling argument for more research on the species-level correlates of migration, particularly studies focusing on migration systems in other parts of the world. Ideally, future studies will better capture the detail and continuous nature of the variation in both food resource variability among habitats and the variation in migratory behavior across species. Phylogenetically explicit comparative studies could greatly advance our understanding of the processes contributing to the evolution of migration in ecologically very different migratory systems. The evolutionary precursor hypothesis is one of many hypotheses proposed to explain variation in migratory behavior among species that have rarely (if ever) been empirically tested. Yet all of these hypotheses make predictions regarding species-level correlates of migratory behavior. We encourage other researchers to take advantage of the ever-increasing number of phylogenies being published to test predictions of alternative hypotheses explaining the evolution of migration.

Acknowledgments

K. Bildstein, J. Bronstein, K. Bonine, Y. Carrière, R. Montgomerie, D. Levey, B. Steidl, and an anonymous reviewer provided valuable comments on an earlier draft of the manuscript. J. Oliver helped enormously in constructing the supertrees, and F. Michelangeli assisted in formatting the phylogeny figures. T. Chesser reviewed our classifications. M. Ali and G. Bieber assisted in the compilation of raw data. This material is based upon work supported by the National Science Foundation (DDIG No. 0410531), the Natural Sciences and Engineering Research Council of Canada (PGS-B fellowship), the Research Training Group in Biological Diversification at the University of Arizona (NSF-DIR-9113362, BIR-9602246) and the University of Arizona Graduate College.

Literature Cited

Alerstam, T. 1990. Bird Migration. Cambridge University Press, Cambridge, UK.

Alerstam, T., and A. Hedenstrom. 1998. The development of bird migration theory. Journal of Avian Biology 29:343-369.

American Ornithologists' Union. 1998. Checklist of North American Birds. American Ornithologists' Union, Washington, DC.

—. 2005. Forty-sixth supplement to the American Ornithologists' Union *Check-list of North American Birds*. Auk 122:1026-1031.

Bates, J. M., and R. M. Zink. 1994. Evolution into the Andes: molecular evidence for species relationships in the genus *Leptopogon*. Auk 111:507-515.

Beauchamp, G. 2002. Higher-level evolution of intraspecific flock-feeding in birds. Behavioral Ecology and Sociobiology 51:480-487.

Belton, W. 1985. Birds of the Rio Grande do Sul, Brazil. Part 2, Formicariidae through Corvidae. Bulletin of the American Museum of Natural History 180:1-241.

Berthold, P. 2001. Bird Migration: A General Survey. Oxford University Press, Oxford, UK.

Bininda-Emonds, O. R. P. 2004. The evolution of supertrees. Trends in Ecology & Evolution 19:315-322.

Birdsley, J. S. 2002. Phylogeny of the tyrant flycatchers (Tyrannidae) based on morphology and behavior. Auk 119:715-734.

Blake, J. G., and B. A. Loiselle. 2002. Manakins (Pipridae) in second-growth and old-growth forests: patterns of habitat use, movement, and survival. Auk 119:132-148.

Bond, J. 1993. A Field Guide to the Birds of the West Indies. The Peterson Field Guide Series. Houghton Mifflin Company, New York, NY.

Bostwick, K. S. 2000. Display behaviors, mechanical sounds, and evolutionary relationships of the Club-winged Manakin (*Machaeropterus deliciosus*). Auk 117:465-478.

Brown, J. H. 1995. Macroecology. The University of Chicago Press, Chicago, IL.

Brumfield, R. T., and M. J. Braun. 2001. Phylogenetic relationships in bearded manakins (Pipridae: *Manacus*) indicate that male plumage color is a misleading taxonomic marker. Condor 103:248-258.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multi-model Inference: A Practical Information-Theoretic Approach. 2nd edition. Springer-Verlag New York Inc., New York, NY.

Chesser, R. T. 1994. Migration in South America: an overview of the austral system. Bird Conservation International 4:91-107.

—. 1995. Biogeographic, ecological, and evolutionary aspects of South American austral migration, with special reference to the family Tyrannidae. Doctor of Philosophy thesis, Louisiana State University, Baton Rouge, LA.

—. 1997. Patterns of seasonal and geographical distribution of Austral migrant flycatchers (Tyrannidae) in Bolivia. Ornithological Monographs 48:171-204.

—. 1998. Further perspectives on the breeding distribution of migratory birds: South American austral migrant flycatchers. Journal of Animal Ecology 67:69-77.

—. 2000. Evolution in the high Andes: the phylogenetics of *Muscisaxicola* Groundtyrants. Molecular Phylogenetics and Evolution 15:369-380.

—. 2004. Molecular systematics of New World suboscine birds. Molecular Phylogenetics and Evolution 32:11-24.

—. 2005. Seasonal distribution and ecology of South American austral migrant flycatchers, Pages 168-181 *in* R. Greenberg, and P. P. Marra, eds. Birds of Two Worlds: The Ecology and Evolution of Migration. Johns Hopkins University Press, Baltimore, MD.

Chesser, R. T., and D. J. Levey. 1998. Austral migrants and the evolution of migration in New World birds: diet, habitat and migration revisited. American Naturalist 152:311-319.

Cheviron, Z. A., S. J. Hackett, and A. P. Capparella. 2005. Complex evolutionary history of a Neotropical lowland forest bird (*Lepidothrix coronata*) and its implications for historical hypotheses of the origin of Neotropical avian diversity. Molecular Phylogenetics and Evolution 36:338-357.

Cicero, C., and N. K. Johnson. 2002. Phylogeny and character evolution in the *Empidonax* group of tyrant flycatchers (Aves: Tyrannidae): a test of W. E. Lanyon's hypothesis using mtDNA sequences. Molecular Phylogenetics and Evolution 22:289-302.

Conway, C. J., G. V. N. Powell, and J. D. Nichols. 1995. Overwinter survival of neotropical migratory birds in early-successional and mature tropical forest. Conservation Biology 9:855-864.

Cox, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. American Naturalist 126:451-474.

del Hoyo, J., A. Elliot, and D. A. Christie. 2004. Vol. 9. Cotingas to Pipits and Wagtails, Handbook of the Birds of the World. Lynx Editions, Barcelona, Spain.

Díaz-Uriarte, R., and T. Garland. 1998. Effects of branch length errors on the performance of phylogenetically independent contrasts. Systematic Biology 47:654-672.

Didham, R. K., and J. H. Lawton. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica 31:17-30.

Dunning, J. B. 1993. Avian Body Masses. CRC Press, Boca Raton, FL.

Fetcher, N., S. F. Oberbauer, and B. R. Strain. 1985. Vegetation effects on microclimate in lowland tropical forest in Costa Rica. International Journal of Biometeorology 29:145-155.

Fitzpatrick, J. W. 1973. Speciation in the genus *Octhoeca* (Aves: Tyrannidae): Breviora No. 402.

—. 1980. Foraging behavior of Neotropical tyrant flycatchers. Condor 82:43-57.

—. 1985. Form, foraging behavior, and adaptive radiation in the Tyrannidae, Pages 447-470 *in* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, eds. Neotropical Ornithology. Ornithological Monographs. American Ornithologists' Union, Washington, DC.

Fitzpatrick, J. W., J. M. Bates, K. S. Bostwick, I. C. Caballero, B. M. Clock, A. Farnsworth, P. A. Hosner et al. 2004. Family Tyrannidae (Tyrant-flycatchers), Pages 170-462 *in* J. del Hoyo, A. Elliot, and D. A. Christie, eds. Handbook of the Birds of the World, Vol. 9. Cotingas to Pipits and Wagtails. Lynx Editions, Barcelona, Spain.

Fjeldså, J., and N. Krabbe. 1990. Birds of the High Andes. Zoological Museum, University of Copenhagen, Denmark.

Fjeldså, J., D. Zuccon, M. Irestedt, U. S. Johansson, and P. G. P. Ericson. 2003. *Sapayoa aenigma*: a New World representative of 'Old World suboscines'. Proceedings of the Royal Society of London Series B-Biological Sciences 270:S238-S241.

Freckleton, R. P., P. H. Harvey, and M. D. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. American Naturalist 160:712-726.

Fretwell, S. D. 1980. Evolution of migration in relation to factors regulating bird numbers, Pages 517-527 *in* A. Keast, and E. S. Morton, eds. Migrant birds in the Neotropics. Smithsonian Institution Press, Washington, DC.

García-Moreno, J., P. Arctander, and J. Fjeldså. 1998. Pre-pleistocene differentiation among Chat-tyrants. Condor 100:629-640.

Garland, T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18-32.

Gauthreaux , S. A., Jr. 1996. Bird migration: methodologies and major research trajectories (1945-1995). Condor 98:442-453.

Greenberg, R., and P. P. Marra. 2005. Birds of Two Worlds: the Ecology and Evolution of Migration. Johns Hopkins University Press, Baltimore, MD.

Greenberg, R., and V. Salewski. 2005. Ecological correlates of wintering social systems in New World and Old World migratory passerines, Pages 336-358 *in* R. Greenberg, and P. P. Marra, eds. Birds of Two Worlds: the Ecology and Evolution of Migration. Johns Hopkins University Press, Baltimore, MD.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, UK.

Hilty, S. L. 2003. Birds of Venezuela. Princeton University Press, Princeton, N.J.

Hilty, S. L., and W. L. Brown. 1986. A Guide to the Birds of Colombia. Princeton University Press, Princeton, NJ.

Höglund, J., and L. Shorey. 2004. Genetic divergence in the superspecies *Manacus*. Biological Journal of the Linnean Society 81:439-447.

Howell, S. N. G., and S. Webb. 1995. The Birds of Mexico and Northern Central America. Oxford University Press, Oxford, UK.

Irestedt, M., U. S. Johansson, T. J. Parsons, and P. G. P. Ericson. 2001. Phylogeny of major lineages of suboscines (Passeriformes) analysed by nuclear DNA sequence data. Journal of Avian Biology 32:15-25.

Janzen, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54:687-708.

Johansson, U. S., M. Irestedt, T. J. Parsons, and P. G. P. Ericson. 2002. Basal phylogeny of the Tyrannoidea based on comparisons of cytochrome *b* and exons of nuclear *c-myc* and RAG-1 genes. Auk 119:984-995.

Johnson, N. K., and C. Cicero. 2002. The role of ecologic diversification in sibling speciation of *Empidonax* flycatchers (Tyrannidae): multigene evidence from mtDNA. Molecular Ecology 11:2065-2081.

Joseph, L., T. Wilke, E. Bermingham, D. Alpers, and R. Ricklefs. 2004. Towards a phylogenetic framework for the evolution of shakes, rattles, and rolls in *Myiarchus* tyrant-flycatchers (Aves: Passeriformes: Tyrannidae). Molecular Phylogenetics and Evolution 31:139-152.

Keast, A., and E. S. Morton. 1980. Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC.

Lank, D. B., R. W. Butler, J. Ireland, and R. C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. Oikos 103:303-319.

Lanyon, S. M. 1985*a*. Molecular perspective on higher-level relationships in the Tyrannoidae (Aves). Systematic Zoology 34:404-418.

Lanyon, S. M., and W. E. Lanyon. 1989. The systematic position of the Plantcutters, *Phytotoma*. Auk 106:422-432.

Lanyon, W. E. 1984*a*. A phylogeny of the Kingbirds and their allies. American Museum Novitates 2797:1-28.

—. 1984*b*. The systematic position of the Cocos Flycatcher. Condor 86:42-47.

—. 1985*b*. A phylogeny of the myiarchine flycatchers, Pages 361-380 *in* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, eds. Neotropical Ornithology. Ornithological Monographs 36.

—. 1986. A phylogeny of the thirty-three genera in the *Empidonax* assemblage of tyrant flycatchers. American Museum Novitates 2846:1-64.

—. 1988*a*. The phylogenetic affinities of the flycatcher genera *Myiobius* Darwin and *Terenotriccus* Ridgeway. Novitates 2915:1-11.

—. 1988*b*. A phylogeny of the Flatbill and Tody-tyrant assemblage of Tyrant flycatchers. American Museum Novitates 2923:1-41.

—. 1988*c*. A phylogeny of the thirty-two genera in the *Elaenia* assemblage of Tyrant flycatchers. American Museum Novitates 2914:1-57.

Lepczyk, C. A., K. G. Murray, K. Winnett-Murray, P. Bartell, E. Geyer, and T. Work. 2000. Seasonal fruit preferences for lipids and sugars by American Robins. Auk 117:709-717.

Levey, D. J., and C. Martínez del Rio. 2001. It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. Auk 118:819-831.

Levey, D. J., and F. G. Stiles. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. American Naturalist 140:447-476.

Loiselle, B. A., and J. G. Blake. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72:180-193.

MacMillan. 1996. The MacMillan world atlas. MacMillan Publishers, New York, NY.

Maddison, W. P., and D. R. Maddison. 2005. Mesquite: a modular system for evolutionary analysis, version 1.06.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884-1886.

Midford, P. E., T. Garland Jr., and W. P. Maddison. 2005. PDAP Package of Mesquite, version 1.07.

Mobley, J. A., and R. O. Prum. 1995. Phylogenetic relationships of the Cinnamon Tyrant, *Neopipo cinnamomea*, to the tyrant flycatchers (Tyrannidae). Condor 97:650-662.

Morton, E. S. 1971. Food and migration habits of the Eastern Kingbird in Panama. Auk 88:925-926.

—. 1977. Intra-tropical migration in Yellow-green Vireo and Piratic Flycatcher. Auk 94:97-106.

National Geographic Society. 1999. Field Guide to the Birds of North America, 3rd Edition. National Geographic Society, Washington, DC.

O'Neill, J. P., and T. A. Parker III. 1978. Responses of birds to a snow-storm in the Andes of southern Peru. Wilson Bulletin 90:446-449.

Pagel, M. 1993. Seeking the evolutionary regression coefficient: an analysis of what comparative methods measure. Journal of Theoretical Biology 164:191-205.

Parrish, J. D. 1997. Patterns of frugivory and energetic condition in nearctic landbirds during autumn migration. Condor 99:681-697.

Poole, A., and F. Gill. 2000. The Birds of North America: Life Histories for the 21st Century. The Birds of North America Inc., Philadelphia, PA.

Poulin, B., and G. Lefebvre. 1996. Dietary relationships of migrant and resident birds from a humid forest in central Panama. Auk 113:277-287.

Price, T. 1997. Correlated evolution and independent contrasts. Philosophical

Transactions of the Royal Society of London Series B-Biological Sciences 352:519-529.

Prum, R. O. 1990. A test of the monophyly of the manakins (Pipridae) and of the cotingas (Cotingidae) based on morphology. Occasional Papers of the Museum of Zoology, The University of Michigan 723:1-44.

—. 1992. Syringeal morphology, phylogeny, and evolution of the Neotropical manakins (Aves: Pipridae). American Museum Novitates 3042:1-65.

—. 1994*a*. Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves: Pipridae). Evolution 48:1657-1675.

—. 1994*b*. Species status of the White-fronted Manakin, *Lepidothrix serena* (Pipridae), with comments on conservation biology. Condor 96:692-702.

—. 1997. Phylogenetic tests of alternative intersexual selection mechanisms: trait macroevolution in a polygynous clade (Aves: Pipridae). American Naturalist 149:668-692.

Prum, R. O., and W. E. Lanyon. 1989. Monophyly and phylogeny of the *Schiffornis* group (Tyrannoidea). Condor 91:444-461.

Prum, R. O., N. H. Rice, J. A. Mobley, and W. W. Dimmick. 2000. A preliminary phylogenetic hypothesis for the cotingas (Cotingidae) based on mitochondrial DNA. Auk 117:236-241.

Ramos-Olmos, M. A. 1983. Seasonal movements of bird populations at a neotropical study site in southern Veracruz, Mexico. Ph.D. dissertation thesis, University of Minnesota, Minneapolis, MN.

Rappole, J. H., H. Helm, and M. A. Ramos-Olmos. 2003. An integrative framework for understanding the origin and evolution of avian migration. Journal of Avian Biology 34:124-128.

Rappole, J. H., and P. Jones. 2002. Evolution of old and new world migration systems. Ardea 90:525-537.

Remsen, J. V., A. Jaramillo, M. Nores, J. F. Pacheco, M. B. Robbins, T. S. Schulenberg, F. G. Stiles et al. version January 2006. A classification of the bird species of South America http://www.museum.lsu.edu/~Remsen/SACCBaseline.html.

Ridgely, R. S., and G. Tudor. 1994. The Birds of South America, v. II, The Suboscine Passerines. University of Texas Press, Austin, TX.

Roy, M. S., J. C. Torres-Mura, and F. Hertel. 1999. Molecular phylogeny and evolutionary history of the Tit-tyrants (Aves: Tyrannidae). Molecular Phylogenetics and Evolution 11:67-76.

Sanderson, M. J., A. Purvis, and C. Henze. 1998. Phylogenetic supertrees: assembling the trees of life. Trends in Ecology & Evolution 13:105-109.

Sherry, T. W. 1984. Comparative dietary ecology of sympatric, insectivorous neotropical flycatchers (Tyrannidae). Ecological Monographs 54:313-338.

Sibley, C. G., and J. E. Ahlquist. 1990. Phylogeny and Classification of Birds. Yale University Press, New Haven, CT.

Sick, H. 1993. *Ornitologia Brasileira*. Editora Nova Fronteira, Rio de Janiero, Brazil.

Snow, D. W. 1982. The Cotingas. Oxford University Press, Oxford, UK.

—. 2004. Family Pipridae (Manakins), Pages 110-169 *in* J. del Hoyo, A. Elliot, and D.

A. Christie, eds. Handbook of the Birds of the World, Vol. 9. Cotingas to Pipits and Wagtails. Lynx Editions, Barcelona, Spain.

Snow, D. W., M. d. L. Brooke, and B. A. Walther. 2004. Family Cotingidae (Cotingas), Pages 32-109 *in* J. del Hoyo, A. Elliot, and D. A. Christie, eds. Handbook of the Birds of the World. Vol. 9. Cotingas to Pipits and Wagtails. Lynx Editions, Barcelona, Spain.

Stiles, F. G., and A. F. Skutch. 1989. A Field Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, NY.

Stotz, D. F., J. W. Fitzpatrick, T. A. Parker III, and D. K. Moskovits. 1996. Neotropical Birds: Ecology and Conservation. The University of Chicago Press, Chicago, IL.

Swofford, D. 2002. PAUP*: Phylogenetic analysis using parsimony (and other methods) 4.0 beta. Sinauer Associates, Inc., Sunderland, MA.

Traylor, M. A. 1977. A classification of the tyrant Flycatchers (Tyrannidae). Bulletin of the Museum of Comparative Zoology 148:129-184.

Winker, K., P. Escalante, J. H. Rappole, M. A. Ramos, R. O. Oehlenschlager, and D. W. Warner. 1997. Periodic migration and lowland forest refugia in a "sedentary" neotropical bird, Wetmore's Bush-tanager. Conservation Biology 11:692-697.

Zar, J. H. 1999. Biostatistical Analysis. Prentice-Hall, London, UK.

Zink, R. M. 2002. Towards a framework for understanding the evolution of avian migration. Journal of Avian Biology 33:433-436.

Zink, R. M., and N. K. Johnson. 1984. Evolutionary genetics of flycatchers. I. Sibling species in the genera *Empidonax* and *Contopus*. Systematic Zoology 33:205-216.

Tables, Figures, and Appendices

Table 1

Differences in methodological approaches among three studies examining the evolutionary precursor hypothesis to explain why some birds evolved migration when others did not.

	Levey and Stiles (1992)	**Chesser and Levey (1998)**	**This paper**
Geographic scope	Atlantic slope of Costa Rica	S. America	N., Central, and S. America
Taxonomic scope	Landbirds in wet forests	Passerines	Tyranni
n	346	12	379
Taxonomic level	Species	Family/subfamily	Species
Methods to control for phylogeny	None	Ridley (test of association), Maddison (concentrated changes)	Phylogenetically independent contrasts
Migratory behaviors considered	Sedentary, altitudinal, short-distance, intratropical migrants	Sedentary vs. long-distance (austral) migrants	Sedentary vs. migratory, & migratory distance

Habitat categories	4: forest interior, canopy, 2nd growth, aquatic	2: “buffered” (forest interior), & “unbuffered” (canopy/edge)	6: thickets/ground, understory, forest mid- story, canopy, disturbed, open/arid
Diet categories	Many, 3 discussed: no fruit, some fruit, mostly fruit	2: insects, fruits (incl. nectarivores)	4: mostly insects, insects > fruit, fruit > insects, mostly fruit
Habitat & diet in same model?	No	No	Yes
Other correlates?	No	No	Yes

Table 2

Factors associated with migration in 379 species in the Tyranni based on eight analytical models that varied in the response variable (sedentary vs. migratory, or migratory distance), the number of potential explanatory variables (three vs. seven), and whether or not we controlled for phylogeny (raw species means vs. phylogenetically independent contrasts).

	Sedentary vs. migratory species								Migratory distance							
	Restricted model				Complete model				Restricted model				Complete model			
	Raw species		Contrasts		Raw species		Contrasts		Raw species		Contrasts		Raw species		Contrasts	
	χ^2	*P*	*F*	*P*	χ^2	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Whole model	72.0	<0.0001	3.8	<0.0001	85.4	<.0001	4.0	<0.0001	4.9	<0.0001	0.7	0.697	7.6	<0.0001	3.4	0.038
Habitat	50.6	<0.0001	1.3	0.284	63.6	<.0001	1.4	0.223	2.5	0.032	0.4	0.837	3.1	0.013	…[a]	…[a]
Diet	4.4	0.036	11.3	0.001	1.6	0.209	10.2	0.002	0.6	0.457	0.1	0.721	15.7	0.0001	…[a]	…[a]
Habitat*diet	10.2	0.071	5.1	<0.0001	9.8	0.080	5.2	<0.0001	1.3	0.262	1.2	0.309	…[a]	…[a]	…[a]	…[a]
Group size					9.3	0.002	4.2	0.041					8.6	0.004	2.8	0.095
MS flocking					…[a]	…[a]	…[a]	…[a]					…[a]	…[a]	…[a]	…[a]

Elevation	…[a]	…[a]	…[a]	…[a]	2.2	0.143	3.6	0.058
Body mass	4.7	0.031	5.3	0.022	…[a]	…[a]	…[a]	…[a]

Notes: Chi-square and *P*-values for variables in logistic regression models are based on likelihood ratio tests, and *F*- and *P*-values for linear regression models are based on partial sum-of-squares *F*-tests. We report the complete models with variables chosen based on AIC values.

[a] Considered for inclusion in complete model but variable not included in models with the lowest AIC scores.

Figure legends

Figure 1 Percent of Tyranni species varies with diet (highly insectivorous to highly frugivorous) and habitat use. The six lines illustrate how diet and habitat interact; birds of thickets, forest understory and canopy are more likely to be migratory if they are frugivorous. In contrast, increasing frugivory is associated with a decreasing likelihood of being migratory for birds of disturbed and arid habitats. We plotted linear regression lines for each habitat category based on the proportion of species that migrate for each level of diet along a scale from highly insectivorous (1.0) to highly frugivorous (4.0).

Figure 2 Percent of species in the Tyranni that migrate in each of four categories based on habitat (forest vs. non-forest) and diet (mainly frugivorous vs. mainly insectivorous). The number of migratory species in each category appears above the bar.

Figure 3 Relationship between foraging group size and migratory behavior. Values represent the residuals (±1 SE) for likelihood of migration at each level of foraging group size after accounting for the effects of habitat, diet, and body mass.

Online Appendix B Figure 1 A phylogenetic hypothesis for the Tyranni (tree 1). To generate this tree, we constrained both families and genera to be monophyletic during supertree analyses (see text for more details). We used the topologies of this tree to generate the independent contrast results presented in the manuscript. Prior to calculating independent contrasts, we pruned the tree to contain only the 379 species (online appendix A) for which we had complete information for migratory behavior, diet, habitat, foraging group size, mixed-species flocking behavior, elevational range, and body mass. Roman numerals link branches of the phylogeny across page breaks.

Online Appendix B Figure 2 An alternative phylogenetic hypothesis for the Tyranni (tree 2). To generate this tree, we constrained genera (but not families) to be monophyletic and imposed no additional constraints on topology. We repeated all independent contrast analyses using the topology of tree 2 and obtained qualitatively identical results to the analyses using the topology of tree1. Roman numerals link branches of the phylogeny across page breaks.

Figure 1

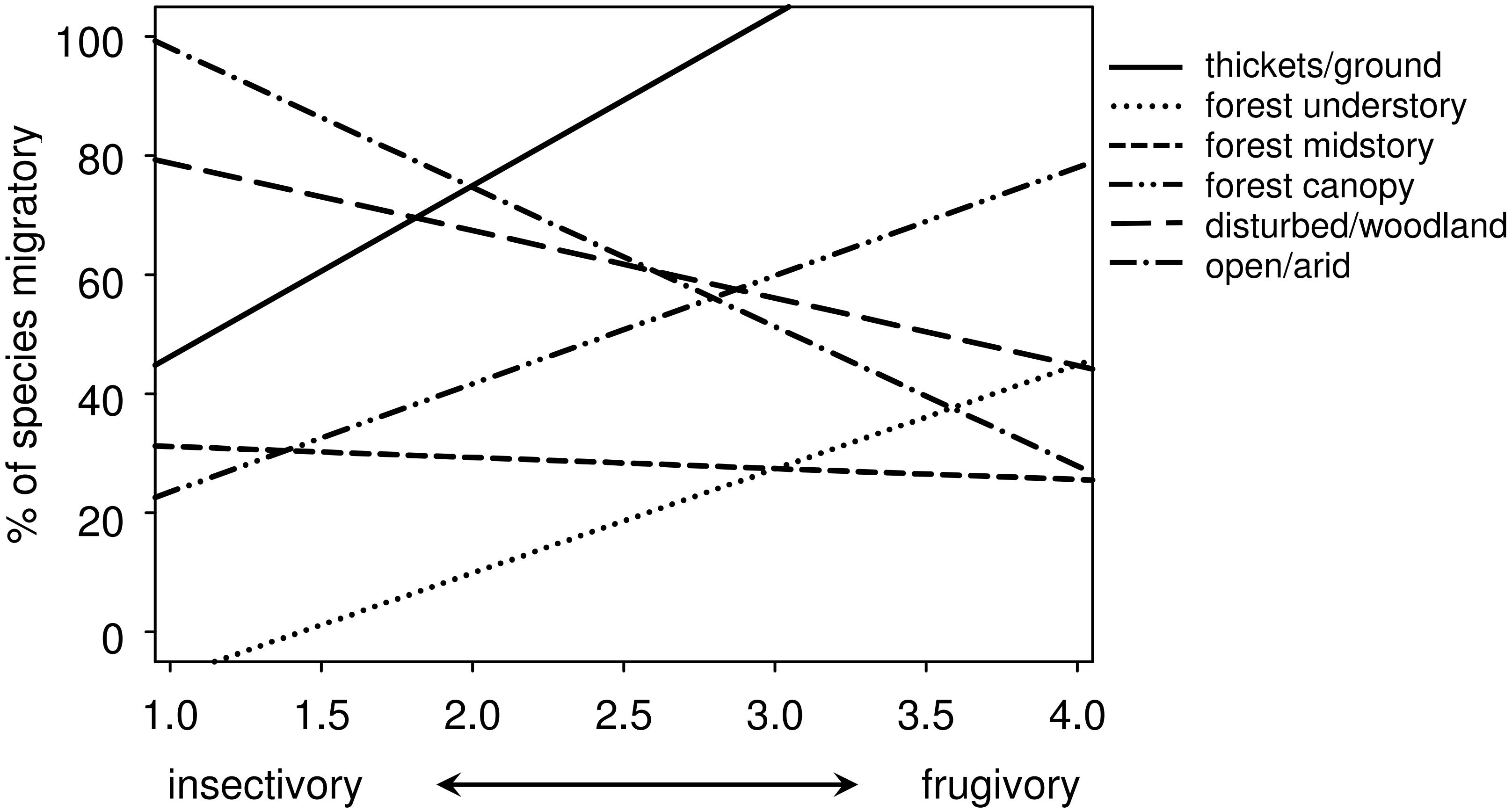

% of species migratory
100
80
60
40
20
0
1.0
1.5
2.0
2.5
3.0
3.5
4.0
insectivory
frugivory
thickets/ground
forest understory
forest midstory
forest canopy
disturbed/woodland
open/arid

Figure 2

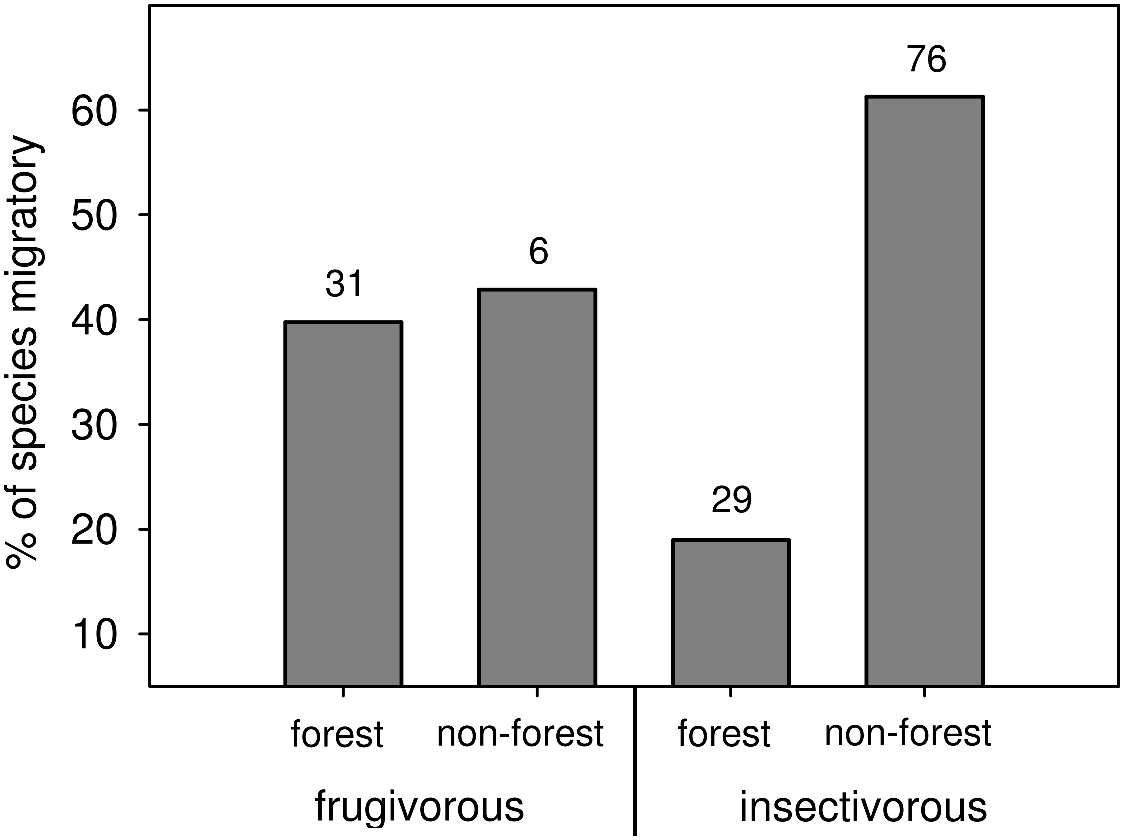
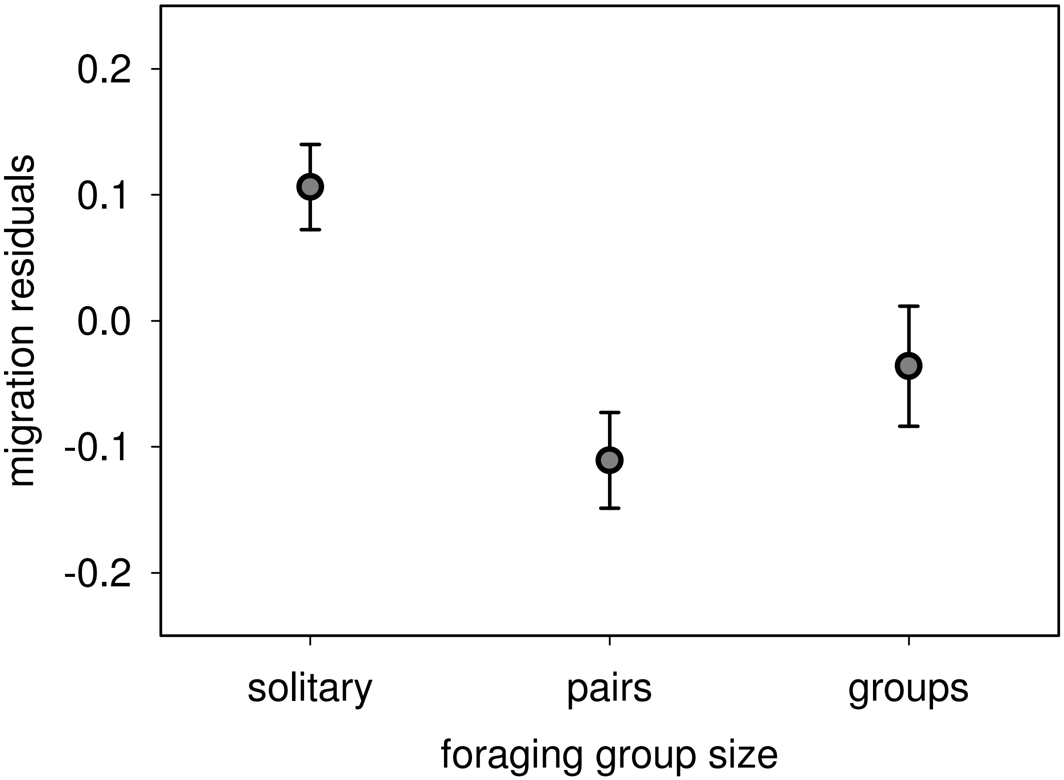

% of species migratory
10
20
30
40
50
60
31
6
29
76
forest
non-forest
forest
non-forest
frugivorous
insectivorous

Figure 3


0.2
0.1
0.0
-0.1
-0.2
migration residuals
solitary
pairs
groups
foraging group size

Online Appendix A

Raw data table for 379 species in the Tyranni used in raw species analyses and used to calculate independent contrasts.

Species[1]	Migration[2]	Diet[3]	Habitat[4]	Foraging group size[5]	Elevation[6]	Mass (g)[7]	Joins mixed-species flocks?[8]
Phyllomyias burmeisteri	4	2.00	4	2	2.0	11.33	yes
Phyllomyias fasciatus	2	2.00	4	2	1.0	11.00	yes
Phyllomyias griseiceps	0	2.00	5	1	1.5	7.67	yes
Phyllomyias uropygialis	1	1.67	4	3	2.0	9.00	yes
Tyrannulus elatus	0	2.67	5	2	1.0	7.75	yes
Myiopagis gaimardii	1	2.00	4	1	1.0	12.67	yes
Myiopagis caniceps	1	2.00	4	1	1.5	10.50	yes
Myiopagis flavivertex	0	1.00	3	2	1.0	11.67	yes
Myiopagis viridicata	4	2.00	4	1	1.0	12.60	yes
Elaenia flavogaster	2	2.40	5	2	1.0	25.20	no
Elaenia spectabilis	4	2.00	5	1	1.0	28.67	no
Elaenia albiceps	5	2.00	5	1	1.5	15.67	yes
Elaenia parvirostris	5	2.50	4	3	1.5	16.67	yes
Elaenia strepera	6	2.00	5	1	1.5	18.33	yes
Elaenia cristata	1	2.50	6	2	1.5	18.00	no
Elaenia chiriquensis	3	2.00	5	2	1.5	15.63	no
Elaenia ruficeps	0	2.00	6	2	1.0	19.00	no
Elaenia frantzii	2	2.40	5	3	2.0	18.25	yes
Elaenia pallatangae	0	2.33	5	1	2.0	16.33	yes
Ornithion brunneicapillus	0	1.33	4	2	1.0	7.25	yes
Ornithion inerme	0	1.00	4	2	1.0	6.67	yes

Camptostoma imberbe	3	1.67	5	1	1.0	7.23	yes
Suiriri suiriri	3	2.00	6	2	1.5	12.67	no
Mecocerculus poecilocercus	0	1.50	4	3	2.0	11.00	yes
Mecocerculus hellmayri	0	1.00	4	1	2.0	11.00	yes
Mecocerculus stictopterus	0	1.33	4	3	2.0	10.67	yes
Mecocerculus calopterus	0	1.00	4	2	2.0	9.00	yes
Mecocerculus minor	0	2.00	5	3	2.0	11.00	yes
Anairetes reguloides	0	1.00	1	3	2.0	6.00	yes
Anairetes alpinus	0	1.00	5	2	2.0	10.00	no
Anairetes flavirostris	4	1.50	6	3	2.0	6.50	yes
Anairetes parulus	4	1.00	5	3	2.0	6.00	yes
Anairetes agraphia	0	1.00	2	3	2.0	10.00	yes
Serpophaga cinerea	0	1.00	6	2	2.0	8.00	no
Serpophaga hypoleuca	1	1.00	1	2	1.0	6.00	no
Serpophaga nigricans	1	1.00	1	2	1.0	9.00	no
Serpophaga munda	3	1.00	4	3	1.0	6.50	no
Phaeomyias murina	4	2.00	1	1	1.0	9.33	yes
Capsiempis flaveola	0	2.00	1	3	1.0	8.00	no
Polystictus pectoralis	4	1.00	6	2	1.5	9.50	yes
Polystictus superciliaris	0	1.00	6	3	2.0	6.00	no
Pseudocolopteryx sclateri	0	1.00	1	3	1.0	7.67	no
Pseudocolopteryx acutipennis	4	1.00	1	3	1.5	8.00	no
Pseudocolopteryx flaviventris	3	1.00	1	3	1.0	8.00	no
Pseudotriccus pelzelni	0	1.00	2	1	2.0	10.50	yes
Pseudotriccus simplex	0	1.00	2	1	2.0	10.00	no
Pseudotriccus ruficeps	0	1.50	2	3	2.0	10.00	no
Corythopis torquatus	0	1.00	1	1	1.0	15.33	no

Corythopis delalandi	0	1.00	1	1	1.0	15.33	no
Euscarthmus meloryphus	3	1.00	1	1	1.0	7.25	no
Euscarthmus rufomarginatus	0	2.00	1	2	1.0	6.00	no
Pseudelaenia leucospodia	0	1.00	6	2	1.0	11.00	no
Stigmatura napensis	0	1.00	5	3	1.0	10.00	no
Stigmatura budytoides	2	1.00	1	3	1.5	11.00	no
Zimmerius vilissimus	1	2.80	4	2	2.0	9.83	yes
Zimmerius cinereicapilla	0	2.50	4	2	2.0	12.00	yes
Zimmerius villarejoi	0	2.00	4	2	1.0	7.00	yes
Zimmerius chrysops	0	2.75	4	2	2.0	11.00	yes
Zimmerius viridiflavus	0	2.50	4	2	2.0	10.00	yes
Phylloscartes poecilotis	0	1.00	3	2	2.0	8.00	yes
Phylloscartes ophthalmicus	0	1.00	3	3	2.0	11.00	yes
Phylloscartes venezuelanus	0	1.00	3	2	2.0	9.00	yes
Phylloscartes eximius	0	1.00	3	2	1.0	9.00	no
Phylloscartes ventralis	0	1.00	3	3	2.0	8.33	yes
Phylloscartes kronei	0	1.00	4	2	1.0	9.00	yes
Phylloscartes beckeri	0	1.00	4	1	2.0	9.00	yes
Phylloscartes flavovirens	0	1.00	4	1	1.5	8.50	yes
Phylloscartes virescens	0	1.00	4	1	1.0	8.50	yes
Phylloscartes gualaquizae	0	1.00	4	2	2.0	8.00	yes
Phylloscartes nigrifrons	0	2.00	4	3	2.0	11.00	yes
Phylloscartes superciliaris	0	2.00	4	3	2.0	8.00	yes
Phylloscartes ceciliae	0	1.00	4	1	1.0	8.00	yes
Phylloscartes flaviventris	0	1.00	4	3	2.0	8.00	yes
Phylloscartes parkeri	0	1.00	4	2	2.0	8.00	yes
Phylloscartes roquettei	0	1.00	3	2	1.0	8.00	no

Phylloscartes paulistus	0	1.00	3	2	1.0	8.00	yes
Phylloscartes oustaleti	0	1.00	4	2	1.0	9.00	yes
Phylloscartes difficilis	0	1.00	2	2	2.0	7.50	no
Phylloscartes sylviolus	0	1.00	4	3	1.0	8.00	yes
Mionectes striaticollis	0	3.00	3	1	2.0	15.00	yes
Mionectes olivaceus	1	3.33	2	1	1.5	14.88	yes
Mionectes oleaginous	1	3.17	2	1	1.0	12.25	yes
Mionectes macconnelli	0	2.67	2	1	2.0	13.33	yes
Leptopogon amaurocephalus	0	2.00	3	1	1.0	11.40	yes
Leptopogon superciliaris	1	2.00	3	1	2.0	12.25	yes
Leptopogon rufipectus	0	2.00	3	2	2.0	13.00	yes
Leptopogon taczanowskii	0	1.50	3	1	2.0	13.00	yes
Sublegatus arenarum	0	2.00	5	1	1.0	13.00	no
Sublegatus obscurior	0	2.00	5	1	1.0	14.00	no
Sublegatus modestus	4	1.50	5	1	1.5	12.17	no
Inezia tenuirostris	0	2.00	5	1	1.0	6.00	yes
Inezia inornata	4	2.00	1	2	1.0	6.00	yes
Myiotriccus ornatus	0	1.00	2	2	2.0	13.50	yes
Tachuris rubrigastra	4	1.00	6	3	1.5	7.00	no
Myiornis atricapillus	0	1.00	4	2	1.0	5.10	no
Myiornis ecaudatus	0	1.00	4	2	1.0	4.67	yes
Oncostoma cinereigulare	0	1.50	2	2	1.5	6.43	no
Oncostoma olivaceum	0	2.00	2	2	1.5	7.00	no
Lophotriccus pileatus	0	1.00	3	1	2.0	7.75	yes
Lophotriccus vitiosus	0	1.00	3	1	1.0	7.00	yes
Lophotriccus eulophotes	0	1.00	3	1	1.0	6.50	yes
Lophotriccus galeatus	0	1.00	3	1	1.0	7.00	yes

Hemitriccus minor	0	1.00	3	2	1.0	7.00	no
Hemitriccus spodiops	0	1.00	1	1	2.0	7.00	no
Hemitriccus flammulatus	0	1.00	2	2	1.0	10.50	yes
Hemitriccus diops	0	1.00	2	2	1.5	10.33	yes
Hemitriccus obsoletus	0	1.00	2	2	2.0	10.00	no
Hemitriccus josephinae	0	1.00	3	2	1.0	10.00	no
Hemitriccus zosterops	0	1.00	3	1	1.0	8.67	yes
Hemitriccus griseipectus	0	1.00	3	1	1.0	9.00	yes
Hemitriccus orbitatus	0	1.00	3	2	1.0	10.00	no
Hemitriccus iohannis	0	1.00	1	3	1.0	11.00	no
Hemitriccus striaticollis	0	1.00	3	2	1.0	9.00	no
Hemitriccus nidipendulus	0	1.00	1	1	1.0	8.00	no
Hemitriccus margaritaceiventer	0	1.00	2	2	1.5	8.33	no
Hemitriccus minimus	0	1.00	4	2	1.0	7.00	no
Hemitriccus granadensis	0	1.00	2	1	2.0	8.00	yes
Hemitriccus rufigularis	0	1.00	3	2	2.0	9.00	yes
Poecilotriccus ruficeps	0	1.00	1	3	2.0	7.00	yes
Poecilotriccus luluae	0	1.00	1	2	2.0	7.00	no
Poecilotriccus capitalis	0	1.00	2	1	1.0	7.50	no
Poecilotriccus russatus	0	1.00	1	2	2.0	7.00	no
Poecilotriccus plumbeiceps	0	1.00	1	2	2.0	6.00	no
Poecilotriccus fumifrons	0	1.00	1	2	1.0	7.00	no
Poecilotriccus latirostris	0	1.00	1	2	1.0	8.50	no
Poecilotriccus sylvia	0	1.50	1	2	1.0	7.33	no
Poecilotriccus calopterus	0	1.00	5	2	1.0	7.50	no
Poecilotriccus pulchellus	0	1.00	1	2	1.5	8.00	no
Taeniotriccus andrei	0	1.00	2	2	1.0	9.00	no

Todirostrum maculatum	0	1.00	5	2	1.0	7.00	no
Todirostrum cinereum	0	1.00	5	2	1.5	6.13	no
Todirostrum nigriceps	1	1.00	4	2	1.0	6.33	yes
Todirostrum pictum	0	1.00	4	2	1.0	7.00	yes
Todirostrum chrysocrotaphum	0	1.00	4	2	1.0	11.33	yes
Cnipodectes subbrunneus	0	1.00	2	1	1.5	23.00	yes
Rhynchocyclus olivaceus	0	1.00	2	1	1.0	20.67	yes
Rhynchocyclus brevirostris	1	1.50	3	1	2.0	22.67	yes
Rhynchocyclus pacificus	0	1.00	2	2	1.0	25.00	yes
Rhynchocyclus fulvipectus	0	1.00	2	1	2.0	26.00	yes
Tolmomyias sulphurescens	0	1.75	5	2	1.5	15.30	yes
Tolmomyias traylori	0	1.00	3	1	1.0	12.00	yes
Tolmomyias assimilis	0	2.00	3	2	1.0	15.50	yes
Tolmomyias poliocephalus	0	1.00	4	2	1.0	11.33	yes
Tolmomyias flaviventris	0	2.00	4	2	1.0	11.33	yes
Platyrinchus cancrominus	0	1.00	2	2	1.0	10.50	no
Platyrinchus saturatus	0	1.00	2	2	1.0	11.00	yes
Platyrinchus mystaceus	0	1.00	2	1	2.0	10.00	yes
Platyrinchus coronatus	0	1.00	2	2	1.0	9.00	yes
Platyrinchus platyrhynchos	0	1.00	3	2	1.0	12.33	no
Platyrinchus leucoryphus	0	1.00	3	1	1.0	17.00	no
Onychorhynchus coronatus	1	1.00	3	1	1.0	16.25	yes
Myiophobus flavicans	0	1.00	2	3	2.0	11.00	no
Myiophobus phoenicomitra	0	1.00	2	3	2.0	11.00	no
Myiophobus roraimae	0	1.00	2	1	2.0	13.00	no
Myiophobus pulcher	0	1.00	4	3	2.0	9.00	yes
Myiophobus lintoni	0	1.00	3	3	2.0	10.00	yes

Myiophobus ochraceiventris	0	1.50	4	3	2.0	11.00	yes
Myiophobus cryptoxanthus	0	2.00	5	2	2.0	11.00	no
Myiophobus fasciatus	4	1.60	1	2	2.0	10.30	no
Myiobius villosus	0	1.00	2	2	2.0	13.33	yes
Myiobius barbatus	0	1.00	2	2	1.0	11.75	yes
Myiobius atricaudus	0	1.00	2	2	1.0	10.00	yes
Terenotriccus erythrurus	0	1.00	3	1	1.0	7.00	yes
Neopipo cinnamomea	0	1.00	3	1	1.0	7.00	yes
Pyrrhomyias cinnamomeus	0	2.00	5	2	2.0	10.67	yes
Hirundinea ferruginea	4	1.00	6	3	1.5	22.50	no
Lathrotriccus euleri	4	1.00	2	1	1.0	11.25	yes
Lathrotriccus griseipectus	1	1.00	2	1	1.5	11.00	no
Aphanotriccus capitalis	0	1.00	1	2	1.5	11.33	no
Aphanotriccus audax	0	1.00	2	2	1.0	11.00	no
Cnemotriccus fuscatus	4	1.00	2	2	1.0	12.75	yes
Empidonax flaviventris	6	1.50	1	1	1.0	11.94	no
Empidonax virescens	6	1.43	4	1	1.5	12.81	yes
Empidonax alnorum	6	1.50	5	1	1.0	13.09	no
Empidonax traillii	6	1.50	5	1	1.0	13.10	no
Empidonax albigularis	3	1.50	1	1	2.0	11.67	no
Empidonax minimus	6	1.00	5	1	1.0	10.11	no
Empidonax hammondii	6	1.00	3	1	2.0	10.33	no
Empidonax wrightii	5	1.00	5	1	1.5	12.13	no
Empidonax oberholseri	6	1.00	5	1	2.0	10.99	no
Empidonax affinis	1	1.00	3	1	2.0	11.50	no
Empidonax difficilis	6	1.50	3	1	1.5	10.59	no
Empidonax occidentalis	5	1.50	3	1	2.0	11.13	no

Empidonax flavescens	1	1.50	5	1	2.0	12.00	no
Empidonax fulvifrons	3	1.00	3	1	2.0	7.97	no
Empidonax atriceps	1	1.00	4	1	2.0	9.00	no
Contopus cooperi	6	1.00	5	1	2.0	32.76	no
Contopus pertinax	4	2.00	5	1	2.0	27.07	yes
Contopus lugubris	0	1.00	5	1	2.0	22.67	no
Contopus fumigatus	0	1.00	5	1	2.0	19.00	no
Contopus ochraceus	0	1.00	5	1	2.0	23.00	no
Contopus sordidulus	6	1.00	4	1	2.0	13.04	no
Contopus virens	6	1.00	4	1	1.0	14.02	no
Contopus cinereus	3	1.00	5	1	1.0	12.13	yes
Contopus nigrescens	0	1.00	4	2	2.0	10.00	no
Mitrephanes phaeocercus	1	1.00	5	2	1.5	8.83	no
Mitrephanes olivaceus	0	1.00	3	2	2.0	9.00	yes
Sayornis nigricans	2	1.00	6	1	1.0	19.05	no
Sayornis phoebe	6	2.00	5	1	1.0	19.60	no
Sayornis saya	6	1.00	6	1	1.5	21.38	no
Pyrocephalus rubinus	4	1.00	6	1	1.0	13.17	no
Lessonia rufa	5	1.00	6	3	1.5	14.00	no
Knipolegus poecilocercus	0	1.00	2	1	1.0	14.00	yes
Knipolegus cyanirostris	4	1.00	5	2	1.5	15.50	no
Knipolegus poecilurus	0	1.00	5	2	2.0	14.67	yes
Knipolegus orenocensis	0	1.00	5	2	1.0	19.00	no
Knipolegus aterrimus	4	1.00	5	1	1.5	24.00	no
Knipolegus lophotes	0	2.00	6	2	1.5	32.00	no
Knipolegus nigerrimus	1	1.00	6	2	2.0	20.00	no
Hymenops perspicillatus	4	1.00	6	1	2.0	24.00	no

Ochthornis littoralis	0	1.00	6	2	1.0	13.00	no
Satrapa icterophrys	5	1.00	5	1	1.5	20.00	no
Agriornis lividus	0	1.00	6	2	1.5	99.00	no
Agriornis micropterus	4	1.00	6	1	1.5	73.00	no
Xolmis dominicanus	0	1.00	6	2	1.5	43.00	no
Myiotheretes striaticollis	1	1.00	5	2	2.0	64.00	no
Myiotheretes fuscorufus	0	1.00	4	3	2.0	32.00	yes
Neoxolmis rufiventris	4	1.00	6	3	1.0	77.00	no
Gubernetes yetapa	0	1.00	6	3	1.0	67.00	no
Muscipipra vetula	3	1.00	5	3	1.5	27.00	no
Fluvicola pica	0	1.00	6	2	1.0	13.00	no
Arundinicola leucocephala	0	1.00	6	2	1.0	14.25	no
Ochthoeca frontalis	0	1.00	2	1	2.0	11.00	yes
Ochthoeca pulchella	0	1.00	2	1	2.0	12.00	no
Ochthoeca cinnamomeiventris	0	1.00	2	2	2.0	12.00	no
Ochthoeca rufipectoralis	0	1.00	5	2	2.0	12.00	yes
Ochthoeca fumicolor	1	1.00	6	2	2.0	16.33	no
Colorhamphus parvirostris	4	1.00	5	1	1.0	9.00	no
Colonia colonus	1	1.00	5	2	1.0	16.40	no
Machetornis rixosa	1	1.00	6	3	1.0	33.67	no
Legatus leucophaius	5	3.67	5	2	1.0	24.00	no
Myiozetetes cayanensis	1	2.00	5	3	1.5	26.00	no
Myiozetetes similis	2	2.33	5	3	1.5	26.25	no
Myiozetetes granadensis	1	2.25	5	3	1.0	29.00	no
Myiozetetes luteiventris	0	2.00	4	3	1.0	17.00	yes
Phelpsia inornata	0	2.00	5	3	1.0	29.00	no
Pitangus sulphuratus	4	2.00	5	3	1.0	65.25	yes

Pitangus lictor	0	1.00	5	3	1.0	24.67	no
Megarynchus pitangua	4	2.00	5	3	1.0	66.80	yes
Conopias albovittatus	0	2.00	4	3	1.0	24.00	yes
Conopias parvus	0	2.00	4	3	1.0	22.50	yes
Myiodynastes hemichrysus	0	1.50	4	3	2.0	41.67	no
Myiodynastes chrysocephalus	1	1.50	5	2	2.0	38.33	yes
Myiodynastes bairdii	0	2.00	5	2	1.0	45.00	no
Myiodynastes luteiventris	6	2.25	4	3	1.5	45.82	no
Tyrannopsis sulphurea	0	2.00	5	3	1.0	55.00	no
Empidonomus varius	5	2.00	5	1	1.0	26.25	yes
Empidonomus aurantioatrocristatus	6	1.33	5	1	1.0	27.75	no
Tyrannus melancholicus	4	1.80	5	1	1.0	38.59	no
Tyrannus couchii	3	2.00	5	3	1.0	41.33	yes
Tyrannus vociferans	5	2.33	6	1	2.0	44.55	no
Tyrannus crassirostris	3	2.00	5	2	1.0	55.55	no
Tyrannus verticalis	6	1.25	6	1	1.5	39.74	yes
Tyrannus forficatus	5	2.00	6	3	1.5	41.28	no
Tyrannus savana	5	1.50	6	3	1.0	30.00	no
Rhytipterna holerythra	0	2.33	3	2	1.0	38.33	yes
Rhytipterna simplex	0	2.00	3	3	1.0	34.67	yes
Sirystes sibilator	1	2.00	4	2	1.0	30.67	yes
Myiarchus tuberculifer	4	2.00	5	1	1.5	19.99	yes
Myiarchus swainsoni	6	2.00	4	1	1.0	24.75	yes
Myiarchus ferox	0	2.00	4	2	1.0	26.67	no
Myiarchus cephalotes	0	1.00	5	1	2.0	23.67	yes
Myiarchus cinerascens	5	2.00	5	1	1.0	27.44	no
Myiarchus nuttingi	0	2.00	5	3	1.5	23.00	no

Myiarchus crinitus	6	2.00	5	1	1.0	34.08	no
Myiarchus tyrannulus	4	2.00	5	2	1.0	34.50	no
Ramphotrigon megacephalum	0	1.00	2	1	1.0	14.00	yes
Ramphotrigon ruficauda	0	1.00	3	2	1.0	18.33	yes
Ramphotrigon fuscicauda	0	1.00	3	2	1.0	19.00	yes
Attila cinnamomeus	0	2.00	3	2	1.0	38.33	yes
Attila citriniventris	0	2.00	4	1	1.0	34.50	yes
Attila bolivianus	0	2.00	3	1	1.0	44.00	yes
Attila rufus	0	2.00	3	2	1.5	43.00	yes
Attila spadiceus	0	2.00	5	1	1.5	37.00	yes
Ampelion rubrocristatus	0	3.00	5	3	2.0	65.33	no
Ampelion rufaxilla	0	3.00	4	1	2.0	73.50	no
Zaratornis stresemanni	1	4.00	5	3	2.0	51.50	no
Doliornis sclateri	0	3.00	4	2	2.0	61.00	no
Phytotoma raimondii	0	4.00	6	2	1.0	40.00	no
Phytotoma rutila	3	4.00	5	3	1.5	36.33	no
Phytotoma rara	1	4.00	5	3	1.5	40.50	no
Carpornis cucullata	0	3.00	3	1	1.5	75.33	no
Carpornis melanocephala	0	4.00	3	1	1.0	64.50	no
Pipreola riefferii	0	4.00	4	3	2.0	51.00	yes
Pipreola arcuata	0	4.00	3	1	2.0	120.00	yes
Pipreola aureopectus	0	4.00	3	1	2.0	47.33	yes
Pipreola pulchra	0	4.00	3	1	2.0	55.50	no
Pipreola frontalis	0	4.00	3	1	2.0	42.50	yes
Pipreola formosa	0	4.00	3	1	2.0	45.00	yes
Ampelioides tschudii	1	3.40	3	3	2.0	81.33	yes
Rupicola rupicola	0	3.00	3	1	1.0	183.33	no

Rupicola peruvianus	0	3.00	3	1	2.0	251.67	no
Phoenicircus carnifex	0	4.00	4	1	1.0	82.67	no
Phoenicircus nigricollis	0	3.67	3	1	1.0	95.50	no
Cotinga amabilis	1	3.00	4	3	1.5	71.67	no
Cotinga ridgwayi	1	4.00	4	1	1.5	56.00	no
Cotinga maynana	0	4.00	4	1	1.0	69.00	yes
Cotinga cayana	1	3.75	4	1	1.0	64.33	yes
Procnias tricarunculatus	2	4.00	4	1	1.5	162.50	no
Procnias albus	1	4.00	4	1	1.5	211.67	no
Procnias averano	1	4.00	4	1	1.0	169.33	no
Procnias nudicollis	1	4.00	4	1	1.0	191.67	no
Tijuca condita	1	4.00	4	1	2.0	80.00	no
Lipaugus fuscocinereus	0	4.00	3	3	2.0	133.50	yes
Lipaugus uropygialis	0	4.00	3	1	2.0	121.00	yes
Lipaugus unirufus	0	3.00	3	1	1.0	79.67	yes
Lipaugus vociferans	0	3.50	3	1	1.0	78.67	yes
Lipaugus lanioides	1	3.00	3	1	1.5	96.50	no
Conioptilon mcilhennyi	0	3.00	3	2	1.0	88.00	yes
Snowornis subalaris	0	2.00	3	1	2.0	83.00	yes
Snowornis cryptolophus	0	2.00	3	1	2.0	84.00	yes
Porphyrolaema porphyrolaema	0	4.00	4	2	1.5	60.00	no
Xipholena punicea	1	3.50	4	1	1.0	66.67	yes
Carpodectes antoniae	1	4.00	4	3	1.0	98.00	no
Carpodectes nitidus	1	4.00	4	3	1.0	105.00	no
Gymnoderus foetidus	1	3.33	4	3	1.0	280.00	no
Querula purpurata	0	2.67	4	3	1.0	103.50	no
Pyroderus scutatus	1	3.50	3	1	2.0	381.75	no

Perissocephalus tricolor	0	3.33	3	1	1.0	343.33	no
Cephalopterus ornatus	0	3.00	3	3	1.0	400.00	no
Cephalopterus penduliger	0	4.00	4	1	2.0	339.00	no
Cephalopterus glabricollis	1	3.00	3	1	1.5	428.33	no
Neopelma pallescens	0	2.00	2	1	1.0	18.00	no
Neopelma chrysocephalum	0	2.50	2	1	1.0	15.67	no
Neopelma aurifrons	0	2.50	2	1	1.0	14.00	no
Tyranneutes stolzmanni	0	3.33	2	1	1.0	8.00	no
Tyranneutes virescens	0	3.00	3	1	1.0	7.00	no
Ilicura militaris	1	3.00	3	1	2.0	15.00	yes
Masius chrysopterus	0	3.33	2	1	2.0	11.00	yes
Corapipo altera	1	4.00	2	1	1.0	12.50	yes
Corapipo gutturalis	0	3.00	2	1	1.5	8.00	yes
Machaeropterus deliciosus	1	3.00	2	1	1.5	12.00	yes
Lepidothrix coronata	0	3.50	2	1	1.0	10.00	yes
Lepidothrix suavissima	0	3.00	2	1	2.0	10.00	yes
Manacus candei	0	3.67	5	3	1.0	18.75	no
Manacus aurantiacus	0	3.00	5	3	1.5	15.75	no
Manacus vitellinus	0	3.25	5	1	1.5	19.00	no
Manacus manacus	0	3.25	5	1	1.0	16.33	no
Chiroxiphia lanceolata	0	3.67	2	3	2.0	18.25	no
Chiroxiphia linearis	0	4.00	2	3	1.5	18.00	no
Xenopipo holochlora	0	2.50	2	1	2.0	15.00	yes
Xenopipo uniformis	1	3.50	2	1	2.0	19.00	no
Xenopipo atronitens	0	3.00	5	3	1.0	15.67	yes
Heterocercus flavivertex	0	2.67	2	1	1.0	21.33	yes
Pipra pipra	1	3.50	2	1	2.0	12.00	yes

Pipra cornuta	0	4.00	2	1	2.0	19.00	no
Pipra mentalis	1	3.50	2	1	1.0	15.67	yes
Pipra erythrocephala	0	3.00	2	1	1.0	13.00	no
Pipra rubrocapilla	0	3.00	2	1	1.0	13.00	no
Laniocera rufescens	0	2.00	3	1	1.0	48.00	yes
Laniocera hypopyrra	0	2.00	3	1	1.0	47.67	yes
Iodopleura isabellae	0	2.00	4	3	1.0	20.00	no
Iodopleura fusca	0	2.00	4	2	1.0	15.33	yes
Iodopleura pipra	1	3.00	4	2	1.0	10.00	yes
Laniisoma elegans	1	3.00	3	1	1.5	47.00	yes
Piprites pileata	1	3.00	4	2	2.0	15.00	yes
Piprites griseiceps	0	3.33	3	1	1.0	16.00	yes
Piprites chloris	0	2.33	4	1	1.5	17.50	yes
Schiffornis major	0	2.00	2	1	1.0	30.67	no
Schiffornis turdina	0	2.33	2	1	1.5	31.00	yes
Xenopsaris albinucha	4	1.00	5	2	1.0	10.00	no
Pachyramphus viridis	0	1.00	4	2	1.0	21.00	yes
Pachyramphus versicolor	0	1.67	4	3	2.0	16.00	yes
Pachyramphus rufus	0	2.00	5	2	1.5	18.33	yes
Pachyramphus cinnamomeus	1	2.33	5	3	1.0	19.50	yes
Pachyramphus castaneus	0	2.00	5	2	1.0	18.25	yes
Pachyramphus polychopterus	2	2.33	5	2	1.5	21.60	yes
Pachyramphus major	1	2.00	4	2	2.0	25.00	yes
Pachyramphus albogriseus	1	2.00	4	2	1.5	19.50	yes
Pachyramphus marginatus	0	2.00	4	2	1.0	18.00	yes
Pachyramphus surinamus	0	2.00	4	2	1.0	19.67	yes
Pachyramphus aglaiae	3	2.00	5	2	1.0	32.00	yes

Pachyramphus homochrous	0	2.00	4	2	1.0	35.00	yes
Pachyramphus minor	0	2.00	3	3	1.0	38.00	yes
Pachyramphus validus	4	1.00	4	1	1.0	47.00	yes
Phibalura flavirostris	2	3.00	5	3	2.0	46.33	yes
Tityra cayana	4	3.33	4	3	1.0	74.75	no
Tityra semifasciata	0	3.25	4	3	1.5	81.75	yes
Oxyruncus cristatus	1	2.67	4	1	2.0	41.25	yes

[1] We follow the American Ornithologists' Union (American Ornithologists' Union 1998; American Ornithologists' Union 2005; Remsen et al. 2006) on all taxonomic issues including the ordering and spelling of species names in this list.

[2] We considered a species as migratory when any source reported migratory populations. Migration categories: 0) no populations of species known or suspected to be migratory, 1) altitudinal movements and other movements less than 100 kms, 2) 100–300 kms, 3) 300–700 kms, 4) 700–1500 kms, 5) 1500–3000 kms, 6) >3000 kms. We assigned a species to the shortest migratory distance category (category 1) when at least some populations of that species migrate locally. Because information on movement patterns for many neotropical species is scant, we also placed species in the shortest migratory category when sources mentioned that movement patterns were suggestive of migration. For all other migratory species, we measured the shortest distance between the reported northern edge of the non-breeding range and the northern edge of the breeding range (for nearctic migrants) or the shortest distance between the reported southern edge of the non-breeding range and the southern edge of the breeding range (for austral migrants). For partially migratory species, we used the longest

estimate of migratory distance which corresponds to the minimum distance individuals of that species must migrate. We placed species in migration category 2 when sources described them as an austral latitudinal migrant but we found no information on migratory distance. We chose the longest distance population to represent the species.

[3] Diet categories: 1) highly insectivorous, 2) more insects (and/or other animals) than fruit, 3) more fruit than insects, 4) highly frugivorous. If diet categories from all sources were in agreement, then we used that category to represent the species. When classifications from different sources resulted in two categories being noted for a species, we entered the mean value from all available sources for that species. If classifications from different sources resulted in three categories being noted, we eliminated these ambiguous species from our dataset.

[4] We classified species on the basis of habitats used for foraging when sources distinguished between habitats occupied for different behaviors. Habitat categories: 1) Generally found near the ground overtopped by vegetation, dense thickets, tangles (including bamboo), and low thickets in forested or non-forested contexts, 2) understory of forest, 3) middle levels of forest, 4) forest canopy, 5) edge or disturbed habitats with matrix of trees and open areas, gardens, orchards, woodlands, scrub, 6) open areas, savannas, deserts, or other places without many trees. For forest-interior species, when foraging height given in height above ground, we defined understory (category 2) as up to ~4 m, and midstory (category 3) as ~4–10 m. When classifying the habitat associations of a species, we entered more than one habitat category from a given source if more than one habitat appeared with equal prominence in descriptions of non-breeding foraging behavior. If only 1

habitat category was common to data from all sources, we chose that category. If no numbers were common to all data, we used the categories resulting from descriptions in del Hoyo et al. (2000) and Stotz et al. (1996) as these were the most taxonomically complete sources we consulted. If these two sources only shared 1 category, we used that category. If these two sources shared more than 1 category, we used the shared category that most commonly appeared in all the sources for that species. If two or more numbers were used equally frequently among del Hoyo et al. (2000), Stotz et al. (1996), and all other sources, we eliminated it from our dataset. If there were no categories in common between del Hoyo et al. (2000) and Stotz et al. (1996) and there was information from other sources, we used the category from either del Hoyo et al. (2000) and Stotz et al. (1996) that appeared most frequently in other sources. When classifications could not be resolved by rechecking original sources, we eliminated these ambiguous species from analyses.

[5] Foraging group size categories refer to the number of conspecifics that typically forage together. We initially categorized foraging group size as: 1) solitary, 2) pairs, 3) small groups, family groups, large groups. To assign a species to a category when more than one foraging group size was noted in sources, we followed these guidelines: if only 1 category was noted among all the sources available for a species, then we used that category. If both categories 1 and 2 were noted we classified a species based on the most common category among sources. If categories 1 and 2 appeared equally commonly, we used the category based on del Hoyo et al. (2000). If del Hoyo et al. (2000) did not mention foraging group size for a given species, and categories 1 and 2 appeared equally commonly, we eliminated the species from analyses. If multiple

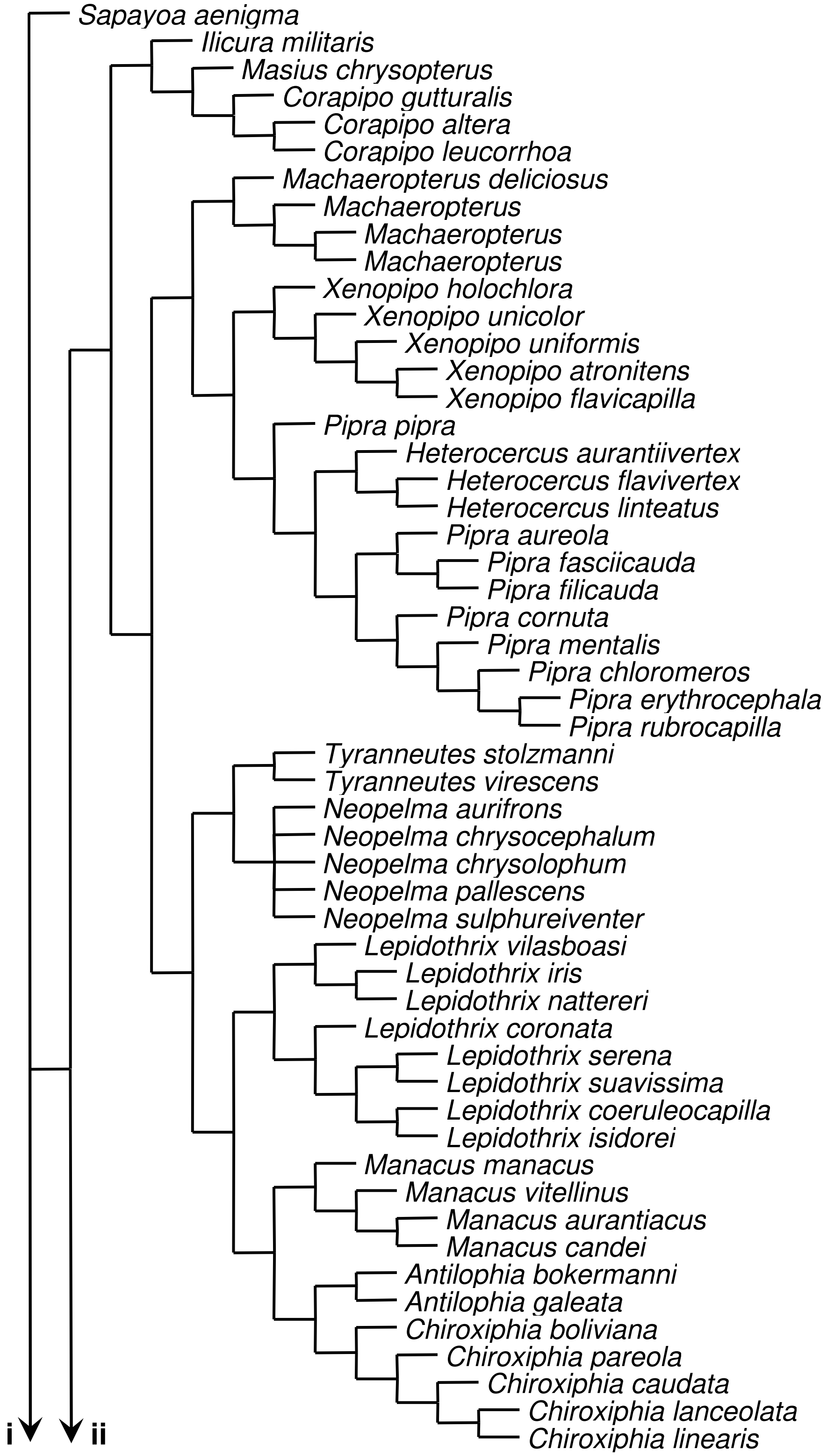
categories were listed for a species, and category 3 appeared more than once or was the categorization based on del Hoyo et al. (2000), we chose the group category to represent the species. If category 3 appeared only once, we used the most common of the designations across all sources to represent the species.

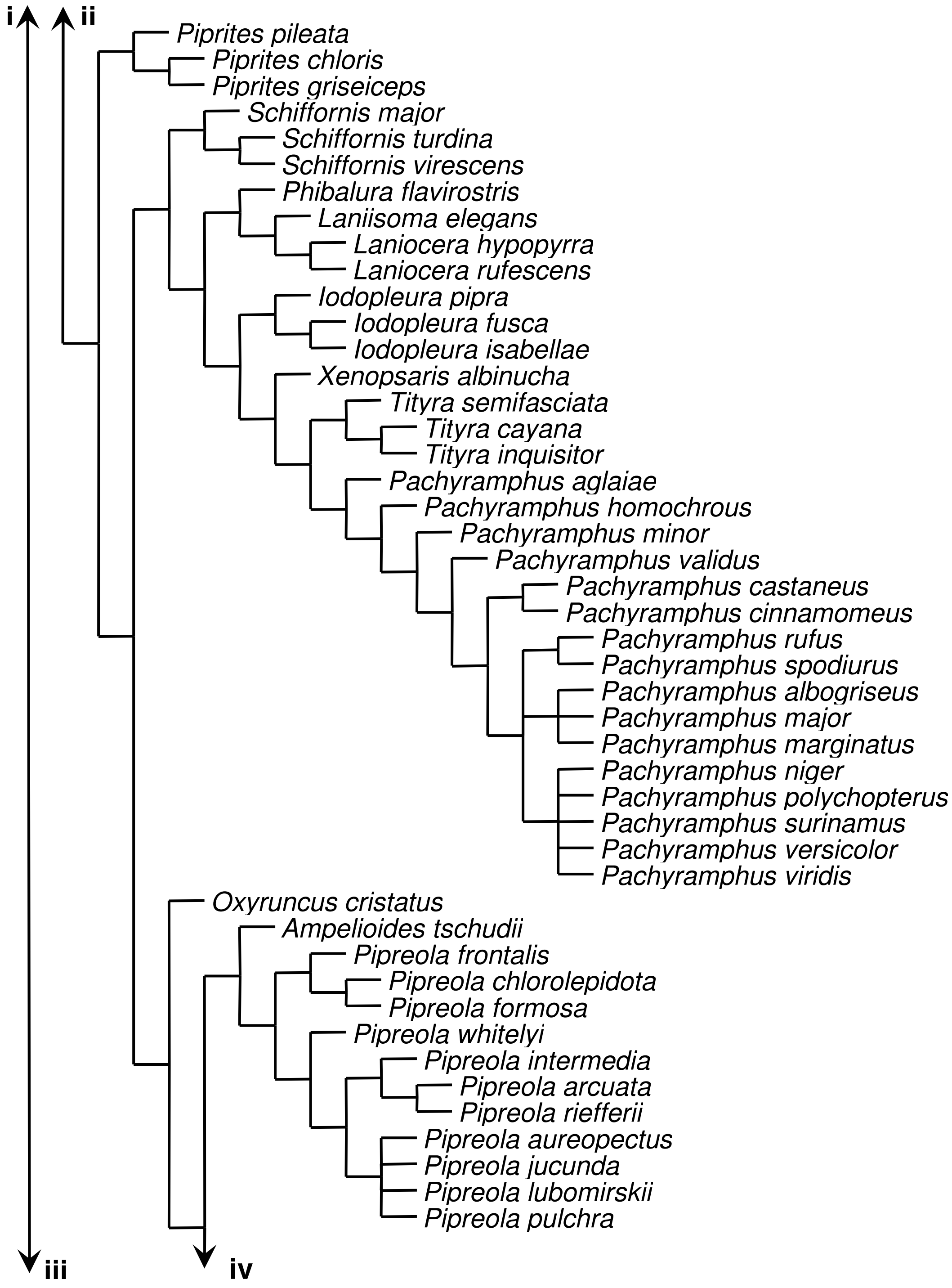
[6] Elevation categories: 1) primarily lowland species, 2) primarily montane species. Montane species were those that primarily spend the non-breeding season above 700 m, not regularly occurring in lowland areas. An intermediate category (1.5) represents species with wide altitudinal ranges, not easily classified as either primarily lowland or primarily montane. Where either category 1 or 2 was noted in combination with category 1.5, we classified the species as 1 or 2. Where both 1 and 2 were noted, or only 1.5 noted, we classified the species as 1.5.

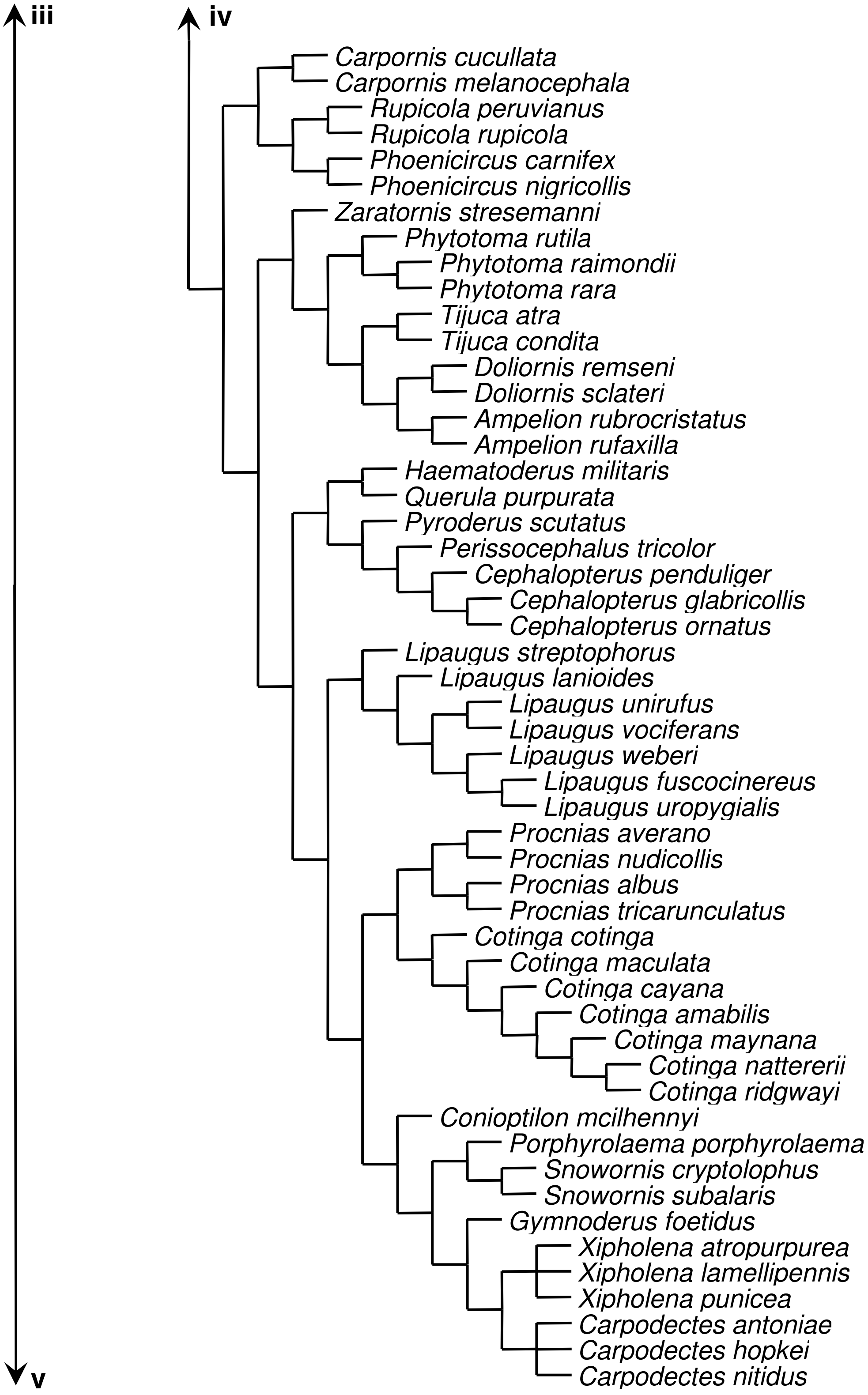
[7] We took the average value of all body mass values available from all sources, males and females combined.

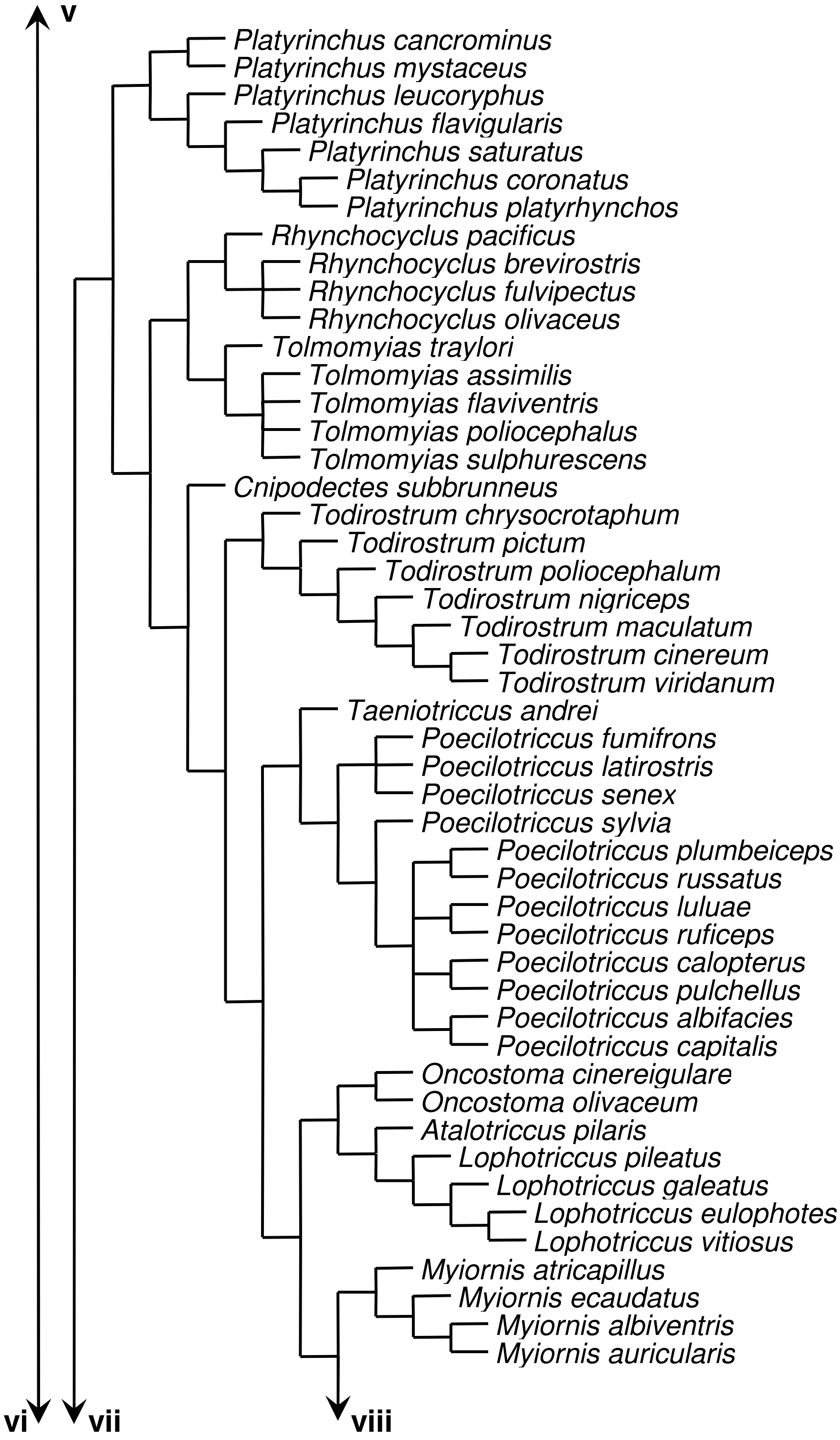
[8] If any source noted that the species joins mixed-species flocks, we classified this species as one that joins mixed-species flocks. If we found descriptions of flocking behavior and foraging group size for a species, but no source ever mentioned the species joining mixed-species flocks, we classified the species as not joining mixed-species flocks.

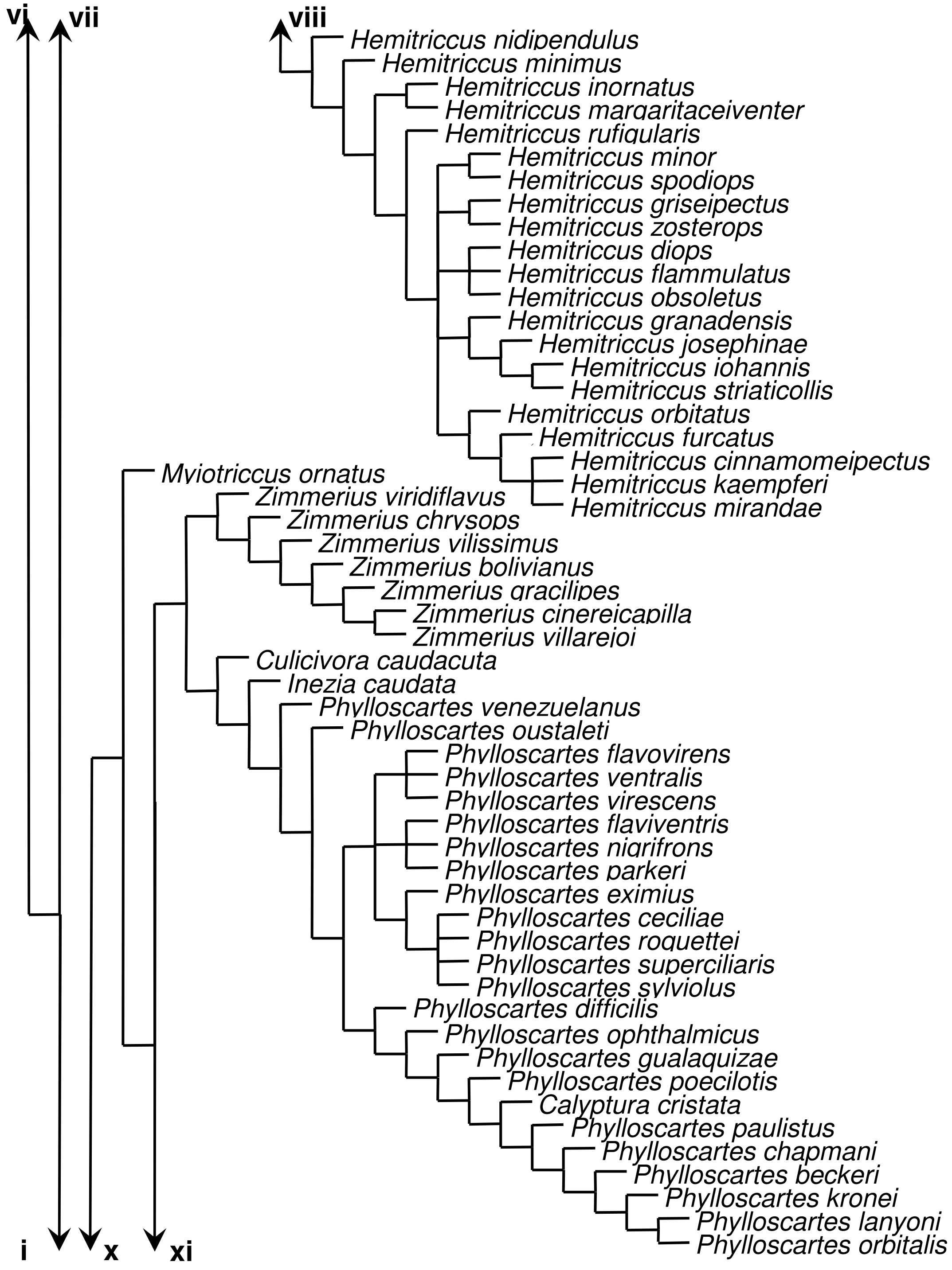
Online Appendix B Figure 1

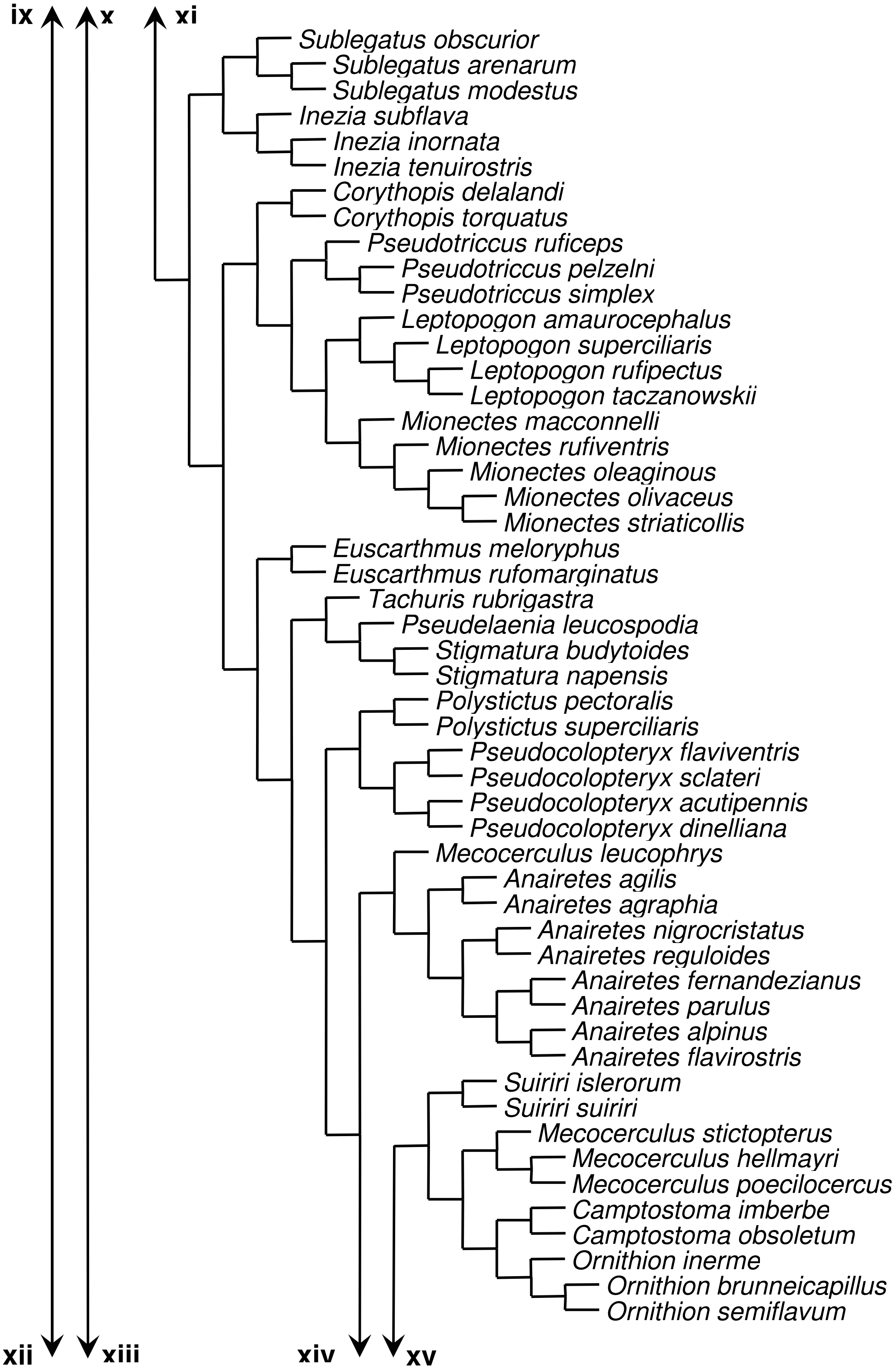


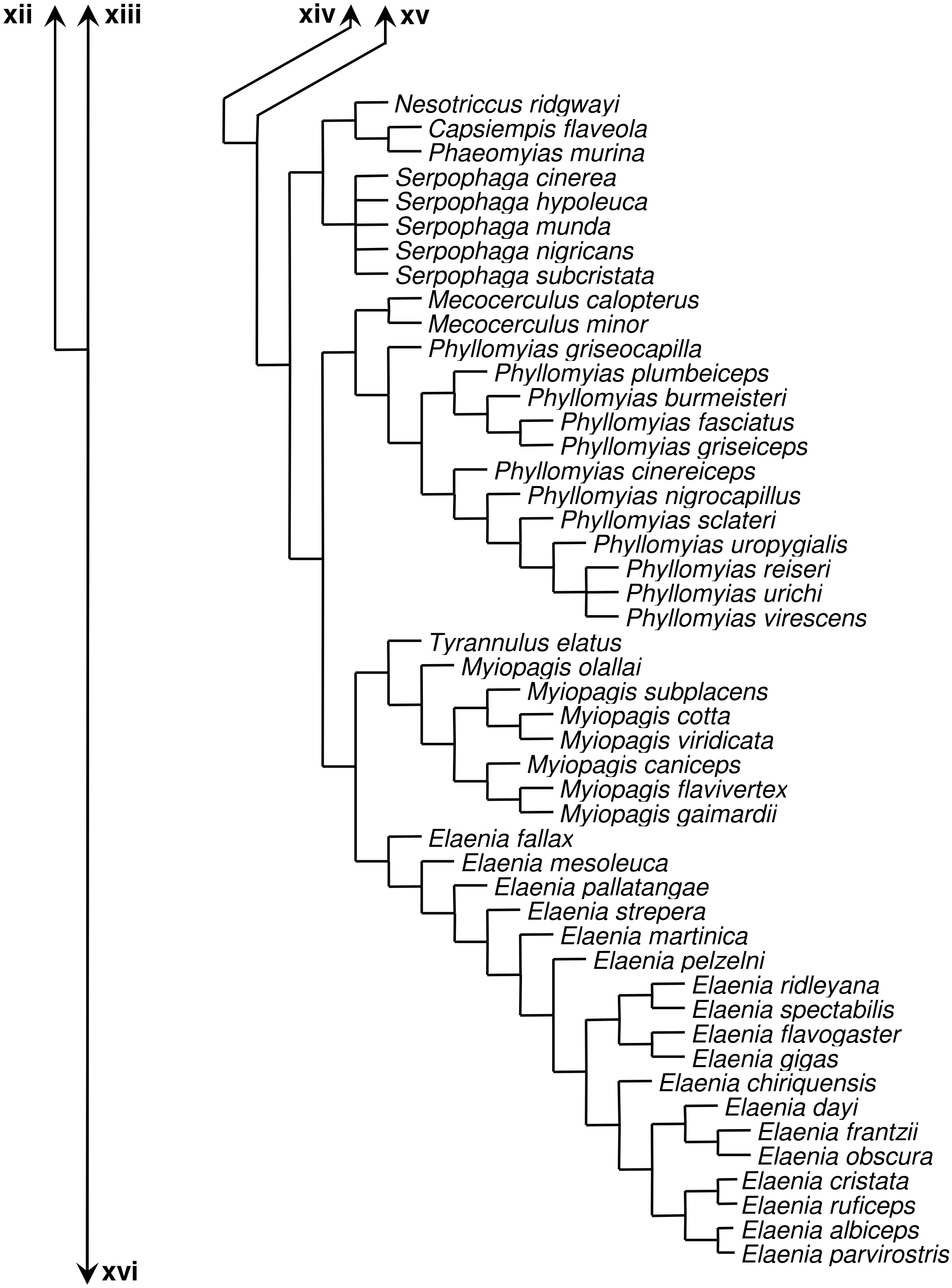

i
ii
iii
iv
Piprites pileata
Piprites chloris
Piprites griseiceps
Schiffornis major
Schiffornis turdina
Schiffornis virescens
Phibalura flavirostris
Laniisoma elegans
Laniocera hypopyrra
Laniocera rufescens
Iodopleura pipra
Iodopleura fusca
Iodopleura isabellae
Xenopsaris albinucha
Tityra semifasciata
Tityra cayana
Tityra inquisitor
Pachyramphus aglaiae
Pachyramphus homochrous
Pachyramphus minor
Pachyramphus validus
Pachyramphus castaneus
Pachyramphus cinnamomeus
Pachyramphus rufus
Pachyramphus spodiurus
Pachyramphus albogriseus
Pachyramphus major
Pachyramphus marginatus
Pachyramphus niger
Pachyramphus polychopterus
Pachyramphus surinamus
Pachyramphus versicolor
Pachyramphus viridis
Oxyruncus cristatus
Ampelioides tschudii
Pipreola frontalis
Pipreola chlorolepidota
Pipreola formosa
Pipreola whitelyi
Pipreola intermedia
Pipreola arcuata
Pipreola riefferii
Pipreola aureopectus
Pipreola jucunda
Pipreola lubomirskii
Pipreola pulchra

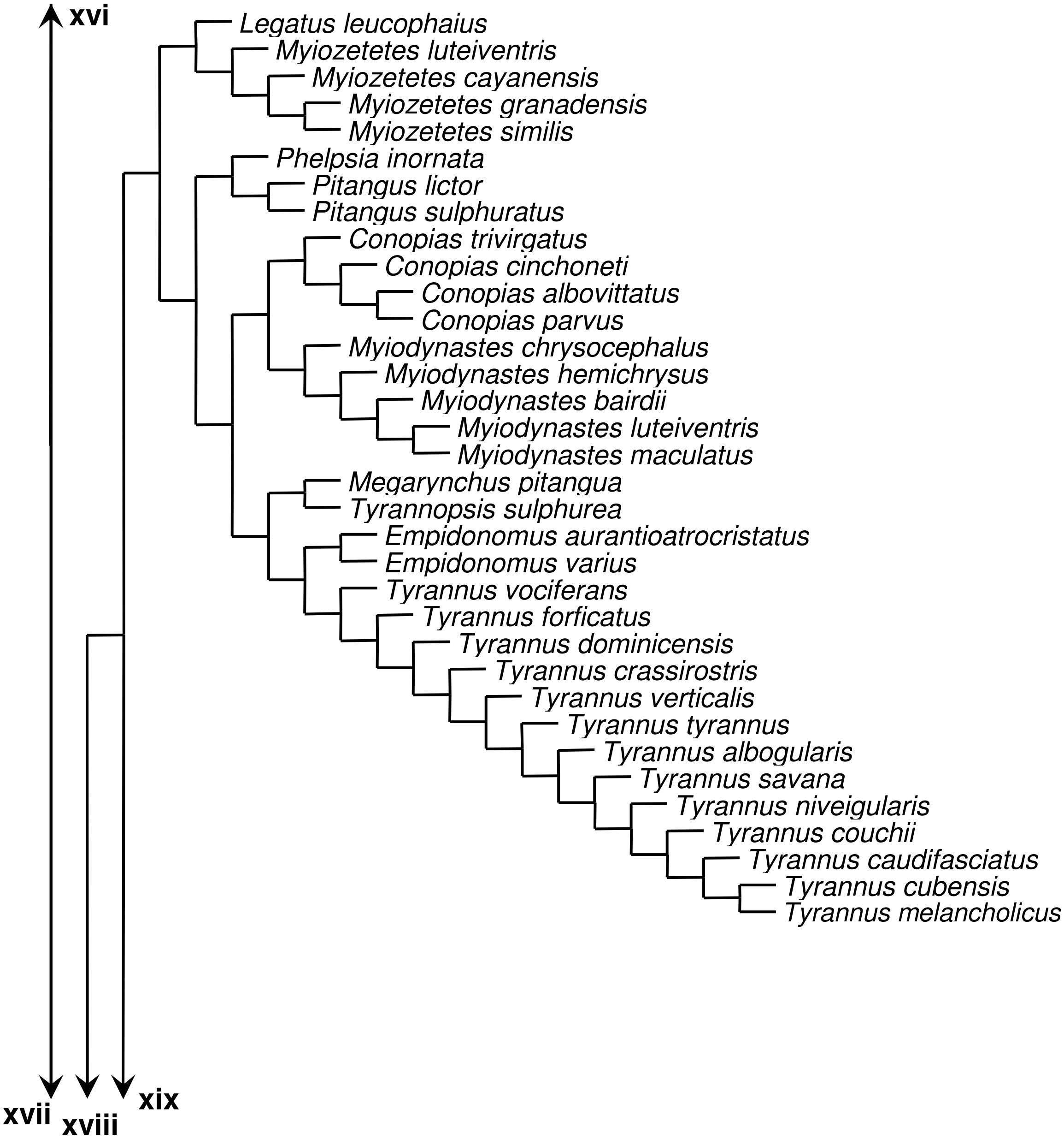

iii
iv
Carpornis cucullata
Carpornis melanocephala
Rupicola peruvianus
Rupicola rupicola
Phoenicircus carnifex
Phoenicircus nigricollis
Zaratornis stresemanni
Phytotoma rutila
Phytotoma raimondii
Phytotoma rara
Tijuca atra
Tijuca condita
Doliornis remseni
Doliornis sclateri
Ampelion rubrocristatus
Ampelion rufaxilla
Haematoderus militaris
Querula purpurata
Pyroderus scutatus
Perissocephalus tricolor
Cephalopterus penduliger
Cephalopterus glabricollis
Cephalopterus ornatus
Lipaugus streptophorus
Lipaugus lanioides
Lipaugus unirufus
Lipaugus vociferans
Lipaugus weberi
Lipaugus fuscocinereus
Lipaugus uropygialis
Procnias averano
Procnias nudicollis
Procnias albus
Procnias tricarunculatus
Cotinga cotinga
Cotinga maculata
Cotinga cayana
Cotinga amabilis
Cotinga maynana
Cotinga nattererii
Cotinga ridgwayi
Conioptilon mcilhennyi
Porphyrolaema porphyrolaema
Snowornis cryptolophus
Snowornis subalaris
Gymnoderus foetidus
Xipholena atropurpurea
Xipholena lamellipennis
Xipholena punicea
Carpodectes antoniae
Carpodectes hopkei
Carpodectes nitidus
v

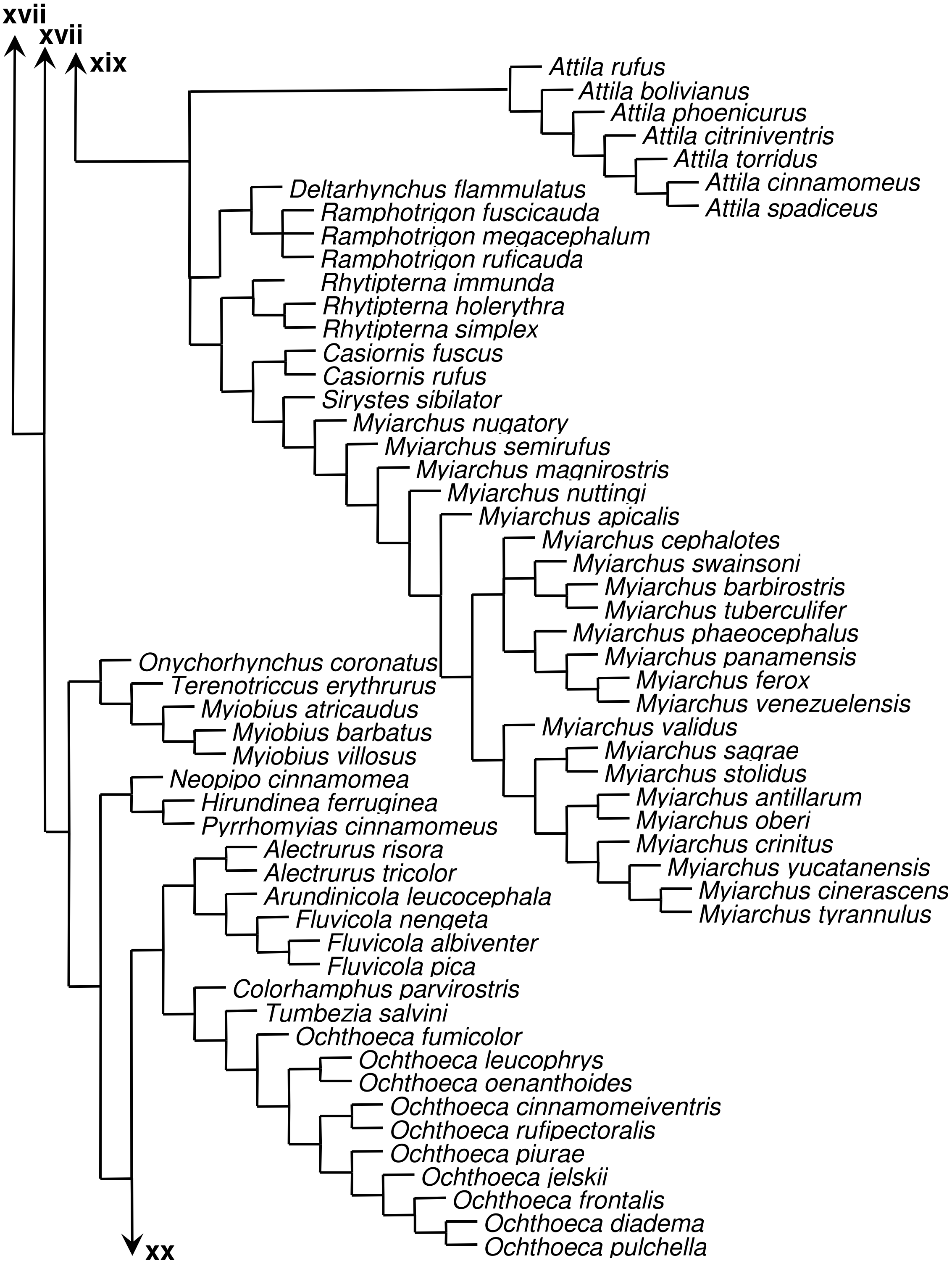

v
Platyrinchus cancrominus
Platyrinchus mystaceus
Platyrinchus leucoryphus
Platyrinchus flavigularis
Platyrinchus saturatus
Platyrinchus coronatus
Platyrinchus platyrhynchos
Rhynchocyclus pacificus
Rhynchocyclus brevirostris
Rhynchocyclus fulvipectus
Rhynchocyclus olivaceus
Tolmomyias traylori
Tolmomyias assimilis
Tolmomyias flaviventris
Tolmomyias poliocephalus
Tolmomyias sulphurescens
Cnipodectes subbrunneus
Todirostrum chrysocrotaphum
Todirostrum pictum
Todirostrum poliocephalum
Todirostrum nigriceps
Todirostrum maculatum
Todirostrum cinereum
Todirostrum viridanum
Taeniotriccus andrei
Poecilotriccus fumifrons
Poecilotriccus latirostris
Poecilotriccus senex
Poecilotriccus sylvia
Poecilotriccus plumbeiceps
Poecilotriccus russatus
Poecilotriccus luluae
Poecilotriccus ruficeps
Poecilotriccus calopterus
Poecilotriccus pulchellus
Poecilotriccus albifacies
Poecilotriccus capitalis
Oncostoma cinereigulare
Oncostoma olivaceum
Atalotriccus pilaris
Lophotriccus pileatus
Lophotriccus galeatus
Lophotriccus eulophotes
Lophotriccus vitiosus
Myiornis atricapillus
Myiornis ecaudatus
Myiornis albiventris
Myiornis auricularis
vi
vii
viii

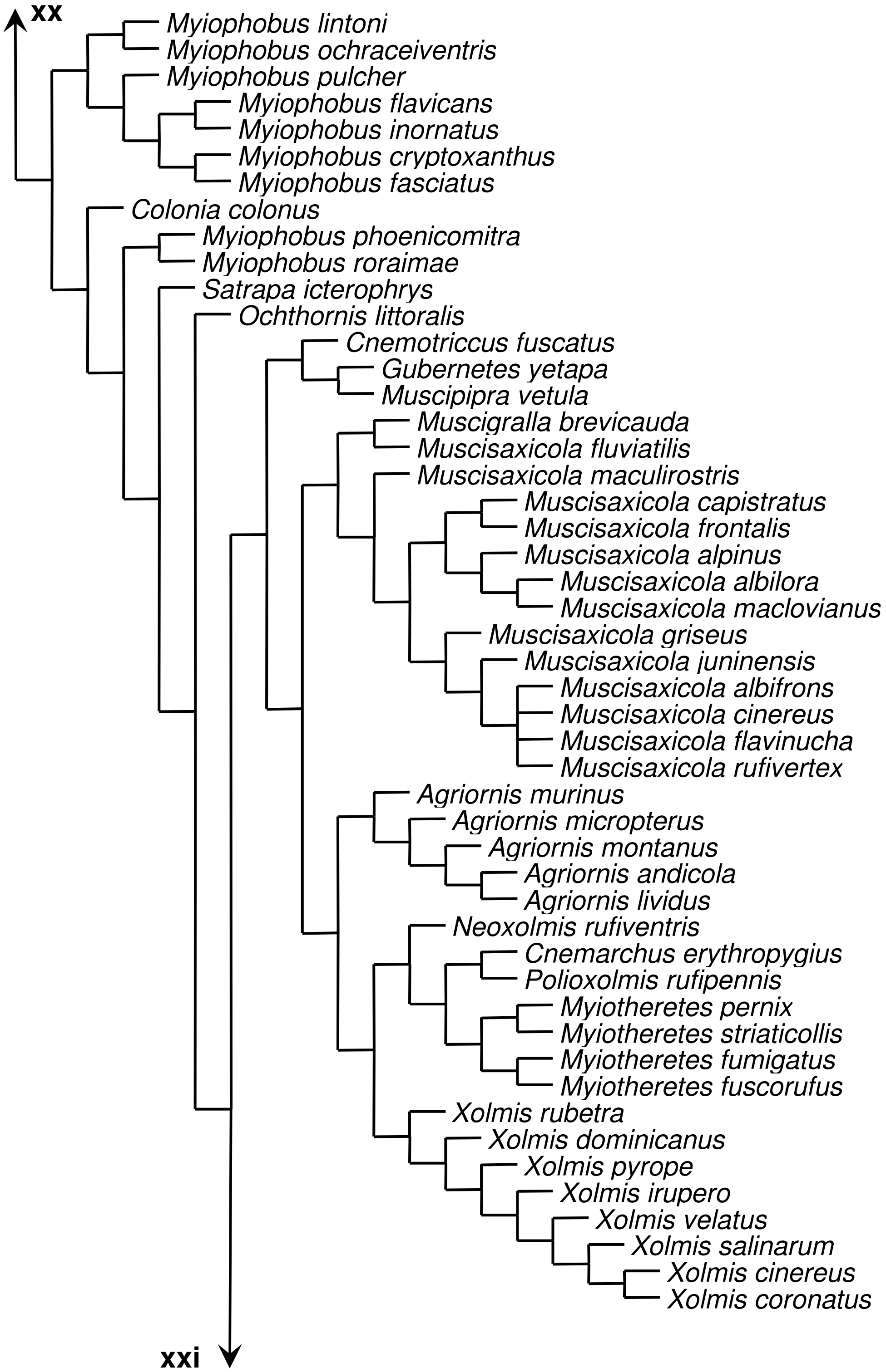

vi
vii
viii
Hemitriccus nidipendulus
Hemitriccus minimus
Hemitriccus inornatus
Hemitriccus margaritaceiventer
Hemitriccus rufigularis
Hemitriccus minor
Hemitriccus spodiops
Hemitriccus griseipectus
Hemitriccus zosterops
Hemitriccus diops
Hemitriccus flammulatus
Hemitriccus obsoletus
Hemitriccus granadensis
Hemitriccus josephinae
Hemitriccus iohannis
Hemitriccus striaticollis
Hemitriccus orbitatus
Hemitriccus furcatus
Hemitriccus cinnamomeipectus
Hemitriccus kaempferi
Hemitriccus mirandae
Myiotriccus ornatus
Zimmerius viridiflavus
Zimmerius chrysops
Zimmerius vilissimus
Zimmerius bolivianus
Zimmerius gracilipes
Zimmerius cinereicapilla
Zimmerius villarejoi
Culicivora caudacuta
Inezia caudata
Phylloscartes venezuelanus
Phylloscartes oustaleti
Phylloscartes flavovirens
Phylloscartes ventralis
Phylloscartes virescens
Phylloscartes flaviventris
Phylloscartes nigrifrons
Phylloscartes parkeri
Phylloscartes eximius
Phylloscartes ceciliae
Phylloscartes roquettei
Phylloscartes superciliaris
Phylloscartes sylviolus
Phylloscartes difficilis
Phylloscartes ophthalmicus
Phylloscartes gualaquizae
Phylloscartes poecilotis
Calyptura cristata
Phylloscartes paulistus
Phylloscartes chapmani
Phylloscartes beckeri
Phylloscartes kronei
Phylloscartes lanyoni
Phylloscartes orbitalis
i
x
xi

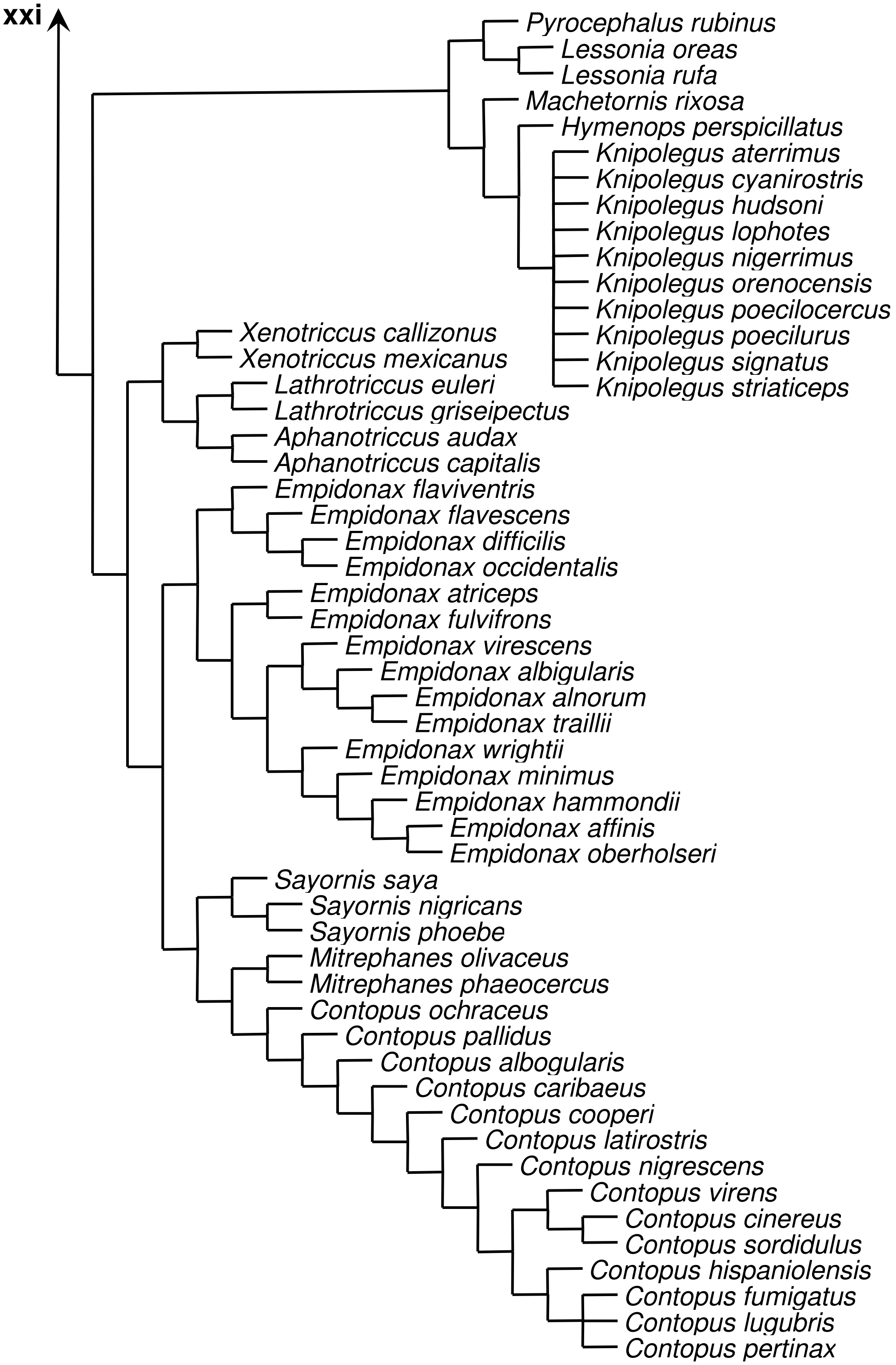

ix
x
xi
Sublegatus obscurior
Sublegatus arenarum
Sublegatus modestus
Inezia subflava
Inezia inornata
Inezia tenuirostris
Corythopis delalandi
Corythopis torquatus
Pseudotriccus ruficeps
Pseudotriccus pelzelni
Pseudotriccus simplex
Leptopogon amaurocephalus
Leptopogon superciliaris
Leptopogon rufipectus
Leptopogon taczanowskii
Mionectes macconnelli
Mionectes rufiventris
Mionectes oleaginous
Mionectes olivaceus
Mionectes striaticollis
Euscarthmus meloryphus
Euscarthmus rufomarginatus
Tachuris rubrigastra
Pseudelaenia leucospodia
Stigmatura budytoides
Stigmatura napensis
Polystictus pectoralis
Polystictus superciliaris
Pseudocolopteryx flaviventris
Pseudocolopteryx sclateri
Pseudocolopteryx acutipennis
Pseudocolopteryx dinelliana
Mecocerculus leucophrys
Anairetes agilis
Anairetes agraphia
Anairetes nigrocristatus
Anairetes reguloides
Anairetes fernandezianus
Anairetes parulus
Anairetes alpinus
Anairetes flavirostris
Suiriri islerorum
Suiriri suiriri
Mecocerculus stictopterus
Mecocerculus hellmayri
Mecocerculus poecilocercus
Camptostoma imberbe
Camptostoma obsoletum
Ornithion inerme
Ornithion brunneicapillus
Ornithion semiflavum
xii
xiii
xiv
xv


xii
xiii
xiv
xv
Nesotriccus ridgwayi
Capsiempis flaveola
Phaeomyias murina
Serpophaga cinerea
Serpophaga hypoleuca
Serpophaga munda
Serpophaga nigricans
Serpophaga subcristata
Mecocerculus calopterus
Mecocerculus minor
Phyllomyias griseocapilla
Phyllomyias plumbeiceps
Phyllomyias burmeisteri
Phyllomyias fasciatus
Phyllomyias griseiceps
Phyllomyias cinereiceps
Phyllomyias nigrocapillus
Phyllomyias sclateri
Phyllomyias uropygialis
Phyllomyias reiseri
Phyllomyias urichi
Phyllomyias virescens
Tyrannulus elatus
Myiopagis olallai
Myiopagis subplacens
Myiopagis cotta
Myiopagis viridicata
Myiopagis caniceps
Myiopagis flavivertex
Myiopagis gaimardii
Elaenia fallax
Elaenia mesoleuca
Elaenia pallatangae
Elaenia strepera
Elaenia martinica
Elaenia pelzelni
Elaenia ridleyana
Elaenia spectabilis
Elaenia flavogaster
Elaenia gigas
Elaenia chiriquensis
Elaenia dayi
Elaenia frantzii
Elaenia obscura
Elaenia cristata
Elaenia ruficeps
Elaenia albiceps
Elaenia parvirostris
xvi

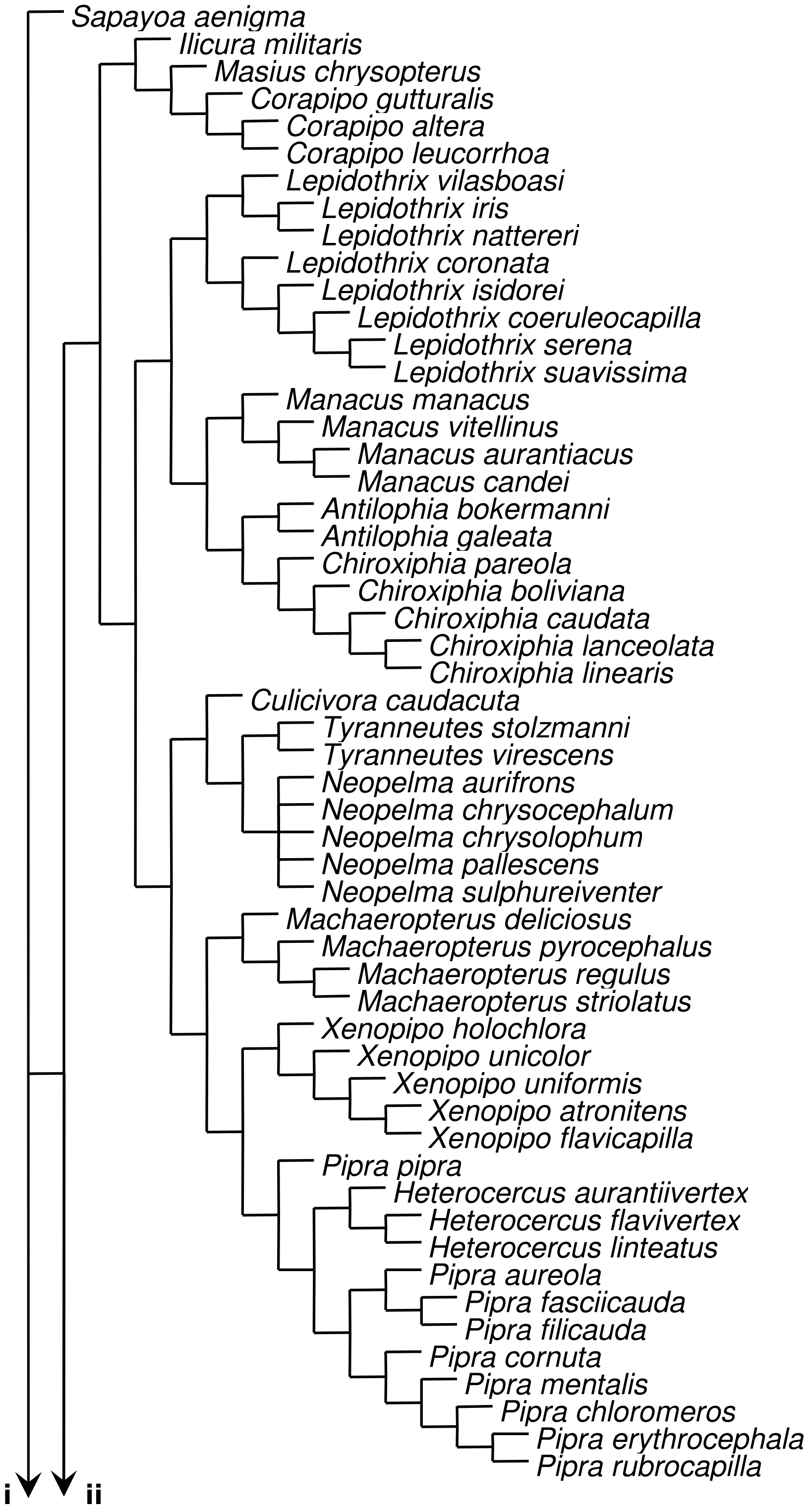

xvi
Legatus leucophaius
Myiozetetes luteiventris
Myiozetetes cayanensis
Myiozetetes granadensis
Myiozetetes similis
Phelpsia inornata
Pitangus lictor
Pitangus sulphuratus
Conopias trivirgatus
Conopias cinchoneti
Conopias albovittatus
Conopias parvus
Myiodynastes chrysocephalus
Myiodynastes hemichrysus
Myiodynastes bairdii
Myiodynastes luteiventris
Myiodynastes maculatus
Megarynchus pitangua
Tyrannopsis sulphurea
Empidonomus aurantioatrocristatus
Empidonomus varius
Tyrannus vociferans
Tyrannus forficatus
Tyrannus dominicensis
Tyrannus crassirostris
Tyrannus verticalis
Tyrannus tyrannus
Tyrannus albogularis
Tyrannus savana
Tyrannus niveigularis
Tyrannus couchii
Tyrannus caudifasciatus
Tyrannus cubensis
Tyrannus melancholicus
xvii
xviii
xix

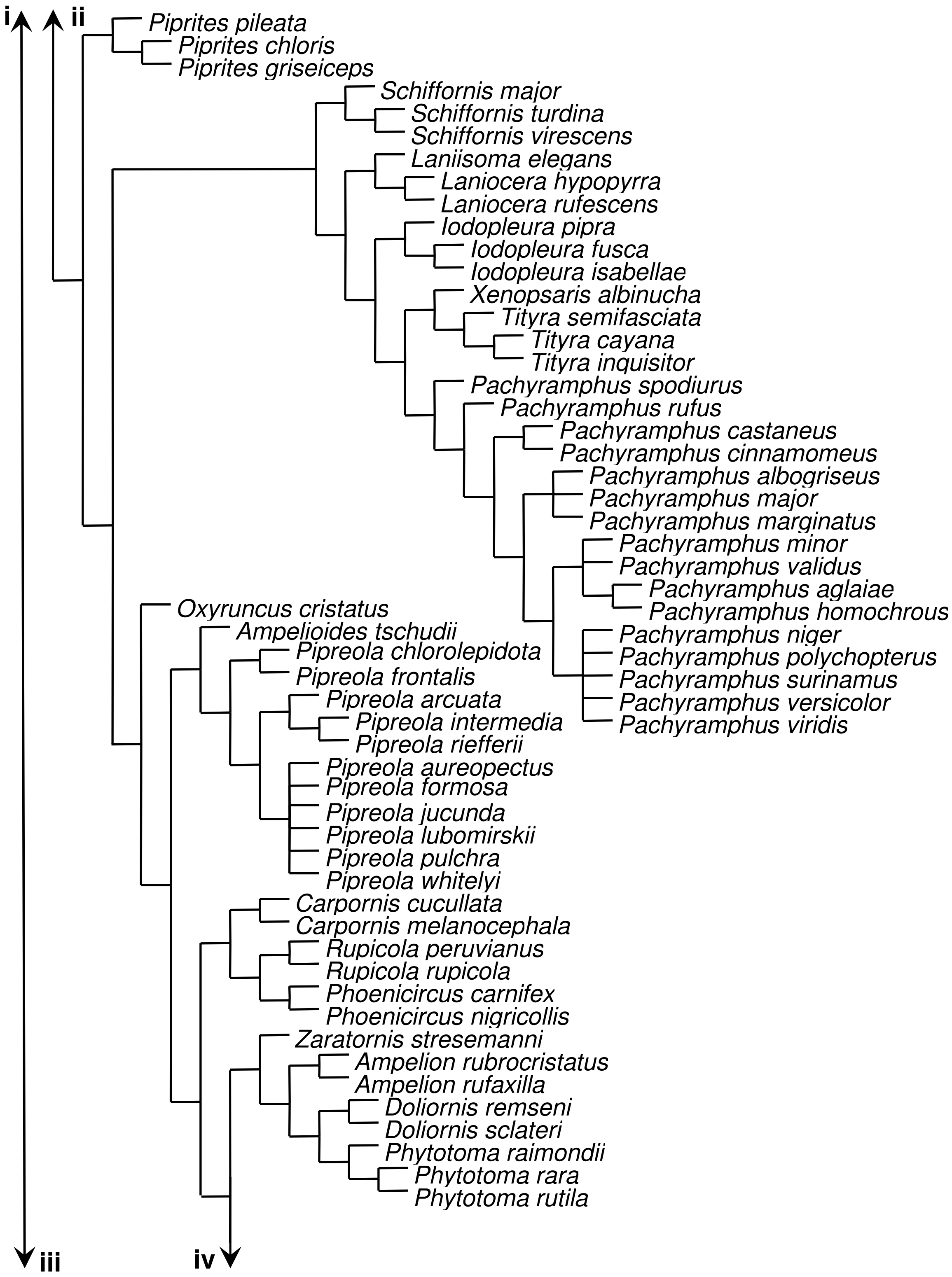

xvii
xvii
xix
Attila rufus
Attila bolivianus
Attila phoenicurus
Attila citriniventris
Attila torridus
Attila cinnamomeus
Attila spadiceus
Deltarhynchus flammulatus
Ramphotrigon fuscicauda
Ramphotrigon megacephalum
Ramphotrigon ruficauda
Rhytipterna immunda
Rhytipterna holerythra
Rhytipterna simplex
Casiornis fuscus
Casiornis rufus
Sirystes sibilator
Myiarchus nugatory
Myiarchus semirufus
Myiarchus magnirostris
Myiarchus nuttingi
Myiarchus apicalis
Myiarchus cephalotes
Myiarchus swainsoni
Myiarchus barbirostris
Myiarchus tuberculifer
Myiarchus phaeocephalus
Myiarchus panamensis
Myiarchus ferox
Myiarchus venezuelensis
Myiarchus validus
Myiarchus sagrae
Myiarchus stolidus
Myiarchus antillarum
Myiarchus oberi
Myiarchus crinitus
Myiarchus yucatanensis
Myiarchus cinerascens
Myiarchus tyrannulus
Onychorhynchus coronatus
Terenotriccus erythrurus
Myiobius atricaudus
Myiobius barbatus
Myiobius villosus
Neopipo cinnamomea
Hirundinea ferruginea
Pyrrhomyias cinnamomeus
Alectrurus risora
Alectrurus tricolor
Arundinicola leucocephala
Fluvicola nengeta
Fluvicola albiventer
Fluvicola pica
Colorhamphus parvirostris
Tumbezia salvini
Ochthoeca fumicolor
Ochthoeca leucophrys
Ochthoeca oenanthoides
Ochthoeca cinnamomeiventris
Ochthoeca rufipectoralis
Ochthoeca piurae
Ochthoeca jelskii
Ochthoeca frontalis
Ochthoeca diadema
Ochthoeca pulchella
xx

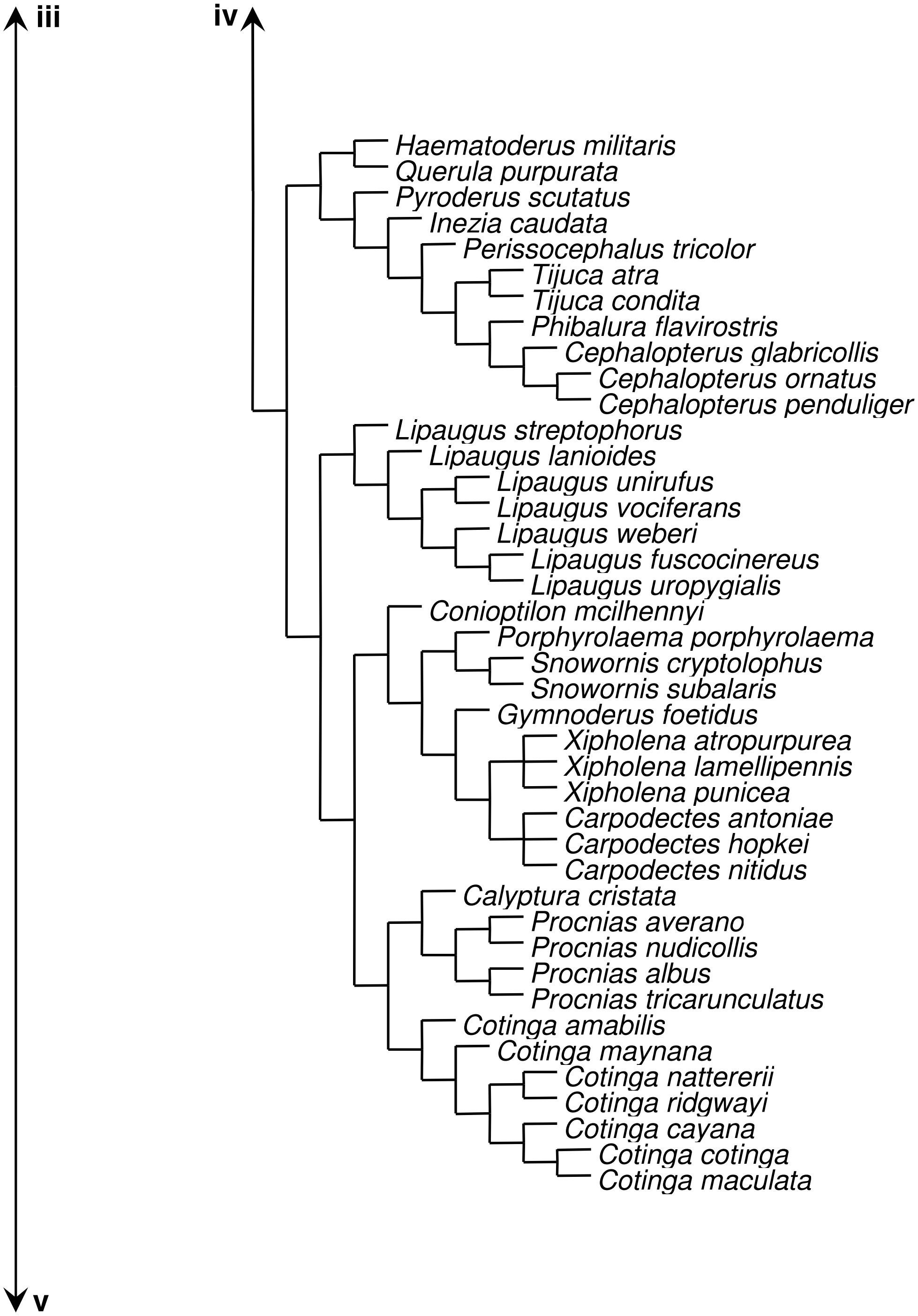

xx
Myiophobus lintoni
Myiophobus ochraceiventris
Myiophobus pulcher
Myiophobus flavicans
Myiophobus inornatus
Myiophobus cryptoxanthus
Myiophobus fasciatus
Colonia colonus
Myiophobus phoenicomitra
Myiophobus roraimae
Satrapa icterophrys
Ochthornis littoralis
Cnemotriccus fuscatus
Gubernetes yetapa
Muscipipra vetula
Muscigralla brevicauda
Muscisaxicola fluviatilis
Muscisaxicola maculirostris
Muscisaxicola capistratus
Muscisaxicola frontalis
Muscisaxicola alpinus
Muscisaxicola albilora
Muscisaxicola maclovianus
Muscisaxicola griseus
Muscisaxicola juninensis
Muscisaxicola albifrons
Muscisaxicola cinereus
Muscisaxicola flavinucha
Muscisaxicola rufivertex
Agriornis murinus
Agriornis micropterus
Agriornis montanus
Agriornis andicola
Agriornis lividus
Neoxolmis rufiventris
Cnemarchus erythropygius
Polioxolmis rufipennis
Myiotheretes pernix
Myiotheretes striaticollis
Myiotheretes fumigatus
Myiotheretes fuscorufus
Xolmis rubetra
Xolmis dominicanus
Xolmis pyrope
Xolmis irupero
Xolmis velatus
Xolmis salinarum
Xolmis cinereus
Xolmis coronatus
xxi

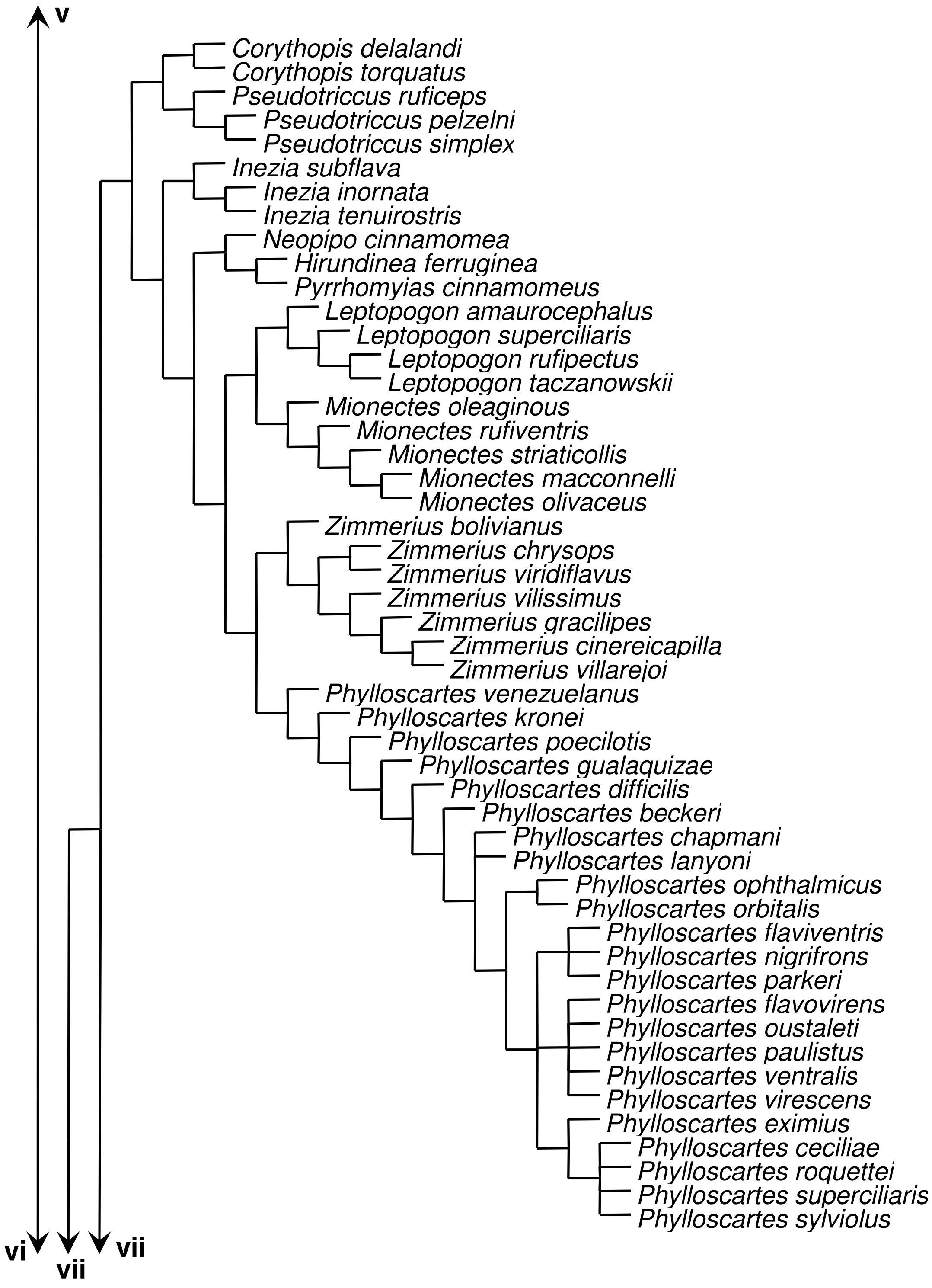

xxi
Pyrocephalus rubinus
Lessonia oreas
Lessonia rufa
Machetornis rixosa
Hymenops perspicillatus
Knipolegus aterrimus
Knipolegus cyanirostris
Knipolegus hudsoni
Knipolegus lophotes
Knipolegus nigerrimus
Knipolegus orenocensis
Knipolegus poecilocercus
Knipolegus poecilurus
Knipolegus signatus
Knipolegus striaticeps
Xenotriccus callizonus
Xenotriccus mexicanus
Lathrotriccus euleri
Lathrotriccus griseipectus
Aphanotriccus audax
Aphanotriccus capitalis
Empidonax flaviventris
Empidonax flavescens
Empidonax difficilis
Empidonax occidentalis
Empidonax atriceps
Empidonax fulvifrons
Empidonax virescens
Empidonax albigularis
Empidonax alnorum
Empidonax traillii
Empidonax wrightii
Empidonax minimus
Empidonax hammondii
Empidonax affinis
Empidonax oberholseri
Sayornis saya
Sayornis nigricans
Sayornis phoebe
Mitrephanes olivaceus
Mitrephanes phaeocercus
Contopus ochraceus
Contopus pallidus
Contopus albogularis
Contopus caribaeus
Contopus cooperi
Contopus latirostris
Contopus nigrescens
Contopus virens
Contopus cinereus
Contopus sordidulus
Contopus hispaniolensis
Contopus fumigatus
Contopus lugubris
Contopus pertinax

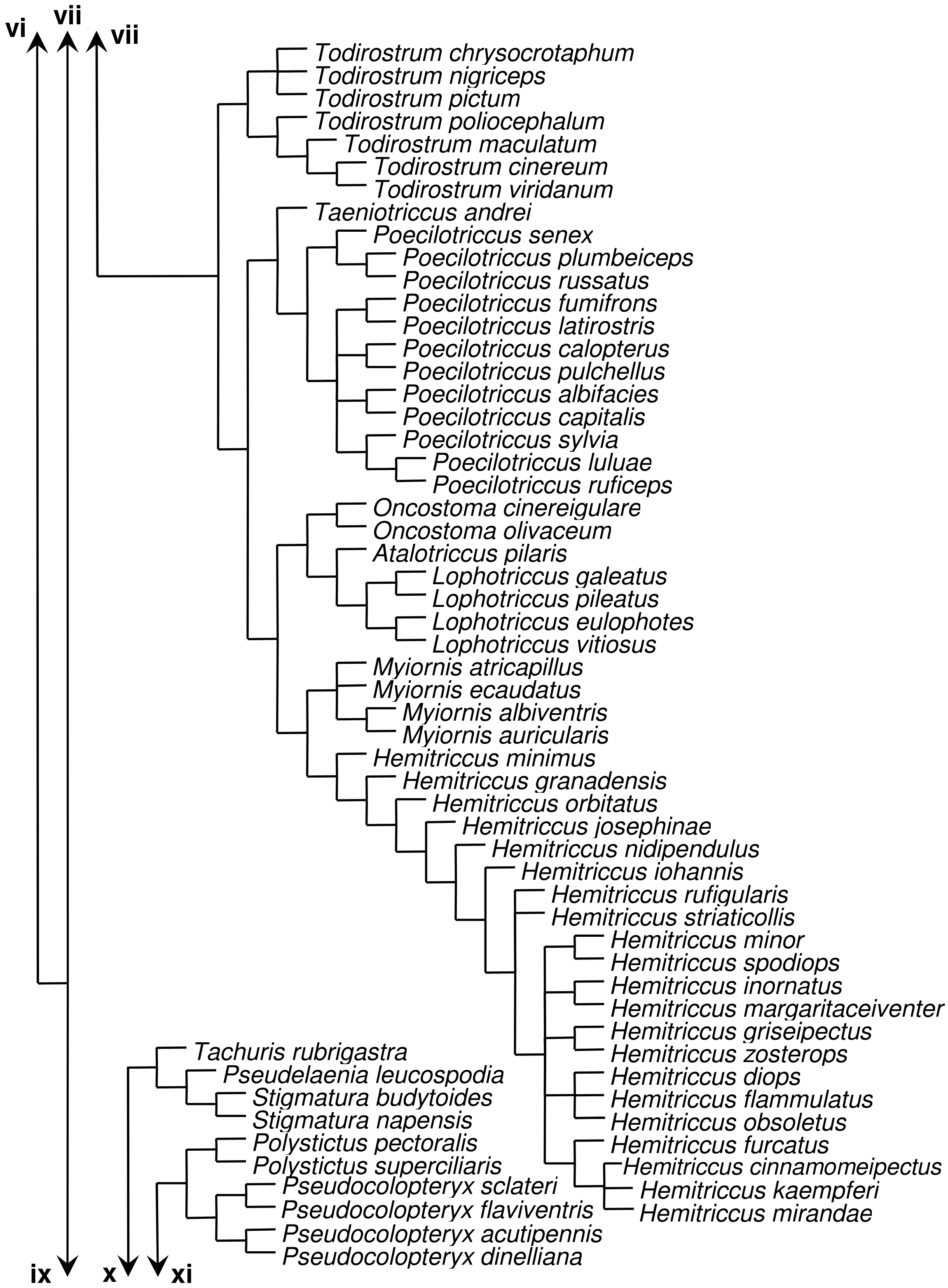
Online Appendix B Figure 2

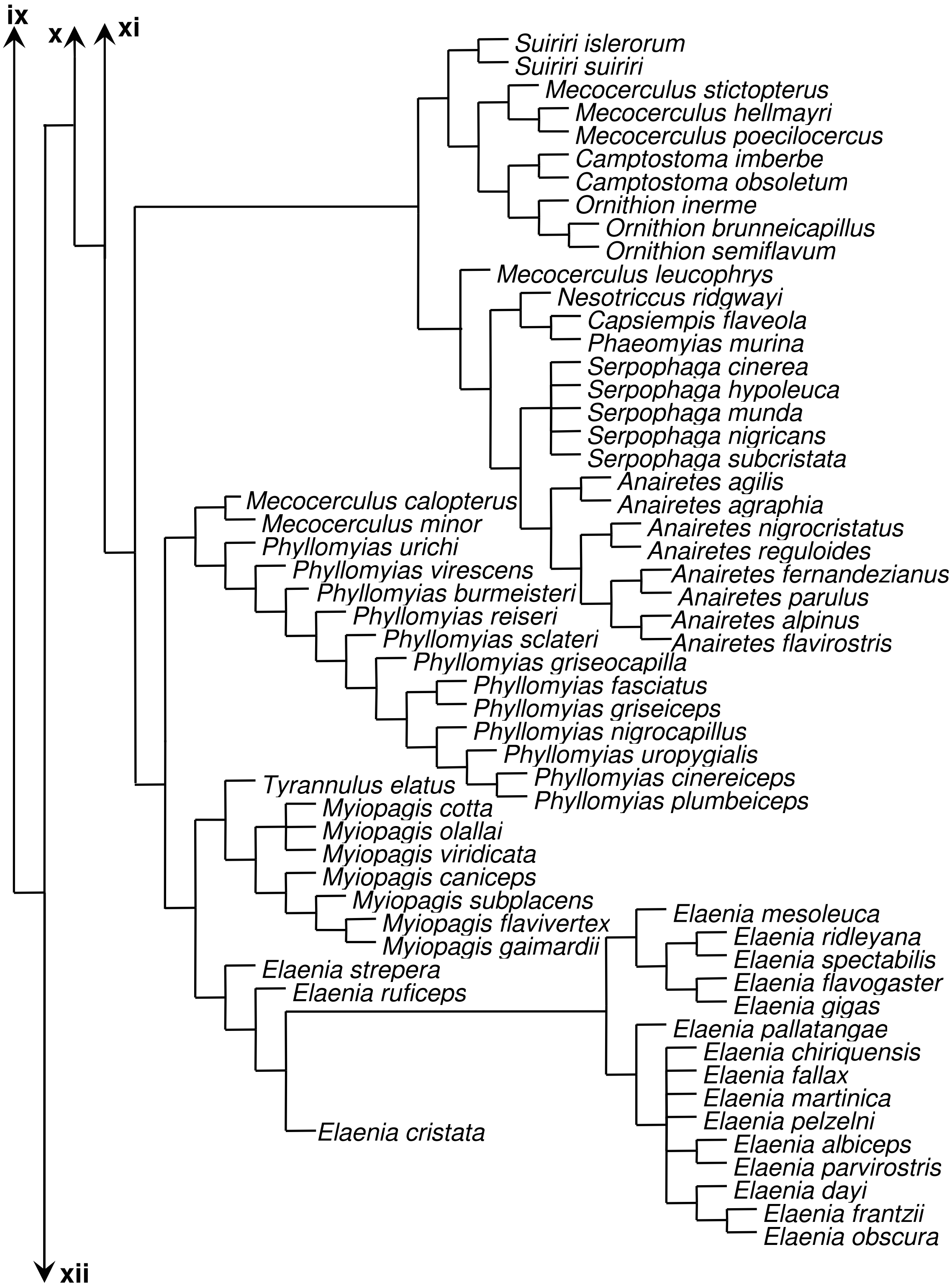


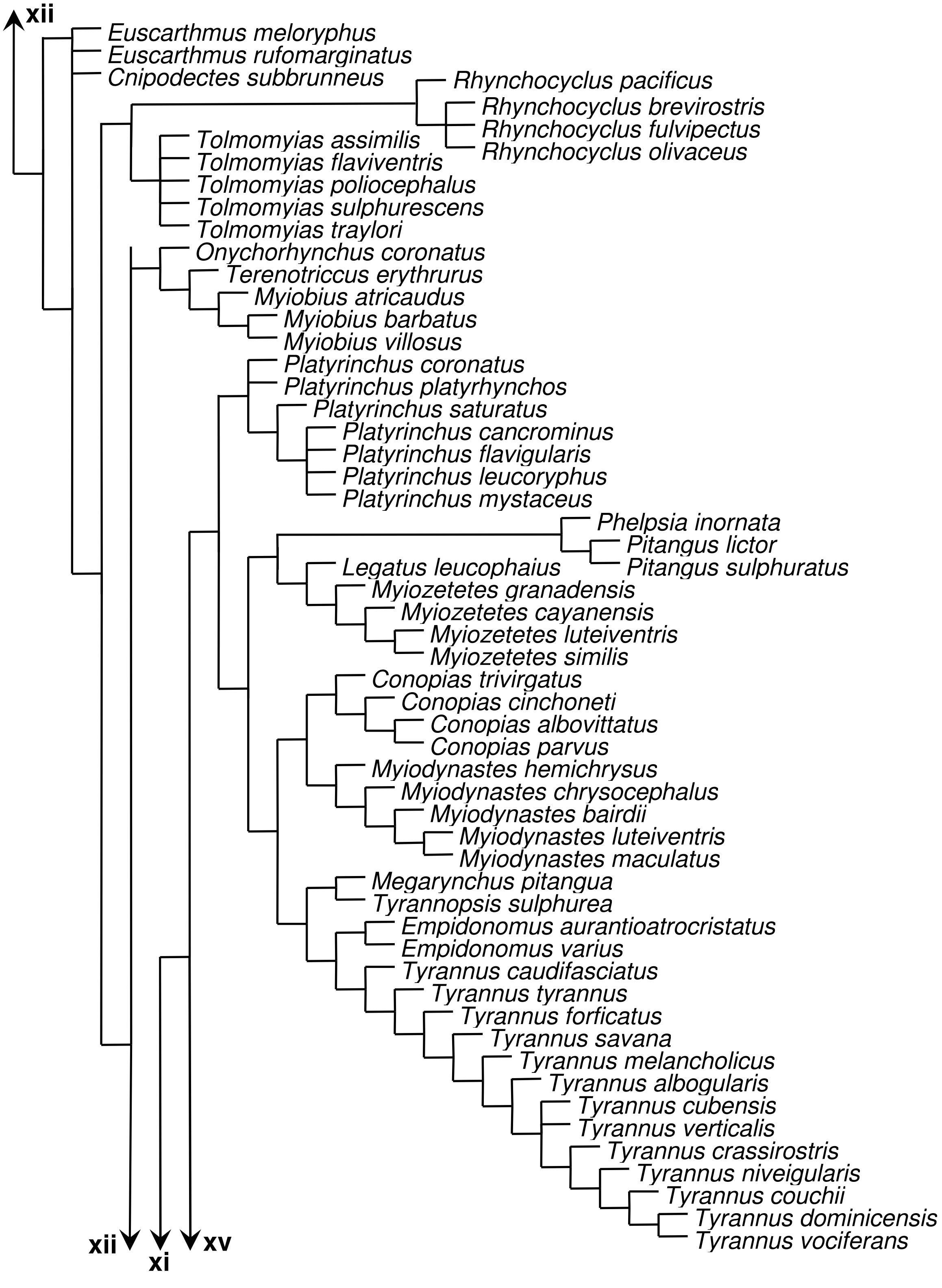

i
ii
Piprites pileata
Piprites chloris
Piprites griseiceps
Schiffornis major
Schiffornis turdina
Schiffornis virescens
Laniisoma elegans
Laniocera hypopyrra
Laniocera rufescens
Iodopleura pipra
Iodopleura fusca
Iodopleura isabellae
Xenopsaris albinucha
Tityra semifasciata
Tityra cayana
Tityra inquisitor
Pachyramphus spodiurus
Pachyramphus rufus
Pachyramphus castaneus
Pachyramphus cinnamomeus
Pachyramphus albogriseus
Pachyramphus major
Pachyramphus marginatus
Pachyramphus minor
Pachyramphus validus
Pachyramphus aglaiae
Pachyramphus homochrous
Pachyramphus niger
Pachyramphus polychopterus
Pachyramphus surinamus
Pachyramphus versicolor
Pachyramphus viridis
Oxyruncus cristatus
Ampelioides tschudii
Pipreola chlorolepidota
Pipreola frontalis
Pipreola arcuata
Pipreola intermedia
Pipreola riefferii
Pipreola aureopectus
Pipreola formosa
Pipreola jucunda
Pipreola lubomirskii
Pipreola pulchra
Pipreola whitelyi
Carpornis cucullata
Carpornis melanocephala
Rupicola peruvianus
Rupicola rupicola
Phoenicircus carnifex
Phoenicircus nigricollis
Zaratornis stresemanni
Ampelion rubrocristatus
Ampelion rufaxilla
Doliornis remseni
Doliornis sclateri
Phytotoma raimondii
Phytotoma rara
Phytotoma rutila
iii
iv

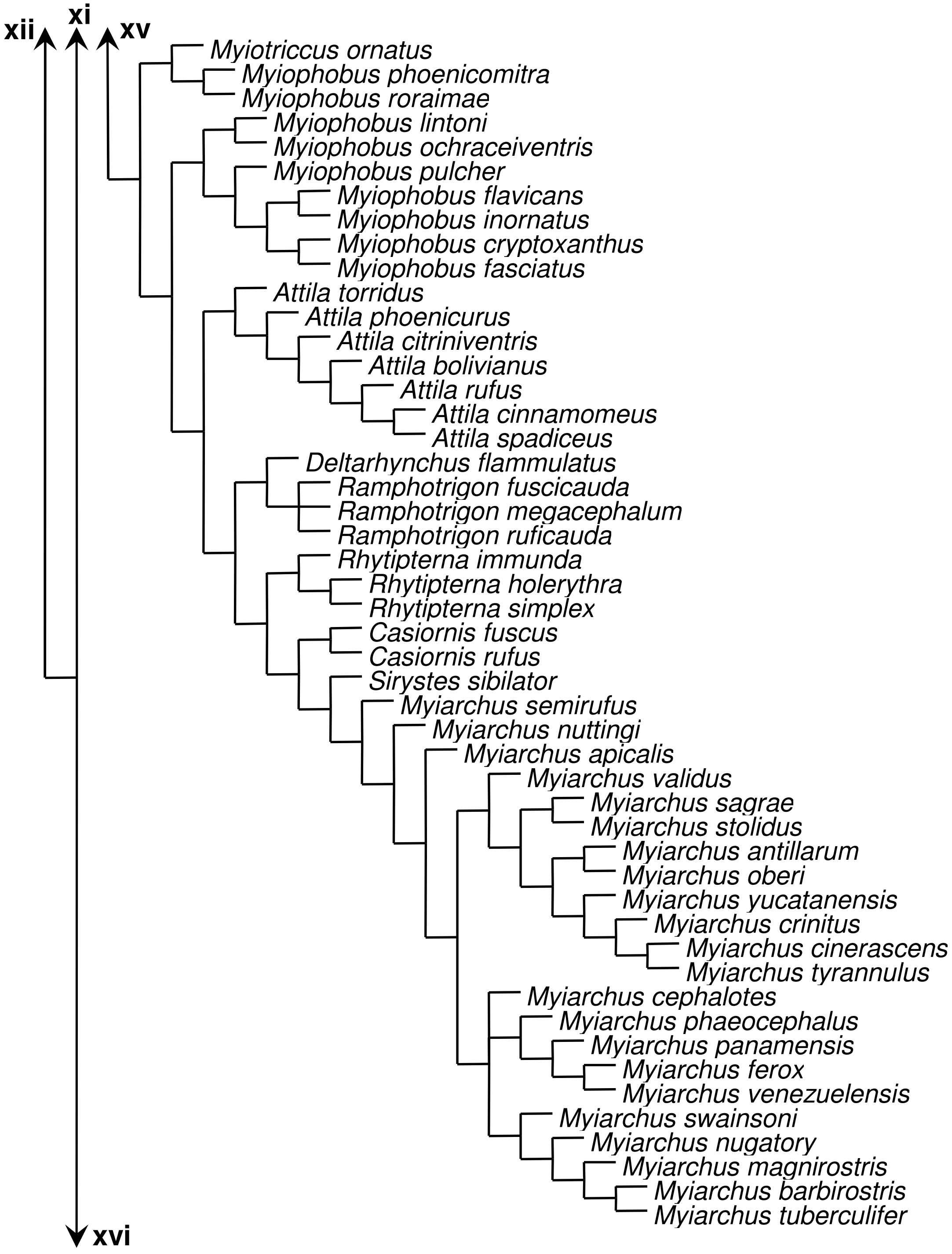

iii
iv
Haematoderus militaris
Querula purpurata
Pyroderus scutatus
Inezia caudata
Perissocephalus tricolor
Tijuca atra
Tijuca condita
Phibalura flavirostris
Cephalopterus glabricollis
Cephalopterus ornatus
Cephalopterus penduliger
Lipaugus streptophorus
Lipaugus lanioides
Lipaugus unirufus
Lipaugus vociferans
Lipaugus weberi
Lipaugus fuscocinereus
Lipaugus uropygialis
Conioptilon mcilhennyi
Porphyrolaema porphyrolaema
Snowornis cryptolophus
Snowornis subalaris
Gymnoderus foetidus
Xipholena atropurpurea
Xipholena lamellipennis
Xipholena punicea
Carpodectes antoniae
Carpodectes hopkei
Carpodectes nitidus
Calyptura cristata
Procnias averano
Procnias nudicollis
Procnias albus
Procnias tricarunculatus
Cotinga amabilis
Cotinga maynana
Cotinga nattererii
Cotinga ridgwayi
Cotinga cayana
Cotinga cotinga
Cotinga maculata
v


v
Corythopis delalandi
Corythopis torquatus
Pseudotriccus ruficeps
Pseudotriccus pelzelni
Pseudotriccus simplex
Inezia subflava
Inezia inornata
Inezia tenuirostris
Neopipo cinnamomea
Hirundinea ferruginea
Pyrrhomyias cinnamomeus
Leptopogon amaurocephalus
Leptopogon superciliaris
Leptopogon rufipectus
Leptopogon taczanowskii
Mionectes oleaginous
Mionectes rufiventris
Mionectes striaticollis
Mionectes macconnelli
Mionectes olivaceus
Zimmerius bolivianus
Zimmerius chrysops
Zimmerius viridiflavus
Zimmerius vilissimus
Zimmerius gracilipes
Zimmerius cinereicapilla
Zimmerius villarejoi
Phylloscartes venezuelanus
Phylloscartes kronei
Phylloscartes poecilotis
Phylloscartes gualaquizae
Phylloscartes difficilis
Phylloscartes beckeri
Phylloscartes chapmani
Phylloscartes lanyoni
Phylloscartes ophthalmicus
Phylloscartes orbitalis
Phylloscartes flaviventris
Phylloscartes nigrifrons
Phylloscartes parkeri
Phylloscartes flavovirens
Phylloscartes oustaleti
Phylloscartes paulistus
Phylloscartes ventralis
Phylloscartes virescens
Phylloscartes eximius
Phylloscartes ceciliae
Phylloscartes roquettei
Phylloscartes superciliaris
Phylloscartes sylviolus
vi
vii
vii

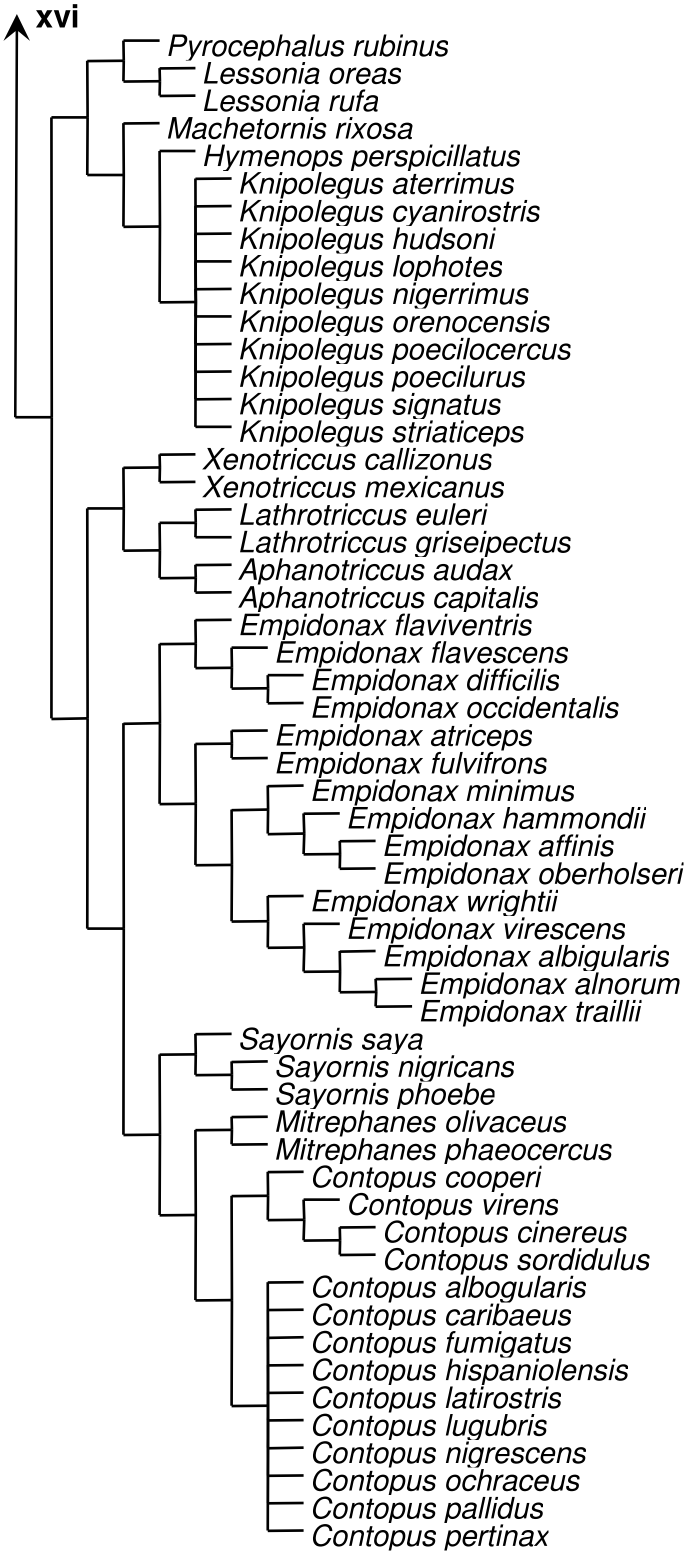

vi
vii
vii
Todirostrum chrysocrotaphum
Todirostrum nigriceps
Todirostrum pictum
Todirostrum poliocephalum
Todirostrum maculatum
Todirostrum cinereum
Todirostrum viridanum
Taeniotriccus andrei
Poecilotriccus senex
Poecilotriccus plumbeiceps
Poecilotriccus russatus
Poecilotriccus fumifrons
Poecilotriccus latirostris
Poecilotriccus calopterus
Poecilotriccus pulchellus
Poecilotriccus albifacies
Poecilotriccus capitalis
Poecilotriccus sylvia
Poecilotriccus luluae
Poecilotriccus ruficeps
Oncostoma cinereigulare
Oncostoma olivaceum
Atalotriccus pilaris
Lophotriccus galeatus
Lophotriccus pileatus
Lophotriccus eulophotes
Lophotriccus vitiosus
Myiornis atricapillus
Myiornis ecaudatus
Myiornis albiventris
Myiornis auricularis
Hemitriccus minimus
Hemitriccus granadensis
Hemitriccus orbitatus
Hemitriccus josephinae
Hemitriccus nidipendulus
Hemitriccus iohannis
Hemitriccus rufigularis
Hemitriccus striaticollis
Hemitriccus minor
Hemitriccus spodiops
Hemitriccus inornatus
Hemitriccus margaritaceiventer
Hemitriccus griseipectus
Hemitriccus zosterops
Hemitriccus diops
Hemitriccus flammulatus
Hemitriccus obsoletus
Hemitriccus furcatus
Hemitriccus cinnamomeipectus
Hemitriccus kaempferi
Hemitriccus mirandae
Tachuris rubrigastra
Pseudelaenia leucospodia
Stigmatura budytoides
Stigmatura napensis
Polystictus pectoralis
Polystictus superciliaris
Pseudocolopteryx sclateri
Pseudocolopteryx flaviventris
Pseudocolopteryx acutipennis
Pseudocolopteryx dinelliana
ix
x
xi


ix
x
xi
Suiriri islerorum
Suiriri suiriri
Mecocerculus stictopterus
Mecocerculus hellmayri
Mecocerculus poecilocercus
Camptostoma imberbe
Camptostoma obsoletum
Ornithion inerme
Ornithion brunneicapillus
Ornithion semiflavum
Mecocerculus leucophrys
Nesotriccus ridgwayi
Capsiempis flaveola
Phaeomyias murina
Serpophaga cinerea
Serpophaga hypoleuca
Serpophaga munda
Serpophaga nigricans
Serpophaga subcristata
Anairetes agilis
Anairetes agraphia
Anairetes nigrocristatus
Anairetes reguloides
Anairetes fernandezianus
Anairetes parulus
Anairetes alpinus
Anairetes flavirostris
Mecocerculus calopterus
Mecocerculus minor
Phyllomyias urichi
Phyllomyias virescens
Phyllomyias burmeisteri
Phyllomyias reiseri
Phyllomyias sclateri
Phyllomyias griseocapilla
Phyllomyias fasciatus
Phyllomyias griseiceps
Phyllomyias nigrocapillus
Phyllomyias uropygialis
Phyllomyias cinereiceps
Phyllomyias plumbeiceps
Tyrannulus elatus
Myiopagis cotta
Myiopagis olallai
Myiopagis viridicata
Myiopagis caniceps
Myiopagis subplacens
Myiopagis flavivertex
Myiopagis gaimardii
Elaenia strepera
Elaenia ruficeps
Elaenia cristata
Elaenia mesoleuca
Elaenia ridleyana
Elaenia spectabilis
Elaenia flavogaster
Elaenia gigas
Elaenia pallatangae
Elaenia chiriquensis
Elaenia fallax
Elaenia martinica
Elaenia pelzelni
Elaenia albiceps
Elaenia parvirostris
Elaenia dayi
Elaenia frantzii
Elaenia obscura
xii


xii
Euscarthmus meloryphus
Euscarthmus rufomarginatus
Cnipodectes subbrunneus
Rhynchocyclus pacificus
Rhynchocyclus brevirostris
Rhynchocyclus fulvipectus
Rhynchocyclus olivaceus
Tolmomyias assimilis
Tolmomyias flaviventris
Tolmomyias poliocephalus
Tolmomyias sulphurescens
Tolmomyias traylori
Onychorhynchus coronatus
Terenotriccus erythrurus
Myiobius atricaudus
Myiobius barbatus
Myiobius villosus
Platyrinchus coronatus
Platyrinchus platyrhynchos
Platyrinchus saturatus
Platyrinchus cancrominus
Platyrinchus flavigularis
Platyrinchus leucoryphus
Platyrinchus mystaceus
Phelpsia inornata
Pitangus lictor
Pitangus sulphuratus
Legatus leucophaius
Myiozetetes granadensis
Myiozetetes cayanensis
Myiozetetes luteiventris
Myiozetetes similis
Conopias trivirgatus
Conopias cinchoneti
Conopias albovittatus
Conopias parvus
Myiodynastes hemichrysus
Myiodynastes chrysocephalus
Myiodynastes bairdii
Myiodynastes luteiventris
Myiodynastes maculatus
Megarynchus pitangua
Tyrannopsis sulphurea
Empidonomus aurantioatrocristatus
Empidonomus varius
Tyrannus caudifasciatus
Tyrannus tyrannus
Tyrannus forficatus
Tyrannus savana
Tyrannus melancholicus
Tyrannus albogularis
Tyrannus cubensis
Tyrannus verticalis
Tyrannus crassirostris
Tyrannus niveigularis
Tyrannus couchii
Tyrannus dominicensis
Tyrannus vociferans
xii
xi
xv


xii
xi
xv
Myiotriccus ornatus
Myiophobus phoenicomitra
Myiophobus roraimae
Myiophobus lintoni
Myiophobus ochraceiventris
Myiophobus pulcher
Myiophobus flavicans
Myiophobus inornatus
Myiophobus cryptoxanthus
Myiophobus fasciatus
Attila torridus
Attila phoenicurus
Attila citriniventris
Attila bolivianus
Attila rufus
Attila cinnamomeus
Attila spadiceus
Deltarhynchus flammulatus
Ramphotrigon fuscicauda
Ramphotrigon megacephalum
Ramphotrigon ruficauda
Rhytipterna immunda
Rhytipterna holerythra
Rhytipterna simplex
Casiornis fuscus
Casiornis rufus
Sirystes sibilator
Myiarchus semirufus
Myiarchus nuttingi
Myiarchus apicalis
Myiarchus validus
Myiarchus sagrae
Myiarchus stolidus
Myiarchus antillarum
Myiarchus oberi
Myiarchus yucatanensis
Myiarchus crinitus
Myiarchus cinerascens
Myiarchus tyrannulus
Myiarchus cephalotes
Myiarchus phaeocephalus
Myiarchus panamensis
Myiarchus ferox
Myiarchus venezuelensis
Myiarchus swainsoni
Myiarchus nugatory
Myiarchus magnirostris
Myiarchus barbirostris
Myiarchus tuberculifer
xvi


xv
Alectrurus risora
Alectrurus tricolor
Arundinicola leucocephala
Fluvicola nengeta
Fluvicola albiventer
Fluvicola pica
Colorhamphus parvirostris
Tumbezia salvini
Ochthoeca fumicolor
Ochthoeca leucophrys
Ochthoeca oenanthoides
Ochthoeca cinnamomeiventris
Ochthoeca rufipectoralis
Ochthoeca piurae
Ochthoeca jelskii
Ochthoeca frontalis
Ochthoeca diadema
Ochthoeca pulchella
Satrapa icterophrys
Colonia colonus
Sublegatus obscurior
Sublegatus arenarum
Sublegatus modestus
Ochthornis littoralis
Muscigralla brevicauda
Muscisaxicola fluviatilis
Muscisaxicola maculirostris
Muscisaxicola capistratus
Muscisaxicola frontalis
Muscisaxicola alpinus
Muscisaxicola albilora
Muscisaxicola maclovianus
Muscisaxicola griseus
Muscisaxicola juninensis
Muscisaxicola albifrons
Muscisaxicola cinereus
Muscisaxicola flavinucha
Muscisaxicola rufivertex
Cnemotriccus fuscatus
Gubernetes yetapa
Muscipipra vetula
Neoxolmis rufiventris
Xolmis rubetra
Xolmis dominicanus
Xolmis pyrope
Xolmis salinarum
Xolmis velatus
Xolmis irupero
Xolmis cinereus
Xolmis coronatus
Agriornis lividus
Agriornis murinus
Agriornis micropterus
Agriornis andicola
Agriornis montanus
Cnemarchus erythropygius
Polioxolmis rufipennis
Myiotheretes pernix
Myiotheretes striaticollis
Myiotheretes fumigatus
Myiotheretes fuscorufus
xvi


xvi
Pyrocephalus rubinus
Lessonia oreas
Lessonia rufa
Machetornis rixosa
Hymenops perspicillatus
Knipolegus aterrimus
Knipolegus cyanirostris
Knipolegus hudsoni
Knipolegus lophotes
Knipolegus nigerrimus
Knipolegus orenocensis
Knipolegus poecilocercus
Knipolegus poecilurus
Knipolegus signatus
Knipolegus striaticeps
Xenotriccus callizonus
Xenotriccus mexicanus
Lathrotriccus euleri
Lathrotriccus griseipectus
Aphanotriccus audax
Aphanotriccus capitalis
Empidonax flaviventris
Empidonax flavescens
Empidonax difficilis
Empidonax occidentalis
Empidonax atriceps
Empidonax fulvifrons
Empidonax minimus
Empidonax hammondii
Empidonax affinis
Empidonax oberholseri
Empidonax wrightii
Empidonax virescens
Empidonax albigularis
Empidonax alnorum
Empidonax traillii
Sayornis saya
Sayornis nigricans
Sayornis phoebe
Mitrephanes olivaceus
Mitrephanes phaeocercus
Contopus cooperi
Contopus virens
Contopus cinereus
Contopus sordidulus
Contopus albogularis
Contopus caribaeus
Contopus fumigatus
Contopus hispaniolensis
Contopus latirostris
Contopus lugubris
Contopus nigrescens
Contopus ochraceus
Contopus pallidus
Contopus pertinax

APPENDIX B

WHY DO SOME, BUT NOT ALL, TROPICAL BIRDS MIGRATE ALTITUDINALLY?

Why do some, but not all, tropical birds migrate altitudinally?

W. Alice Boyle, Dept. of Ecology and Evolutionary Biology, University of Arizona, alboyle@email.arizona.edu

Courtney J. Conway, USGS Arizona Cooperative Fish and Wildlife Research Unit, School of Natural Resources, University of Arizona, cconway@ag.arizona.edu

Judith L. Bronstein, Dept. of Ecology and Evolutionary Biology, University of Arizona, judieb@email.arizona.edu

Key words: Costa Rica, elevational gradients, diet, frugivory, fruit preference, interspecific competition, nutrient, Neotropical forests, resource variation, specialization

Abstract

Many tropical birds migrate relatively short distances over altitudinal gradients. Because most tropical altitudinal migrant species are primarily frugivorous, hypotheses explaining why tropical birds migrate altitudinally have focused on how spatial and temporal patterns of fruit availability might favor migratory behavior. However, previous tests of food-related hypotheses have used inappropriate metrics of food availability and the hypotheses tested failed to explain either (1) species-specific patterns of migration, or (2) why many frugivorous birds living in sympatry with altitudinal migrants do not migrate. We formulated and tested two mechanistic hypotheses to explain why some but not all tropical frugivores migrate. The competitive exclusion hypothesis casts migrants as competitively inferior foragers for fruit compared to residents, whereas the dietary specialization hypothesis casts migrants and residents as differing in fruit preferences. We tested predictions of these hypotheses by comparing diet breadth, fruit preference, and the relationship between diet and preference among related pairs of migrant and resident species. Based on fecal samples and experimental choice trials, migrants and residents differed in all aspects of diet and preference that we evaluated. Migrant species consumed a greater diversity of fruits and fewer arthropods than their resident counterparts. Migrant species had stronger fruit preferences than their resident counterparts, and despite sharing preferences for fruits of the same plant species (within migrant-resident species pairs), diets of migrants more closely reflected those preferences than did the diets of their resident counterparts. Our results suggest that migrants may be competitively superior fruit foragers to

residents, allowing us to eliminate the competitive exclusion hypothesis and to refine the dietary specialization hypothesis. Additionally, our results are consistent with the previously-noted broad taxonomic correlation between diet (frugivory) and short-distance migration. We suggest that future studies should attempt to distinguish whether a frugivorous diet is a consequence or a cause of migratory behavior, and to directly test underlying assumptions regarding resource availability on which the dietary specialization hypothesis relies to explain variation in migratory behavior in birds.

Introduction

Migration is among the most complex and impressive of animal behaviors (Dingle 1996, Berthold 2001). We know a great deal about migration patterns, and the proximate causes and physiological adaptations for migration, but the ultimate causes of migration are still poorly understood. This is true even in birds, in which migration has been a topic of extensive study for over a century (Alerstam 1990). Numerous hypotheses have been proposed to explain how and why bird migration evolved (Fretwell 1980, Greenberg 1980, Levey and Stiles 1992, Alerstam et al. 2003, Rappole et al. 2003), but few of these hypotheses have been tested empirically (but see Appendix A). Furthermore, ecologically similar and closely related sympatric species often differ in migratory tendency, and few hypotheses can account for this difference. Consequently, the question of why birds migrate is more appropriately phrased, “why do some, but not all, bird species migrate?” (Fretwell 1980). Answering such a question requires formulating and testing mechanistic hypotheses that predict species-level correlates of migratory behavior. An impediment to answering this question lies in the difficulty of studying organisms whose breeding and non-breeding ranges span regions differing dramatically in climate, food, vegetation structure, competitors, and predators. Short-distance altitudinal migrations of tropical birds provide a relatively tractable system in which to examine the function of migratory behavior. Altitudinal migrations occur in mountains around the globe (Ramos-Olmos 1983, Laymon 1989, Loiselle and Blake 1991, Cardoso da Silva 1993, Johnson and Maclean 1994, Burgess and Mlingwa 2000, Solórzano et al. 2000, Galetti 2001, Symes et al. 2001, Hobson et al. 2003) and in many areas constitute a major portion of the montane avifauna.

Spatial and temporal variation in climate (Cox 1985) or predation risk (Fretwell 1980, Greenberg 1980) have both been proposed to explain why birds migrate. However, variation in the availability of food dominate theories explaining the evolution of bird migration (e.g., Cox 1968, Alerstam and Enckell 1979, Fretwell 1980, Levey and Stiles 1992, Holmgren and Lundberg 1993, Kaitala et al. 1993, Bell 2000), including explanations for altitudinal bird migration (Stiles 1980, 1983, Wheelwright 1983, Rosselli 1989, Loiselle and Blake 1991, Solórzano et al. 2000, Chaves-Campos et al. 2003, Chaves-Campos 2004). Empirical studies focusing on altitudinal migrants have all tested a general hypothesis that birds migrate to elevations of highest food abundance to breed, and migrate back when food is more abundant at the non-breeding elevations (Fig. 1A). This hypothesis of “reciprocal food abundance” has received general acceptance (Gill 1994, Alcock 2005) due in part to the commonly observed pattern that most altitudinal migrants belong to predominantly frugivorous or nectarivorous families, and very few are highly insectivorous or carnivorous (Stiles

1983), suggesting that variation in the availability of fruit and nectar is the most important factor leading the evolution of altitudinal migration. Additionally, an explanation for altitudinal migration based on food limitation may have received more attention than alternative explanations because (1) climatic seasonality in many tropical forests is less pronounced than in temperate forests and often varies little over the short distances involved in altitudinal migration (Walsh 1996), and (2) limited data on patterns of nest predation risk across altitudinal gradients has caused most previous authors to ignore predation-based hypotheses (but see Skutch 1985; Appendix C).

Some evidence supports the reciprocal food abundance hypothesis (Wheelwright 1983, Loiselle and Blake 1991, Solórzano et al. 2000) but the evidence is inconclusive. For example, Rosselli (1994), Chaves-Campos et al. (2003), and Chaves-Campos (2004) all concluded that the timing and movement patterns of individual species make little sense if birds simply migrate to track areas with highest seasonal fruit abundance. Most importantly, in all the tropical forests where species-level studies have been conducted, many ecologically-similar and closely-related species do not migrate at all. No previous study has identified the traits possessed by migrants that might confer reproductive or survival benefits to migrating sufficient to outweigh the presumed energetic and survival costs associated with migration. Additionally, previous studies have not used appropriate metrics of fruit abundance to adequately test the reciprocal abundance hypothesis. If forests of different elevations really do differ in the quantity of food resources they produce in seasonally-predictable ways, and birds migrate to exploit those resources, then more and more birds should become migratory until the amount of food available per individual is similar across elevational gradients during seasons when food is most limiting (Fretwell and Lucas 1969; Fig. 1B). Consequently, studies that have tested the reciprocal food abundance hypothesis by correlating migration patterns with the temporal and spatial patterns of surplus standing crops of fruits (Loiselle and Blake 1991, Rosselli 1994, Solórzano et al. 2000, Chaves-Campos et al. 2003) have tested a prediction inconsistent with foraging theory and inconsistent with the reciprocal food abundance hypothesis itself. Instead we need to estimate fruit production rates (not standing crop) across elevational gradients to adequately test the reciprocal food abundance hypothesis.

We propose two hypotheses to explain how spatial and temporal variation in food resources could favor the evolution of migration in some but not all frugivorous birds. The two hypotheses we propose here encompass variations that differ in the details of how food availability, traits of migrants and residents, and migratory behavior might be related. The goals of this study are to shift attention from the level of process to the level of mechanism in our attempt to explain why bird migrate, and to test some of the assumptions and predictions of these hypotheses.

The first hypothesis relies on *competitive exclusion* driving migratory behavior and is similar to mechanisms proposed to explain the evolution of long-distance migration (Cox 1985) and partial bird migration (Cristol et al. 1999). This hypothesis proposes that (a) residents are superior competitors for fruit, and (b) residents and migrants are subject to different trade-offs in the costs and benefits of migrating. If the surplus fruit available to migrant species may be insufficient to meet their needs, they migrate up or downhill to elevations with reduced competition for fruit (Fig. 1C). Residents could reduce fruit availability to migrants either directly through exploitative competition or indirectly through interference competition. Differences between species in the trade-offs associated with migrating could result from differences in the benefits associated with year-round flock maintenance, site occupancy, familiarity with local predator communities and profitable foraging sites, or some combination of these factors. Unlike the reciprocal fruit abundance hypothesis, migrants are not necessarily predicted to visit elevations during the season when overall production rates of fruits peak. The measure of food abundance relevant to this hypothesis is the amount of surplus fruit produced that is not consumed by the resident species at a given elevation relative to other elevations during the same season (Fig. 1C, unhatched portion of bars).

The second hypothesis relies on differences between migrant and resident species in foraging strategy and *dietary specialization*. Migrants are hypothesized to either (1) have narrower diet breadths (less food available to them than residents), (2) be less likely to switch fruit types due to stronger fruit preferences, or (3) have equal preference strengths, but prefer fruits that are only available seasonally. In contrast, residents are hypothesized to either (1) have broader diets, (2) be more likely to switch fruit types due to weaker fruit preferences, or (3) have equal preference strengths, but prefer fruits of plant species that produce year-round. In addition to one of the three requirements above, the dietary specialization hypothesis requires that the production of the fruits preferred by migrant species varies reciprocally between seasons and elevations (Fig. 1D). Like the competitive exclusion hypotheses (and again, unlike the reciprocal fruit abundance hypothesis), migrants are not necessarily predicted to visit elevations during the season when overall production rates of fruits peak at that elevation (i.e., total height of bars, Fig. 1 A–D), nor would they be expected to visit sites during the season when production rates of their preferred fruits peak. This hypothesis predicts only that migrants will visit elevations where the production of preferred fruits is greatest relative to other sites during the same season (Fig. 1D, unhatched portion of bars).

Distinguishing between these two hypotheses directly via estimates of fruit availability would require prior knowledge of the relevant fruit resources to measure (i.e., detailed knowledge of the fruits consumed by migrant species). Additionally, testing the dietary specialization hypothesis would require accurate measurements of production rates (not standing crops) of fruits consumed by migrants over the elevations they migrate. Testing the competitive exclusion hypothesis would require excluding migrants (but not residents) from fruiting plants to assess the marginal surplus of fruit produced that is not consumed by residents. Such studies would be impractical at the community level for altitudinal migrant birds, and at best, could only be attempted for one or a few altitudinal migrant species, thereby greatly reducing the scope of inference. Thus, we used a series of comparative tests in a community of tropical frugivorous birds to distinguish between these two mechanistic hypotheses.

The two hypotheses make different predictions regarding how migrants and residents differ in their diet breadths, their dietary preferences, and the degree to which diets reflect preferences (table 1). We compared diet breadth in two ways. First we compared the diversity of fruits consumed by migrant and resident species—defined here as both the number of plant species from which individuals of each bird species consumes fruit (i.e., the estimated species richness of fruits), and the relative importance of fruits from different plant species in their diets (i.e., the evenness of representation of fruits in diets; table 1, #1). Under the competitive exclusion hypothesis, residents out-compete migrants for the best fruits available. Thus, we predicted that residents would consume high-quality fruits in greater proportions than migrants who must supplement their diets with a broader range of lower-quality fruits. Such foraging patterns would result in a wider diversity of fruits in diets of migrants than residents. Dietary specialization could result in migrants (1) consuming a lower diversity of fruits (if migrants specialize on fruits of a narrower range of plant species), or (2) not differing from residents in the diversity of fruits they consume (if migrants specialize to the same degree as residents, but prefer fruits of a different set of plant species). If birds migrate because they specialize on fruits of plant species with seasonal fruiting phenologies, or because their diets are more restricted, then at the beginning of the migratory period, the diets of residents should be broader than the diets of migrants who leave as their preferred resources are consumed.

We also quantified diet breadth in terms of the relative importance of fruit vs. arthropod prey in the diets of primarily frugivorous species (table 1, #2). Under the competitive exclusion hypothesis, residents should consume a greater proportion of fruit relative to arthropods because they are capable of obtaining the full range of fruits required to fill the majority of their nutritional needs. If migrants are prevented from foraging on the best fruits, they may have to forage for more arthropod prey. Although few fruits contain as much protein as arthropods (Wheelwright et al. 1984), arthropods are likely to cost more in terms of foraging time for forest-understory frugivores because (1) arthropod abundance is low in forest understory (Elton 1973, Janzen 1973), (2) competition with specialized understory insectivores may be high, and (3) frugivores possess few morphological and behavioral adaptations for efficiently detecting and capturing arthropod prey. Under the dietary specialization hypothesis, migrants would be expected to be either more frugivorous (and less insectivorous) than residents, or not to differ in their degree of frugivory, again depending on whether migrants and residents differ in their degree of specialization or specialize to the same degree on different fruits. If residents are more likely to alter their diet, or habitually sample from a broader array of food types, broader diet breadth could be expressed in terms of an increase in the proportion of arthropods relative to fruits. If residents specialize to the same degree as migrants, only differing by specializing on plants producing fruit year-round, then the relative proportion of fruits and arthropods in diets would not be expected to be related to migratory strategy.

The two hypotheses also make different sets of predictions regarding the relationship between migratory tendency and fruit preferences. The competitive exclusion hypothesis assumes that both migrants and residents share preferences for the same fruits (table 1, #3), and that migrants and residents do not differ in the strength of their fruit preferences (only in their abilities to obtain those preferred fruits; table 1, #4). In contrast, the dietary specialization hypothesis relies upon migrants and residents either preferring different fruits, or migrants having stronger fruit preferences than residents if they share preferences.

Finally, the ways that diet and preference are related to each other are predicted to differ as a consequence of migratory strategy (table 1, #5). The competitive exclusion hypothesis makes the prediction that resident species' realized niche (i.e., diet in the wild) will more closely resemble its fundamental niche (i.e., dietary preferences) than in migrant species due to their superior competitive abilities. However, if dietary specialization explains differences in migratory strategy, then the diets of migrants should more closely reflect their preferences than the diets of residents because they will simply migrate when their preferred resources become unavailable.

We tested the competitive exclusion and dietary specialization hypotheses by examining whether the diets and preferences of migrant and resident species differed in all five respects in a community of tropical birds in Costa Rica. We paired altitudinal migrant species with their most-closely-related, resident, sympatric counterpart. By pairing closely-related species, we were able to controlled for the confounding effects of shared evolutionary history (Harvey and Pagel 1991). Consistent results across several species pairs implies that similar selective pressures have been important repeatedly in the evolution of migration, and provide a conservative test of correlated trait evolution when the phylogenetic relationships among all taxa are not known (Ackerly 2000).

Methods

Study site

We studied a community of frugivorous birds at Rara Avis, a privately-owned reserve located on the eastern boundary of Braulio Carrillo National Park on the Atlantic slope of Costa Rica (10°17'3" N, 84°02'47" W, ~700–800 masl). This site is located along an altitudinal gradient of protected forest extending from approx. 30–2900 m elevation. Roughly 30% of the birds in this region migrate altitudinally (Stiles 1983). We restricted our studies of diet and preference to a single location and season to control for variation in the diets of resident species caused by changing availability of fruit resources over the course of the year and in migrant species by the availability of alternative fruit found at different sites. Forests at Rara Avis are classified as Premontane Pluvial (Holdridge 1967), receiving a mean annual rainfall of 8279 mm (± SE 263 mm, Rara Avis, unpublished data). We studied the diets of birds during Jun–Jul in 2001, 2002, and 2004. These months correspond to the end of the breeding season, immediately post-breeding, and the beginning of the downhill migratory period. We conducted all preference trials during Jun–Jul 2002.

Bird capture and fecal sample collection

We placed 6–16 understory mist nets (12 m wide x 3 m tall, 38-mm mesh) and three canopy mist nets (3 m wide x 12 m tall, 38-mm mesh) in both old-growth forest and selectively-logged forest for 4–7 days at each of 15 sets of net locations. We opened mist nets at 0600, keeping them open until noon or until rain began, checking nets every 20 min. We immediately released birds belonging to highly nectarivorous, insectivorous, or carnivorous families, as they were not the focus of our study. We collected fecal samples from birds in all the primarily frugivorous lineages at our site:

trogons (Trogonidae), toucanets (Ramphastidae), manakins (Pipridae), cotingas (Cotingidae), tityras and becards (uncertain familial affinities), thrushes (Turdidae), tanagers (Thraupidae), and the genus *Mionectes* (Tyrannidae).

To collect fecal samples, we placed individual birds in small commercial bird cages. We lined the bottom of each cage with plastic wrap and covered the cage with light cotton cloth. Birds were kept in the cages for ~30 min, during which time they voided seeds via either regurgitation or defecation (hereafter "fecal" samples). We collected fecal matter from the cages and from the cloth bags in which birds were transported, preserving samples in 75% alcohol. We washed the bird bags after every soiling, and changed the plastic wrap lining cages after each capture. We placed numbered aluminum bands on birds prior to releasing them.

Field collection of seed reference collection

Because no published references were available with which to identify seeds of neotropical plants, we made botanical collections of any species of tree, shrub, liana, or epiphyte observed fruiting on or near our site over the course of 19 mo of field work. We used extendable clipper poles to collect small fruiting branches of trees and lianas up to 14 m above ground. We prepared herbarium specimens and deposited plant collections at the following institutions: Museo Nacional de Costa Rica, Instituto Nacional de Biodiversidad (INBio), Missouri Botanical Garden, and University of Arizona. Additionally, we preserved whole fruits and seeds in alcohol to build a reference seed collection. We identified plants at INBio using published materials and by matching with herbarium specimens with help of INBio botanists. When we encountered a seed in fecal samples that we could not match to our collection, we assigned it a unique morphospecies name, and preserved it as we did for our reference collection. A complete photographic library of our seed collection is available online (Boyle 2003).

Pairing of migrant and resident species

We categorized all frugivorous species captured as either altitudinal migrants or as residents at our site. We relied primarily upon Stiles and Skutch (1989) and Loiselle and Blake (1991) for categorization of species' migratory status in this region. The migratory status for two of our 19 species was ambiguous; Stiles and Skutch (1989) do not mention altitudinal movements for *Pipra pipra* or *Mionectes oleagineus*, but Loiselle and Blake (1991) categorize these species as 'complete' and 'partial' altitudinal migrants, respectively. We resolved the classification of these two species (and verified classifications of all species) by examining the seasonal pattern of capture rates from 2001–2004 from four study sites that varied in elevation (100 m, 300 m, Rara Avis, and 1100 m, W. A. Boyle, unpublished data). Our data strongly suggest that *Pipra pipra* is in fact an altitudinal migrant breeding at higher elevations than Rara Avis, and that most *Mionectes oleagineus* in the region do not migrate.

We collected fecal samples from individuals of eight migratory and 11 resident species. Six of the eight altitudinal migrant species could be paired with resident species in either the same genus or family (table 2). We paired a seventh migratory species (*C. altera*) with *Schiffornis turdina*. *S. turdina* was recently moved out of the Pipridae, placed in the Cotingidae (Snow et al. 2004), and is now placed within a clade of uncertain affinities within the Tyranni (Remsen et al. 2006). Because *Corapipo* is believed to be basal in the manakin lineage and thus, less closely related to *Manacus* than is the other migrant manakin in this study (*Pipra*; Prum 1992), *Schiffornis* was the closest sympatric relative to *Corapipo* for which we had dietary data. *Corapipo* was paired with *Manacus* for analyses of preferences because we lacked preference data for either *Schiffornis* or *Pipra*. Body mass of migrants was not consistently lighter or heavier than their resident counterparts (paired-sample t-test, $t = 0.4$, $P = 0.718$).

We conducted preference trials with 38 individuals of eight bird species (*n* individuals): *Corapipo altera* (10), *Manacus candei* (5), *Mionectes olivaceus* (6), *M. oleagineus* (2), *Myadestes melanops* (8), *Catharus mexicanus* (2), *Tanagara icterocepahala* (3), and *Tachyphonus delatrii* (2). However, 10 individuals consumed no fruits during trials, including all *C. mexicanus* and *T. icterocepahala*. Thus, we were able to pair data from preference trials two manakin species and two flycatcher species, but lacked a resident thrush species to pair with *M. melanops* and a migratory tanager species to pair with *T. delatrii*. Because thrushes (Turdidae) and tanagers (Thraupidae) are believed to be more closely related to each other than either family is to manakins or flycatchers (Sibley and Ahlquist 1990), we paired *M. melanops* with *T. delatrii* for species-pair analyses of fruit preference (predictions 3 and 5).

Characterization of diets

We examined the contents of each fecal sample under a 40 x microscope on a filter-paper-lined Petri dish. We drew lines on the filter paper liners to divide the dish into 12 quadrants of roughly the same area and systematically examined each quadrant, separating fecal matter using forceps. Small seeds and large seeds are often handled differently by birds, influencing the time that the seeds are present in the digestive tract (Martínez del Río and Restrepo 1993, Murray et al. 1993). Such differences could bias attempts to estimate relative contributions of different fruits in diets based on quantitative measures of seed abundance in fecal samples. Hence, we did not use measures of relative abundance of seeds in our analyses, but rather presence/absence of seeds from each plant species. We analyzed 207 fecal samples from 14 paired species (table 2) and identified seeds from 82 distinct plant species or morphospecies in samples (online appendix S1). Of those, 62 seed types (75.6%) could be matched to one of the 144 species of plants we collected in the region.

We estimated the proportion of fecal matter consisting of arthropod remains in each sample by inspecting the relative amount of arthropod pieces in each quadrant and comparing this to the amount of all fruit pulp and seeds, averaging estimates among quadrants within a sample. Separating all arthropod pieces from fruit matter and weighing arthropod mass was not possible due to the extremely small size of most arthropod fragments. Although this method may not accurately represent the volume or mass of arthropods in samples, it provides a quantitative index of the relative importance of arthropods and fruit in diets, and is similar to methods used in other studies of frugivorous birds (e.g., Herrera 1998). When possible, we noted the orders of arthropods found in samples (online appendix S1). Arthropod taxa differ in the robustness of their exoskeleton and thus, degradation during passage through a bird's digestive system; hence, our ability to confidently identify them differs as well

(Rosenberg and Cooper 1990). Consequently, our list of arthropod taxa found in the diets of frugivorous birds is unlikely to be complete.

Fruit preference trials

To examine fruit preferences, we conducted choice experiments with birds of the same species from which we collected fecal sample data. These species were not selected at random from among all the frugivorous species at our site, but represented the species of birds that tolerated being kept in cages. To ensure that preference data were not influenced by which fruits had been consumed immediately beforehand, we fed birds an artificial diet (Denslow et al. 1987) colored red or black. We released birds that would not eat the artificial diet within four hours. We conducted fruit preference trials after a bird had been maintained in captivity under ambient temperature and light on artificial diet for at least 24 hours (and up to three days), removing food from cages one hour prior to trials.

We conducted trials in a cloth flight cage measuring 3 m x 2 m x 2 m with a mesh ceiling. The cage was protected from rain with translucent roofing material that allowed natural light into the interior. We positioned the flight cage in an area where the bird could see no trees or natural landscape features. In the center of the cage, we placed one bamboo perching structure. On one side of the cage, we placed seven bamboo stakes to which we attached infructescences. Each stake was equipped with a single transverse perch 10 cm from the top to allow birds easy access to fruits. The opposite wall of the cage contained a zippered doorway and a small (~ 5 cm diameter) mesh panel through which an observer recorded a bird’s foraging behavior.

We offered birds fruits from up to seven plant species during trials. We chose fruits based on preliminary analyses of fecal samples and the availability of wild fruits in our study area. Arrays differed among species pairs from different families. We attempted to offer all individuals of the species pair the same arrays of fruits. However, because the fruiting period of a few plant species used in trials ended before all trials were complete, fruits of a few plant species were not offered to all birds. We left one or a pair of leaves subtending each infructescence, and we did not manipulate the number of fruits on infructescences in order to preserve as many visual cues of leaf shape, leaf size, and infructescence morphology as possible. We assigned plant species randomly to perches before each trial. An observer noted the time and identity of all fruits consumed throughout the 45 min trial. We aborted the trial if the bird ignored all fruit and repeatedly attempted to escape the cage or appeared to be in distress. We fed birds following trials and released them in the vicinity of the capture location.

Analyses

We compared diet breadth (in terms of fruits consumed) between migrant and resident bird species in two ways. First, we used Fisher's α diversity index based on presence/absence matrices of plant species (represented by seeds identified to species or distinct seed morphospecies) found in fecal samples. We chose Fisher's α index because it incorporates both information regarding the total number of plant species a bird species forages on, as well as the evenness of those plant species among samples. Furthermore, the use of Fisher's α permits a comparison of fruit diversity in diets of different species represented by unequal numbers of fecal samples (Magurran 1988).

We compared the diversity indices between species pairs using paired-sample *t*-tests (prediction 1). Second, we counted the total number of plant species found in fecal samples (all individuals pooled) within a species. To correct for differences among species within a pair in the number of fecal samples available for analysis, we rarefied the number of fecal samples of the species in a pair with more samples to the number of samples of the species with fewer samples. By using both diversity as well as the number of species of plants whose seeds we found in fecal samples, we were able to evaluate the species richness as well as the evenness of fruits in diets. These two metrics provide complementary information the foraging behavior of different species.

We compared the relative predominance of fruits vs. arthropod prey in diets of migrant and non-migrant species using the proportion of arthropod remains in each fecal sample. We analyzed these proportions (arcsine square-root transformed) using a 2-factor mixed-model ANOVA in which migrant status was a fixed effect and species pair was a random effect to control for among-pair variation independent of migratory behavior (prediction 2).

We estimated the relative strength of fruit preference for each individual bird by calculating the number of plant species from which individual birds consumed fruits during preference trials. We assumed that birds with strong fruit preferences would consume fruits of only one or a few plant species during trials, and that birds with weaker fruit preferences would consume fruits from a wider range of plant species. We compared preference strengths between migrant and resident species pairs using a 2-factor mixed-model ANOVA with migrant status as a fixed effect and species pair as a random effect (prediction 3). To ensure that preference results were not biased by unequal arrays of fruits offered to individuals within a species, we conducted all analyses of preference twice: first using all data, and then restricting analyses to fruits that all individuals within a species were offered. Our results did not differ qualitatively between sets of analyses, and we present only the results based on the complete trial data.

To examine whether fruit preference ranks were shared between species pairs and the extent to which observed diets reflected fruit preferences within a species, we calculated fruit preference ranks for each individual bird based on the order in which fruits of each plant species were consumed. To obtain overall fruit preference ranks for each bird species, we summed ranks for each plant species from all individuals of each bird species. We explored alternative methods of ranking fruit preference, and rankings derived from all methods were all highly correlated (W. A. Boyle, unpublished data). Thus, we present results based on a single method of ranking fruit preferences based on the order that birds consumed fruits. To investigate whether migrant and non-migrant species share preferences for fruits of the same or different plant species, we used Spearman rank correlations to compare fruit preference ranks between species pairs (prediction 4).

Finally, we calculated the proportion of fecal samples of a given bird species that contained seeds of each plant species. We constructed diet ranks based on these proportions for the plant species also used in preference trials (for each bird species). We examined whether the ranking of plant species based on dietary data reflected the ranking of those same plant species based on preference trials by conducting non-parametric Spearman rank correlations (diet rank vs. preference rank) for each bird species. We then compared the correlation coefficients of migrant and resident species pairs using a paired-sample *t*-test (prediction 5).

Results

Diet breadth

Indices of diet diversity differed among migrant and resident species pairs. The diversity of plant species from which birds consumed fruits (i.e., seed types in fecal samples) was on average 8.0 (± 1.7 SE) units greater in migrant species than in resident species ($t = 4.3$, df = 6, $P = 0.005$; Fig. 2A). All species pairs but one (*Tangara icterocephala–Tachyphonus*) were consistent in the direction of this association. The Fisher's α score of resident species was on average half the value of the corresponding score of their migrant counterparts. Additionally, all migrant species except for *Tangara icterocephala* consumed fruits from on average 25% more plant species than the resident species with which they were paired, although this trend was not statistically significant ($t = 1.5$, df = 6, $P = 0.175$). In contrast, the relative importance of arthropod prey was greater in resident species than in migrant species ($F_{7, 206} = 10.1$, $P < 0.0001$; Fig. 2B). Fecal samples collected from migrant birds contained on average 5.0% (± 1.8% SE) arthropod remains, whereas samples from resident birds contained on average 21.9% (± 2.1% SE) arthropod remains. All species pairs but one (*Manacus–Pipra*) were consistent in the direction of this association.

Fruit preference

We found some suggestive evidence of stronger fruit preferences in migrant birds compared to resident birds ($t = -1.6$, $P = 0.118$, Fig. 3A). In all three species pairs, the migrant species consumed fruits from on average 0.4 (± 0.25) fewer plant species during preference trials than did the corresponding resident species. This difference was not simply due to migrant birds eating more individual fruits during trials; migrants and residents did not differ in the total number of individual fruits consumed ($t = -0.8$, $P = 0.880$). Migrants and residents had similar fruit preferences (flycatchers, $r = 0.932$, $P < 0.0001$; manakins, $r = 0.901$, $P = 0.006$; Fig. 4). However, realized diets were less similar (flycatchers, $r = 0.843$, $P = 0.002$; manakins, $r = 0.181$, $P = 0.698$).

Relationship between diet and preference

We found suggestive evidence that the realized diets of migrant species more closely resembled their preferences (as estimated by experimental choice trails) compared to their resident counterparts: the correlation coefficients between diet and preference ranks were consistently higher in each of the migrant species than in their resident counterparts ($t = -3.2$, df = 2, $P = 0.086$; Fig. 3B). Furthermore, in all three migrant species, the highest ranked fruit based on preference trials was the same as the highest ranked fruit based on diet. In contrast, in all three resident species, the highest ranked fruit based on preference trials was different from the highest ranked fruit based on diet.

Discussion

The results of our analyses of diet and preference show that migrant birds differed from resident birds in both diet breadth and diet composition, and provide mixed support for each of the two hypotheses. The competitive exclusion hypothesis relies on differences in migratory behavior between closely related species being attributable to residents have a competitive advantage over their migrant counterparts. The dietary specialization hypothesis, in contrast, relies upon differences in dietary specialization explaining differences in migratory strategy between species. Consistent with the competitive exclusion hypothesis, diets were broader (in terms of fruit diversity) in migrant species than in resident species, potentially implying that residents fill more of their dietary needs with the best fruits available, and migrants sample from a broader array of fruits and consume those in more equal proportions in compensation (prediction 1). Also consistent with the competitive exclusion hypothesis was the finding that within species pairs, migrants and residents share preferences for the same fruits (prediction 3). This suggests that specialization on different types of fruit does not explain species-level differences in migratory behavior. However, the results of predictions 2, 4, and 5 were inconsistent with the competitive exclusion hypothesis. The relative importance of fruits vs. arthropods suggested that resident diets are broader in terms of broad dietary classes, not narrower than migrants; migrants consume proportionately more arthropods. Furthermore, the results of our preference trials suggest that despite sharing preferences, migrants tend to exhibit stronger fruit preferences, which would only be expected under the dietary specialization hypothesis. Most importantly, the degree to which the diets of residents reflect their preferences strongly suggests that Cox's (1985) mechanism of interspecific competition does not explain the differences in migratory strategy between these species. It also suggests that the broader diversity of fruits in migrant diets is not caused by migrants being out-competed by residents for those fruits.

Several of our results were consistent with the dietary specialization hypothesis. Consistent with predictions 2, 4, and 5, migrant species were more frugivorous, they had stronger fruit preferences, and their diets more closely resembled their preferences relative to resident species. Wheelwright (1983) provided evidence suggesting that dietary specialization could explain altitudinal migration in Resplendent Quetzals (*Pharomachrus mocinno*) who appear to migrate in response to the fruiting phenology of trees in a single plant family, the Lauraceae. Because our two indices of diet breadth differed in their association with migratory behavior, we suggest that future studies carefully examine how each of these two indices of diet breadth might be constrained. We suggest that perhaps because migrants have diets more restricted to fruit, they are obliged to sample more broadly from the fruits available in the community. Most fruits are low in protein (Wheelwright et al. 1984) and nutritionally imbalanced relative to arthropod prey. Sampling broadly from the fruiting community may thus be necessary in order to complete the nutritional needs of an obligate frugivore.

Our finding of shared fruit preferences between migrants and residents within pairs (prediction 3) does not refute the dietary specialization hypothesis as a whole, but allows us to narrow the range of variations on this hypothesis that future studies should consider. In particular, this result suggests that birds do not migrate because they prefer fruits that are only available seasonally. The results of our dietary comparisons (prediction 2) do suggest, however, that residents' diets involve more switching from fruits to arthropods when their preferred fruits are difficult to obtain. We can further narrow the scope of the dietary specialization hypothesis by considering the diversity of fruits in migrants' diets. High diversity of fruits in diets suggests that most migrants are unlikely to track the fruiting of a single genus or family of fruits over the course of their migratory cycle. Instead, they may migrate in response to changing fruit nutrient profiles or abundance of a suite of complementary fruits available at different elevations over the course of the year.

The results of this study demonstrate that previously noted correlations between a frugivorous diet and short-distance migration (Levey and Stiles 1992, Appendix A) are also apparent at much finer scales than previously suggested (i.e., between closely-related species within several lineages of frugivorous birds). In particular, these findings provide further evidence that food limitation plays a role in causing some birds to migrate while others do not. We suggest two approaches that will be necessary to further our understanding of the causes of variation in migratory behavior in birds.

The first is to test the dietary specialization hypothesis against alternative hypotheses that do not rely on food limitation. Because manipulative experiments have been logistically impractical, neither our data nor previous data can distinguish whether a frugivorous diet is a cause of migration or a consequence of migration in tropical birds. Migration could occur in response to variation in ecological factors other than food, such as unfavorable weather or nest predator avoidance. If so, migrants could be constrained to eat whatever foods are easiest to find. Tropical forests are believed to be places of intense competition for insects and other protein-rich prey (Janzen 1973, Sherry 1984), contrasting with the view that fruits and flowers (unlike most other types of food resources) “want” to be eaten (Snow 1971). Thus, migrants may be forced to eat fruit because it is the easiest food to find. Under alternative hypotheses based on ecological processes other than food limitation, the direction of the causal arrow between diet and migration would be reversed, whereby the observed differences in diet between migrants and residents are caused by migration itself. As yet, only one test of alternative hypotheses exists (Appendix C), and this study suggests that the role of nest predation indeed merits further consideration when explaining altitudinal migration.

The second approach will be to directly and appropriately test the fundamental assumption of all food-based hypotheses of underlying variation in some portion of the fruit resources in a community. Such variation is not an assumption of the alternative hypotheses that do not invoke food limitation. Thus, to provide compelling support for any food-based hypothesis, we need a careful study of fruit availability across elevations used by altitudinal migrants. We argue that this should be undertaken in new ways, going beyond community-level counts of standing crop of fruits. First, we must identify which fruits are consumed and preferred by altitudinal migrant species, and accurately quantify the variation in fruit availability on those preferred fruits. The diet data presented here (online appendix S1) and by many previous authors (e.g., Moermond and Denslow 1983, Levey et al. 1984, Wheelwright et al. 1984, Gautier-Hion et al. 1985, Loiselle and Blake 1990, Stiles and Rosselli 1993, Fuentes 1994, Giles and Lill 1999) clearly show that frugivores do not forage indiscriminately on all fleshy fruits available. Second, we must measure availability of fruits using techniques that capture the spatial variation in *production rates* rather than counting standing crops of fruits. Even if one elevation produces three or four times as much fruit per day as another, standing crops could be identical between elevations if fruit consumption rates differ between those areas; a pattern that would be expected if spatial variation in fruit availability does influence the migratory behavior of frugivores.

Ours is the first study that has demonstrated a link between frugivorous birds' diets and their preferred foods, an approach that has allowed us refute competitive exclusion as an explanation for why tropical bird migrate altitudinally. Our data are the first to reveal associations between realized diet, dietary preference, and migration within several lineages of oscine and sub-oscine birds, implying that similar ecological conditions have acted similarly across taxonomic groups in the evolution of altitudinal migration. Our conclusions lend support to the body of theoretical work suggesting that food limitation drives the evolution of bird migration. The next steps will be to further explore the mechanisms by which food limitation has resulted in differences among species and individuals in migratory behavior in both short- and long-distance migratory systems.

Acknowledgments

We are grateful to L. Cholodenko, M. Hill, J. Montoya-Morera, P. Sanchez, A. Zambrano, and especially R. Repasky and H. Reider for assistance in the field. B. Boyle, B. Hammel, F. Morales, N. Zamora, C. Taylor, R. Kriebel, J. Gonzalez, and O. Vargas helped identify plants, and S. White sorted many fecal samples. A. Bien and staff of Rara Avis, J. Guevara and R. Tenorio at MINAE and the ACCVC, and the University of Arizona's IACUC committee assisted with logistics, permits, and support in the field. D. Papaj, B. Enquist, B. Steidl, and B. Boyle commented on earlier drafts. Financial support was provided by the National Science Foundation (Grant No. 0410531), NSERC (PGS-B fellowship), RTG in Biological Diversification, the Center for Insect Science, the Silliman Memorial Research Award, the International Arid Lands Consortium, the American Ornithologists' Union, the Explorer's Club, the department of EEB, and the graduate college of the University of Arizona.

Literature Cited

Ackerly, D. D. 2000. Taxon sampling, correlated evolution, and independent contrasts. Evolution **54**:1480-1492.

Alcock, J. 2005. Animal behavior: an evolutionary approach, eighth edition. Sinauer Associates, Inc., Sunderland, MA.

Alerstam, T. 1990. Bird Migration, English edition. Cambridge University Press, Cambridge, UK.

Alerstam, T., and P. H. Enckell. 1979. Unpredictable habitats and evolution of bird migration. Oikos **33**:228-232.

Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. Oikos **103**:247-260.

American Ornithologists' Union. 1998. Checklist of North American Birds, seventh edition. American Ornithologists' Union, Washington, DC.

American Ornithologists' Union. 2005. Forty-sixth supplement to the American Ornithologists' Union *Check-list of North American Birds*. Auk **122**:1026-1031.

Bell, C. P. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. Journal of Avian Biology **31**:258-265.

Berthold, P. 2001. Bird Migration: A General Survey, Second edition. Oxford University Press, Oxford, UK.

Boyle, W. A. 2003. Seed images from the Atlantic Slope of Costa Rica. http://eebweb.arizona.edu/grads/alice/SeedPhotos.html.

Burgess, N. D., and C. O. F. Mlingwa. 2000. Evidence for altitudinal migration of forest birds between montane Eastern Arc and lowland forests in East Africa. Ostrich **71**:184-190.

Cardoso da Silva, J. M. 1993. The Sharpbill in the Serra dos Carajás, Para, Brazil, with comments on altitudinal migration in the Amazon Region. Journal of Field Ornithology **64**:310-315.

Chaves-Campos, J. 2004. Elevational movements of large frugivorous birds and temporal variation in abundance of fruits along an elevational gradient. Ornitología Neotropical **15**:433-445.

Chaves-Campos, J., J. E. Arévalo, and M. Araya. 2003. Altitudinal movements and conservation of Bare-necked Umbrellabird *Cephalopteris glabricollis* of the Tilarán Mountains, Costa Rica. Bird Conservation International **13**:45-58.

Cox, G. W. 1968. The role of competition in the evolution of migration. Evolution **22**:180-192.

Cox, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. American Naturalist **126**:451-474.

Cristol, D. A., M. C. Baker, and C. Corbone. 1999. Differential migration revisited: latitudinal segregation by age and sex class. Current Ornithology **15**:33-88.

Denslow, J. S., D. J. Levey, T. C. Moermond, and B. C. Wentworth. 1987. A synthetic diet for fruit-eating birds. Wilson Bulletin **99**:131-135.

Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, NY.

Elton, C. S. 1973. The structure of invertebrate populations inside neotropical rain forest. Journal of Animal Ecology **42**:55-104.

Fretwell, S. D. 1980. Evolution of migration in relation to factors regulating bird numbers. Pages 517-527 *in* A. Keast and E. S. Morton, editors. Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica **19**:16-36.

Fuentes, M. 1994. Diets of fruit-eating birds: what are the causes of interspecific differences? Oecologia **97**:134-142.

Galetti, M. 2001. Seasonal movements and diet of the Plumbeous Pigeon (*Columba plumbea*) in a Brazilian Atlantic Forest. Melopsittacus **4**:39-43.

Gautier-Hion, A., J. M. Duplantier, R. Quris, F. Feer, C. Sourd, J. P. Decoux, G. Dubost, L. Emmons, C. Erard, P. Hecketsweiler, A. Moungazi, C. Roussilhon, and J. M. Thiollay. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia **65**:324-337.

Giles, S., and A. Lill. 1999. The effect of fruit abundance, conspicuousness and sugar concentration on fruit colour choice by captive silvereyes. Ethology Ecology & Evolution **11**:229-242.

Gill, F. 1994. Ornithology, second edition. W. H. Freeman and Company, New York.

Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493-504 *in* A. Keast and E. S. Morton, editors. Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC.

Harvey, P. H., and M. D. Pagel. 1991. The Comparative Method in Evolutionary

Biology. Oxford University Press, Oxford, UK.

Herrera, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-yr study. Ecological Monographs **68**:511-538.

Hobson, K. A., L. I. Wassenaar, B. Mila, I. Lovette, C. Dingle, and T. B. Smith. 2003. Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. Oecologia **136**:302-308.

Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.

Holmgren, N., and S. Lundberg. 1993. Despotic behavior and the evolution of migration patterns in birds. Ornis Scandinavica **24**:103-109.

Janzen, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology **54**:687-708.

Johnson, D. N., and G. L. Maclean. 1994. Altitudinal migration in Natal. Ostrich **65**:86-94.

Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A theory of partial migration. American Naturalist **142**:59-81.

Laymon, S. A. 1989. Altitudinal migration movements of Spotted Owls in the Sierra Nevada, California. Condor **91**:837-841.

Levey, D. J., T. C. Moermond, and J. S. Denslow. 1984. Fruit choice in Neotropical birds: the effects of distance between fruits on preference patterns. Ecology **65**:844-850.

Levey, D. J., and F. G. Stiles. 1992. Evolutionary precursors of long-distance migration:

resource availability and movement patterns in Neotropical landbirds. American Naturalist **140**:447-476.

Loiselle, B. A., and J. G. Blake. 1990. Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. Studies in Avian Biology **13**:91-103.

Loiselle, B. A., and J. G. Blake. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology **72**:180-193.

Magurran, A. 1988. Ecological diversity and its measurement. Chapman and Hall, London, UK.

Martínez del Río, C., and C. Restrepo. 1993. Ecological and behavioral consequences of digestion in frugivorous animals. Vegetatio **107/108**:205-216.

Moermond, T. C., and J. S. Denslow. 1983. Fruit choice in Neotropical birds: effects of fruit type and accessibility on selectivity. Journal of Animal Ecology **52**:407-420.

Murray, K. G., K. Winnettmurray, E. A. Cromie, M. Minor, and E. Meyers. 1993. The influence of seed packaging and fruit color on feeding preferences of American Robins. Vegetatio **108**:217-226.

Prum, R. O. 1992. Syringeal morphology, phylogeny, and evolution of the neotropical manakins (Aves: Pipridae). American Museum Novitates **3042**:1-65.

Ramos-Olmos, M. A. 1983. Seasonal movements of bird populations at a Neotropical study site in southern Veracruz, Mexico. Ph.D. dissertation. University of Minnesota, Minneapolis, MN.

Rappole, J. H., H. Helm, and M. A. Ramos-Olmos. 2003. An integrative framework for understanding the origin and evolution of avian migration. Journal of Avian Biology

34:124-128.

Remsen, J. V., A. Jaramillo, M. Nores, J. F. Pacheco, M. B. Robbins, T. S. Schulenberg, F. G. Stiles, J. M. C. da Silva, D. F. Stotz, and K. J. Zimmer. version January 2006. A classification of the bird species of South America. **http://www.museum.lsu.edu/~Remsen/SACCBaseline.html**.

Rosenberg, K. V., and R. J. Cooper. 1990. Approaches to avian diet analysis. Pages 80-90 *in* M. L. Morrison, C. J. Ralph, J. Verner, and J. R. J. Jehl, editors. Avian foraging: theory, methodology and applications. Studies in Avian Biology. Cooper Ornithological Society, Lawrence, Kansas.

Rosselli, L. 1989. El ciclo anual de un ave frugívora migratoria altitudinal, *Corapipo leucorrhoa* (Pipridae) y los frutos que consume. M.Sc. thesis. Universidad de Costa Rica, San José, Costa Rica.

Rosselli, L. 1994. The annual cycle of the White-ruffed Manakin, *Corapipo leucorrhoa*, a tropical frugivorous altitudinal migrant, and its food plants. Bird Conservation International **4**:143-160.

Sherry, T. W. 1984. Comparative dietary ecology of sympatric, insectivorous Neotropical flycatchers (Tyrannidae). Ecological Monographs **54**:313-338.

Sibley, C. G., and J. E. Ahlquist. 1990. Phylogeny and Classification of Birds. Yale University Press, New Haven, CT.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. Pages 575-594 *in* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, editors. Neotropical Ornithology. The American

Ornithologists' Union, Washington, DC.

Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. Ibis **113**:194-202.

Snow, D. W., M. D. L. Brooke, and B. A. Walther. 2004. Family Cotingidae (Cotingas). Pages 32-109 *in* J. del Hoyo, A. Elliot, and D. A. Christie, editors. Handbook of the Birds of the World. Vol. 9. Cotingas to Pipits and Wagtails. Lynx Editions, Barcelona, Spain.

Solórzano, S., S. Castillo, T. Valverde, and L. Avila. 2000. Quetzal abundance in relation to fruit availability in a cloud forest of southeastern Mexico. Biotropica **32**:523-532.

Stiles, F. G. 1980. The annual cycle in a tropical wet forest hummingbird community. Ibis **122**:322-343.

Stiles, F. G. 1983. Birds. Pages 502-530 *in* D. H. Janzen, editor. Costa Rican Natural History. University of Chicago Press, Chicago, IL.

Stiles, F. G., and L. Rosselli. 1993. Consumption of fruits of the Melastomataceae by birds: how diffuse is the coevolution? Vegetatio **108**:57-73.

Stiles, F. G., and A. F. Skutch. 1989. A Field Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, NY.

Symes, C. T., C. T. Downs, and S. McLean. 2001. Seasonal occurrence of the Malachite Sunbird, *Nectarinia famosa*, and Gurney's Sugarbird, *Promerops gurneyi*, in KwaZulu- Natal, South Africa. Ostrich **72**:45-49.

Walsh, R. P. D. 1996. Climate. Pages 157-205 *in* The Tropical Rainforest: an ecological study, second edition. Cambridge University Press, Cambridge, UK.

Wheelwright, N. T. 1983. Fruits and the ecology of Resplendent Quetzals. Auk **100**:286-301.

Wheelwright, N. T., W. A. Haber, K. G. Murray, and C. Guindon. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. Biotropica **16**:173-192.

Tables, Figures and Appendices

Table 1

Summary of the tests used to evaluate the two food-based mechanisms proposed in this paper to explain why some but not all frugivorous birds migrate altitudinally.

	hypotheses	
differences between migrants and resident species in:	competitive exclusion	dietary specialization
DIET BREADTH		
(1) diversity of fruits in diet	higher in migrant than in resident species	lower in migrant than in resident species, or no difference
(2) relative proportion of fruit vs. arthropods in diet	residents more frugivorous	migrants more frugivorous, or no difference
FRUIT PREFERENCE		
(3) preferences for fruit types the same or different between species within pair	fruit preferences shared between migrant and resident species	**EITHER** fruit preferences differ between migrant and resident species; **OR** ↓
(4) strength of preference for preferred fruits	no difference	stronger preference strength in migrants than in residents
RELATIONSHIP BETWEEN DIET AND PREFERENCE		
(5) correlation between preferences and realized diets	stronger in resident than migrant species	weaker in resident than migrant species

Table 2

Species pairs and sample sizes of both fecal samples used in dietary comparisons and preference trials. Species names follow the (American Ornithologists' Union 1998, 2005).

species pair	bird species	migrant status	sample size	
			fecal samples	preference trials
manakin1	*Corapipo altera*	migrant	89	8
	Schiffornis turdina[1]	resident	8	
manakin2	*Pipra pipra*	migrant	13	
	Manacus candei	resident	7	2
flycatcher	*Mionectes olivaceus*	migrant	9	6
	Mionectes oleagineus	resident	11	4
thrush1	*Myadestes melanops*	migrant	10	7
	Catharus mexicanus	resident	10	
thrush2	*Turdus obsoletus*	migrant	12	
	Turdus grayii	resident	5	
tanager1	*Tangara icterocephala*	migrant	11	
	Tachyphonus delatrii	resident	15	1
tanager2	*Tangara florida*	migrant	3	
	Chlorospingus opthalmicus	resident	4	

[1] The familial classification of *Schiffornis turdina* is uncertain. See text for justification of its pairing with *Corapipo altera*.

Figure legends

Figure 1 Hypothetical relationship between food, elevation (high/low), season (breeding/non-breeding) and migratory behavior under four alternative scenarios. The reciprocal food abundance hypothesis tested by previous studies (panel A) assumes that total fruit production fluctuates in a temporally and spatially reciprocal fashion. At high elevations where migrants breed (gray bars) fruit is expected to peak during the breeding season and at low elevations (white bars) fruit is expected to peak during the non-breeding season. The proportion of fruits consumed by resident species is implicitly assumed to be constant between season and elevation. Previous research has tested this hypothesis by looking for differences among seasons and elevations in surplus standing crop of fruit. However, optimal foraging theory (panel B) suggests that if patterns of total fruit abundance fluctuates reciprocally (e.g., total bar height, panels A and B), then the proportions of birds that will migrate should stabilize at levels that equalize the surplus standing crop of fruits between elevations during any given season (unhatched portions of bars). Thus, measurements of standing crop (panel B, unhatched portion of bars) should not differ among elevations, despite seasonal and elevational differences in production rate (total bar height). The groups of hypotheses relying upon either competitive exclusion (panel C) or diet specialization (panel D) to explain differences in migratory strategy among species do not make specific predictions regarding patterns of variation in total fruit production (total bar height) between seasons or elevations. Hypotheses based upon competitive exclusion (panel C) depend upon resident species experiencing higher costs to migrating than migrant species, and being capable of out-competing migrants for fruit. Migrants consume the surplus food not consumed by residents (unhatched portions of bars, panel C) and migrate when this surplus drops below critical levels. In contrast, hypotheses based upon dietary specialization (panel D) depend upon reciprocal patterns of fruit productivity of only plant species that migrants prefer (unhatched portions of bars, panel D), and the ability of migrants to obtain those resources. Stars within bars show the location migrants are predicted to be during each season in panels C and D.

Figure 2 A comparison of the diets of species pairs of frugivorous alitudinal migrant and resident species as represented by Fisher's α index based on presence of plant species in fecal samples (panel A) and relative proportions of arthropod remains in fecal samples (panel B). Error bars in panel B represent 1 SE of the mean.

Figure 3 A comparison of preference strength estimated by the mean (±1 SE) number of plant species from which birds consumed fruits during preference trials (panel A), and the correlation between ranks of fruits observed in diets and those chosen in preference trials among migrant and resident species (panel B). Values in panel B represent the extent to which the preferred fruits (based on preference trials) were actually eaten by birds in the wild. Starred values (*Tachyphonus delatrii* and *Manacus candei*) had diet-preference correlation coefficients indistinguishable from zero. *P*-values of other correlations were: *Mionectes oleagineus*, $P = 0.004$; *M. olivaceus*, $P < 0.0001$; *Corapipo altera*, $P = 0.069$; *Myadestes melanops*, $P = 0.083$.

Figure 4 The similarity of relative fruit preferences (based on preference trials) between migrant and resident species pairs. Values on x- and y-axes represent rank order of preference (high values are most preferred), and dots represent plant species used in preference trials. Plant codes are: CaveComp, *Cavendishia complectans;* CaveEndr, *Cavendishia endresii;* ClusGrac, *Clusia gracilis;* ClusSten, *Clusia stenophylla;* ConoMicr, *Conostegia micrantha;* DoliMult, *Doliocarpus multiflora;* MicoCent, *Miconia centrodesma;* OssaMicr, *Ossaea micrantha;* PsycBuch, *Psychotria buchtienii;* ShefSyst, *Schefflera systyla.*

Figure 1

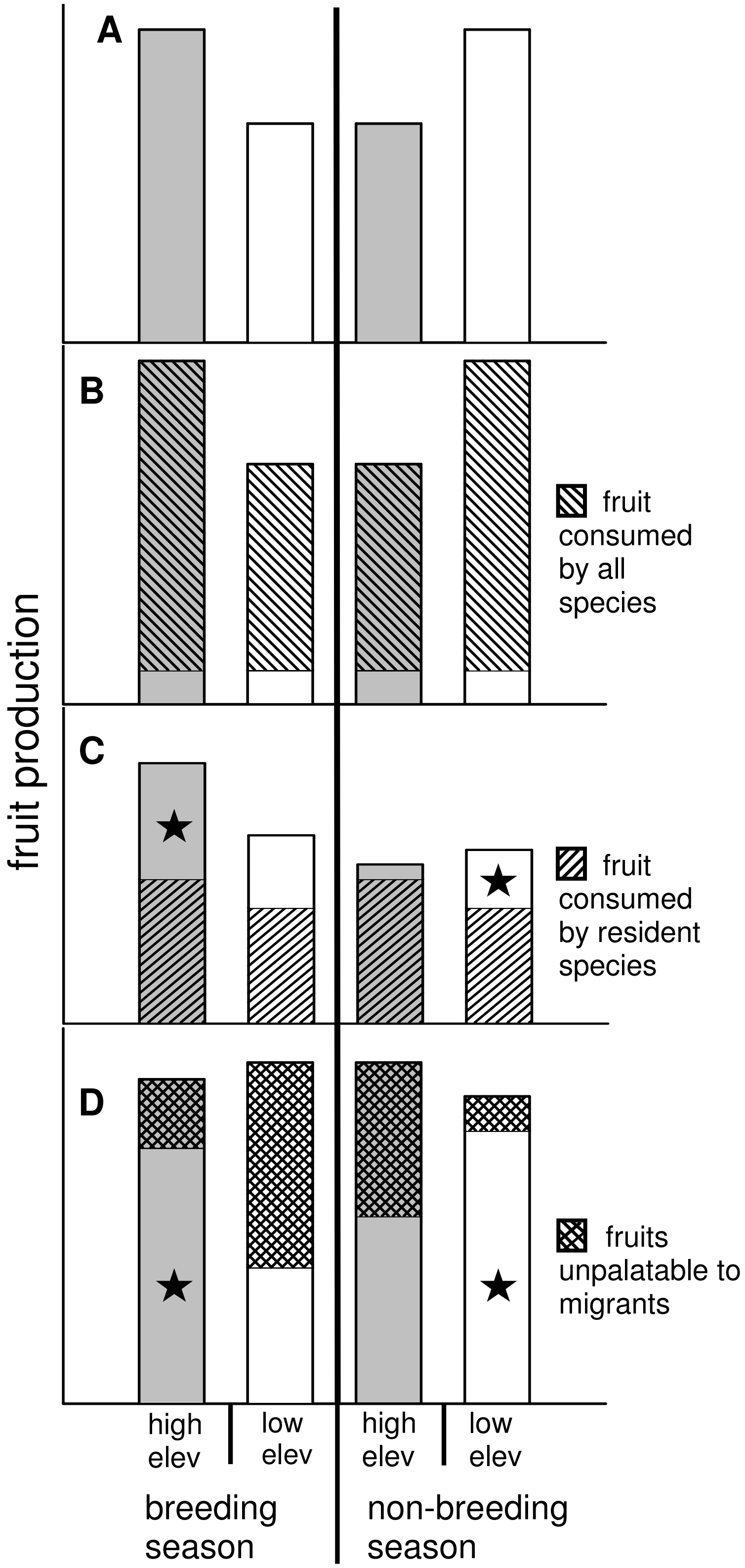

A
B
C
D
fruit production
fruit consumed by all species
fruit consumed by resident species
fruits unpalatable to migrants
high elev
low elev
high elev
low elev
breeding season
non-breeding season

Figure 2

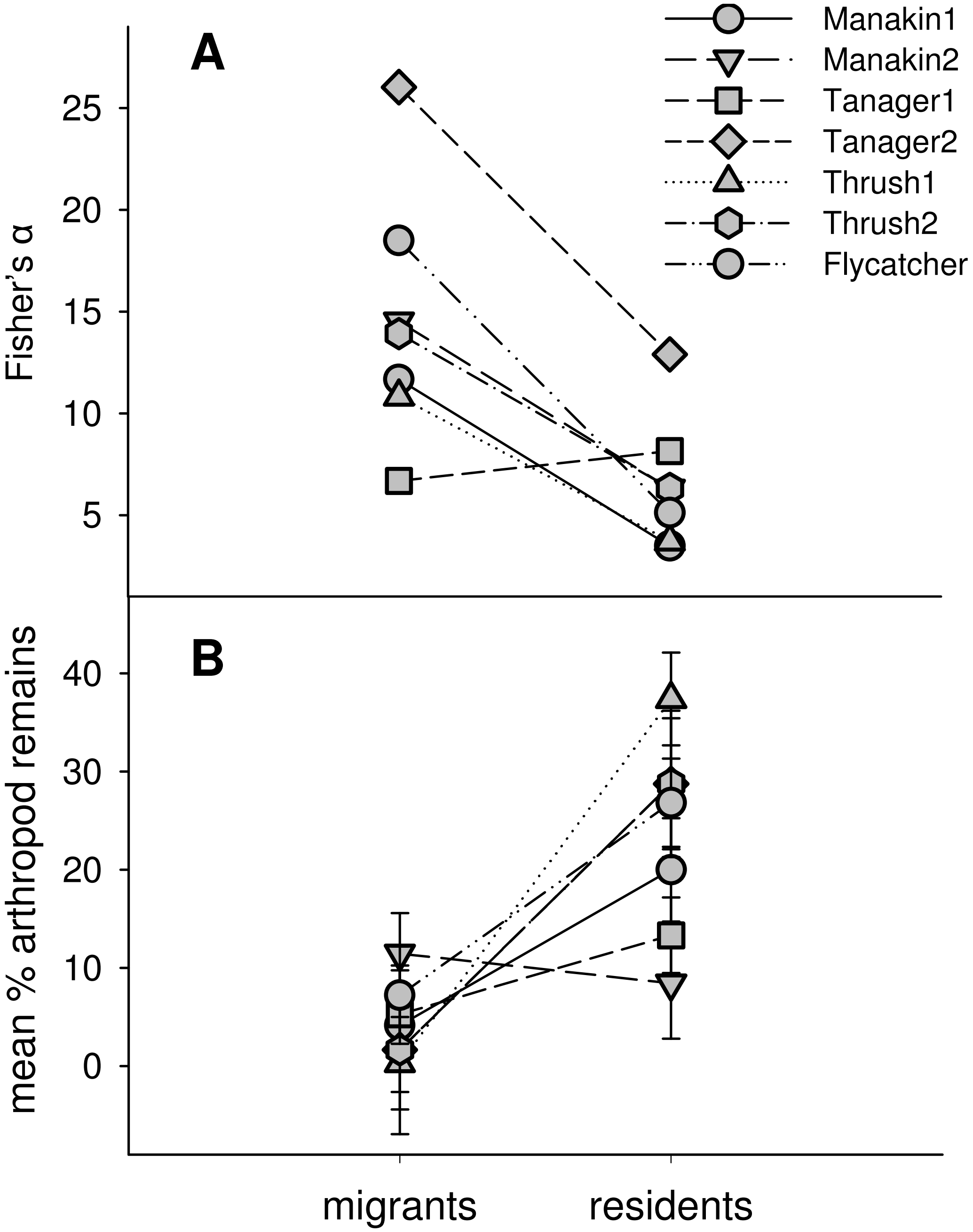

A
B
Fisher's α
25
20
15
10
5
mean % arthropod remains
40
30
20
10
0
migrants
residents
Manakin1
Manakin2
Tanager1
Tanager2
Thrush1
Thrush2
Flycatcher

Figure 3

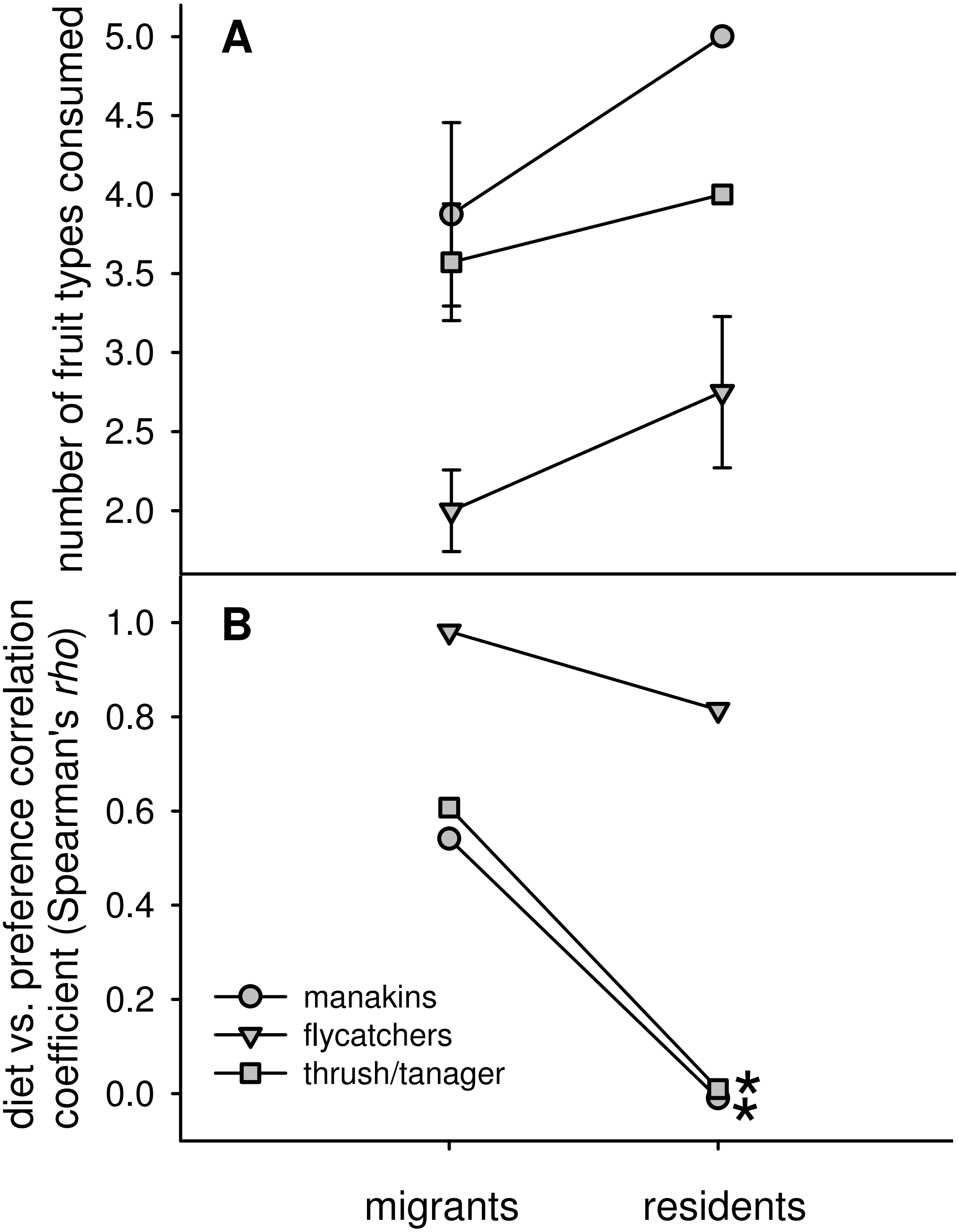
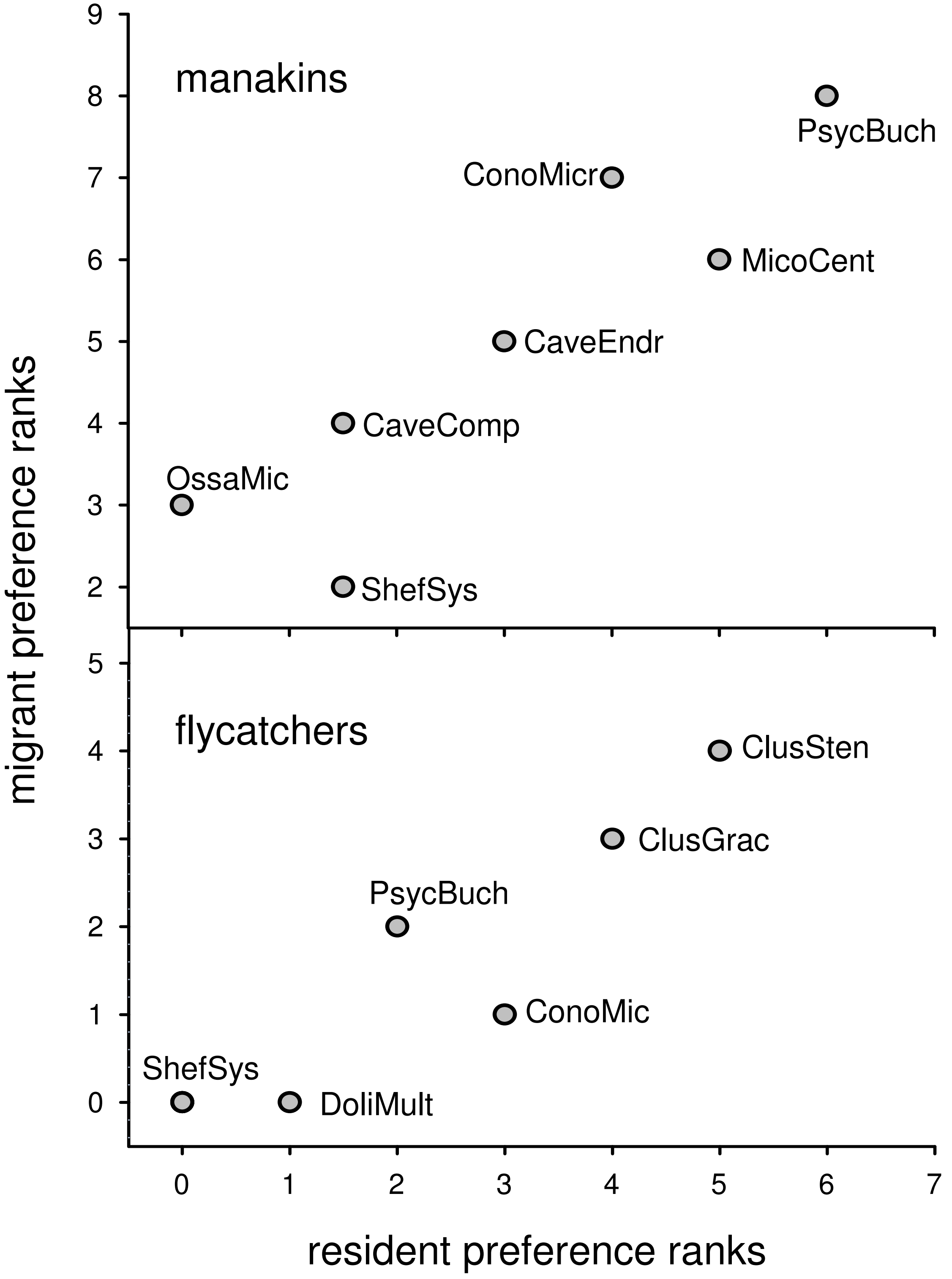

A
B
number of fruit types consumed
5.0
4.5
4.0
3.5
3.0
2.5
2.0
diet vs. preference correlation coefficient (Spearman's *rho*)
1.0
0.8
0.6
0.4
0.2
0.0
manakins
flycatchers
thrush/tanager
*
*
migrants
residents

Figure 4


manakins
PsycBuch
ConoMicr
MicoCent
CaveEndr
CaveComp
OssaMic
ShefSys
9
8
7
6
5
4
3
2
flycatchers
ClusSten
ClusGrac
PsycBuch
ConoMic
ShefSys
DoliMult
5
4
3
2
1
0
0
1
2
3
4
5
6
7
migrant preference ranks
resident preference ranks

Online Appendix S1

Number of fecal samples in which a given plant species (seed type) was found for each bird species in this study. Plant names and authorities follow the INBio species list for Costa Rica (version July 2006). Presence of arthropod taxa (Order-Family) in fecal samples is indicated by an X. Bird species codes are: SHTU, *Schiffornis turdina*; COAL, *Corapipo altera*; PIPI, *Pipra pipra*; MACA, *Manacus candei*; MIOV, *Mionectes olivaceus*; MIOG, *Mionectes oleagineus*; MYME, *Myadestes melanops*; CAME, *Catharus mexicanus*; TUOB, *Turdus obsoletus*; TUGR, *Turdus grayii*; TGIC, *Tangara icterocephala*; TGFL, *Tangara florida*; TCDE, *Tachyphonus delatrii*; CPOP, *Chlorospingus opthalmicus*.

	bird species													
plant taxa	SHTU	COAL	PIPI	MACA	MIOV	MIOG	MYME	CAME	TUOB	TUGR	TGIC	TGFL	TCDE	CPOP
Annonaceae														
Guatteria aeruginosa Standl.							1							
Aquifloliaceae														
Ilex hemiepiphytica W. J. Hahn				1							3	1	1	
Ilex maxima W. J. Hahn		1				1					2			
Araceae														
Anthurium cuspidatum Mast.			1											
Anthurium michelii Guillaumin		1												

Anthurium tenerum Engl.														1
Araliaceae														
Schefflera nicaraguensis (Standl.) A. C. Sm.		3							1		4			
Schefflera systyla (Donn. Sm.) Vig.		1	1				1		1		3	1		
Arecaceae														
Chamaedorea pinnatifrons (Jacq.) Oerst.	1						1							
Chaemaedorea sp. (Indet13)	1													
Geonoma epetiolata H. E. Moore							1							
Pholidostachys pulchra H. Wendl. ex Burret					1									
Asteraceae														
Clibadium pittieri Greenm.		2												
Chloranthaceae														
Hedyosmum bonplandianum Kunth		2												
Hedyosmum costaricense C. E. Wood		1												
Hedyosmum scaberrimum Standl.		6												
Clusiaceae														
hrysochlamys nicaraguensis (Oerst., Planch. & Triana) Hemsl.					1									
Clusia cretosa Hammel					1									
Clusia gracilis Standl.		3			4	4							5	
Clusia palmana Standl.			1										4	
Clusia stenophylla Standl.		2			3	2							4	
Clusiella isthmensis Hammel	1													
Clusia sp. (Indet 14)[1]					2	2							1	
Clusiaceae *sp.* (Indet15)[1]													3	

Dilleniaceae														
Doliocarpus multiflorus Standl.				1						3				
Ericaceae														
Cavendishia capitulata Donn. Sm.		1												
Cavendishia complectens Hemsl.		2		2					1	1				
Cavendishia endresii Hemsl.		3						1	1					
Sphyrospermum buxifolium Poepp. & Endl.											1			1
Vaccinium orosiense Wilbur & Luteyn							1						1	
Ericaceae *sp.* (Indet16)[1]														1
Ericaceae *sp.* (Indet17)[1]		3												
Euphorbiaceae														
Hyeronima oblonga (Tul.) Mull. Arg.									2					
Tetrorchidium euryphyllum Standl.					1	1								
Gesneriaceae														
Besleria columneoides Hanst.		1												
Besleria notabilis C. V. Morton									2	2				
Columnea parviflora C. V. Morton													1	1
Drymonia sp. (Indet18)			1											
Gesneriaceae *sp.* (Indet19)[1]			1											
Marcgraviaceae														
Marcgravia caudata Triana & Planch.		3							1	1				
Marcgravia pittieri Gilg		1					1		1		1			
Melastomataceae														
Blakea anomala Donn. Sm.			1										4	
Blakea tuberculata Donn. Sm.	3	3										1	2	

Clidemia discolor (Triana) Cogn.							1							
Clidemia epiphytica (Triana) Cogn.		4	2									1		
Conostegia micrantha Standl.	7	72	8	8	1	4	10	8	11	3	9	2	9	4
Conostegia subcrustulata (Beurl.) Triana	1													
Conostegia xalapensis (Bonpl.) D. Don													1	
Henriettea tuberculosa (Donn. Sm.) L. O. William		16	1	1					1				2	
Leandra longicoma Cogn.		1												
Miconia argentea (Sw.) DC.		1							1					
Miconia centrodesma Naudin		5						3			1		1	
Miconia ligulata Almeda				4										
Miconia loreyoides Triana		3	1	2							2	1	4	
Miconia multiplinervia Cogn.		3	1											2
Miconia sp. (AB175)[2]				1										
Ossaea brenesii Standl.	3	17											3	1
Ossaea micrantha (Sw.) Macfad.		2		2									5	
Moraceae														
Ficus colubrinae Standl.		1							1					
Nyctaginaceae														
Neea amplifolia Donn. Sm.		1												
Neea sp. (AB74)[2]					1									
Nyctaginaceae *sp.* (indet20)[1]				1										
Phytolaccaceae														
Phytolacca rivinoides Kunth & Bouche							1							
Rubiaceae														

Hamelia patens Jacq.									1			1		
Palicourea gomezii C. M. Taylor				1			1							
Psychotria buchtienii (H. Winkl.) Standl.		6	1		1									
Psychotria cooperi Standl.		8	1				2							
Psychotria luxurians Rusby		5												
Solanaceae														
Witheringia solanacea L"Her.		1						1						
Viscaceae														
Phoradendron chrysocladon A. Gray								1						1
Seeds not identified to family[1]														
Indet1								1						
Indet2					1									
Indet3											1			
Indet4		1												
Indet5							1							1
Indet6						1								
Indet7		1			1									
Indet8									2	2				
Indet9									1					
Indet10											1			
Indet11		1												
Indet12		2												
arthropod taxa														
Spiders (Arachnida-Araneae)	X	X	X		X	X	X	X			X	X		

Wasps (Hymenoptera-Vespidae)	X			X	X
Ants (Hymenoptera-Formicidae)				X	
Flies (Diptera)		X	X		
Beetles (Coleoptera)				X	
Mantises (Dictyoptera-Mantodea)				X	

[1] All plant taxa with the word “indet” in name represent seeds from distinct morphospecies, in some cases identified either to family or genus.

[2] Seeds matched to plant taxa collected at our study sites (collection numbers of W. A. Boyle in parentheses), but collections not yet identified to species.

APPENDIX C

CAN VARIATION IN RISK OF NEST PREDATION EXPLAIN ALTITUDINAL MIGRATION IN TROPICAL BIRDS?

Can variation in risk of nest predation explain altitudinal migration in tropical birds?

W. Alice Boyle, Dept. of Ecology and Evolutionary Biology, University of Arizona,
alboyle@email.arizona.edu

Running title: Altitudinal migration and nest predation

Mailing address: Alice Boyle, Biological Sciences West Bldg., room 310, P.O. Box 210088, Tucson, AZ 85721-0088, alboyle@email.arizona.edu, tel (520) 624-8253, fax (520) 621-9190

Abstract

Migration is among the best-studied of animal behaviors, yet few empirical studies have tested hypotheses proposed to explain the ultimate causes of these cyclical annual movements. Fretwell's (1980) hypothesis predicts that if nest predation explains why many tropical birds migrate uphill to breed, then predation risk must be negatively associated with elevation. Data from 385 artificial nests spanning 2740 m of elevation show an overall decline in predation with increasing elevation. However, nest predation risk was highest at intermediate elevations (500–650 m), not at lowest elevations. The proportion of nests depredated by different types of predators differed among elevations. My results suggest that breeding areas of many altitudinal migrant birds are safer areas to nest than their non-breeding areas, suggesting that the role nest predation should be considered in future studies of altitudinal migration. However, elevational patterns of predation risk cannot explain why lowland birds migrate to mid-elevations to breed, implying that other processes likely influence the migratory patterns of lower-elevation birds.

Keywords**:** cloud forest, Costa Rica, elevational gradients, evolution of migration, nest predation, tropical rainforest

Introduction

Animals from all major vertebrate and many invertebrate lineages engage in annual migrations. These cyclical movements have long fascinated the scientific community and have been the subject of an extensive literature (Alerstam 1990; Dingle 1996). An overwhelming majority of the research on migration has sought to elucidate spatial patterns of migration and identify the proximate cues responsible for the initiation of annual migratory movements (Keast 1995; Gauthreaux 1996; Berthold 2001). In contrast, mechanistic hypotheses that explain why this behavior evolved have rarely been tested. Consequently, we still lack an understanding of the underlying ecological reasons why some species have evolved migratory movements, while others remain at a single site year-round.

In birds, migration is commonly explained as a response to temporal and spatial variation in food resources (Morton 1977; Alerstam and Enckell 1979; Chesser and Levey 1998; Alerstam et al. 2003). However, alternative explanations invoke variation in physiologically optimal climatic conditions (Ramos-Olmos 1983) or in quality of breeding sites. In particular, differences in the relative risk of nest predation among regions may be a factor promoting the evolution of migration (Fretwell 1980; Greenberg 1980). Fretwell (1980) proposed that birds migrate away from their non-breeding areas to minimize density-dependent risks of nest predation on their breeding grounds. Although variation in predation risk has been shown to influence many aspects of avian life-history strategies (e.g., Conway and Martin 2000; Martin et al. 2000; Ghalambor and Martin 2001), few studies have examined the role of nest predation in shaping avian migratory behavior.

Bird migration occurs over a range of spatial scales. Short distance migrations such as altitudinal migrations are common, especially among tropical bird species. Altitudinal migration involves annual movements of all or many individuals in a population between breeding and non-breeding grounds that differ in elevation. Most migrants breed at higher elevations than where they spend their non-breeding season, despite considerable variation in the elevational ranges occupied by each species (Pearson 1980; Ramos-Olmos 1983; Rabenold and Rabenold 1985; Laymon 1989; Loiselle and Blake 1991; Cardoso da Silva 1993; Johnson and Maclean 1994; Burgess and Mlingwa 2000; Solórzano et al. 2000). For example, in Costa Rica, approximately 30% of bird species breeding in Atlantic slope forests migrate altitudinally (Stiles 1983), and roughly 85% of these altitudinal migrant species migrate uphill to breed.

As with latitudinal migration, spatial and temporal variation in food resources has often been invoked to explain altitudinal migration (Loiselle and Blake 1991; Solórzano et al. 2000; Chaves-Campos et al. 2003). However, results of several studies provide mixed support for a food-based explanation for observed migration patterns. For example, Chaves-Campos (2004) reported no relationship between food resources and bird abundance of two species of altitudinal migrant birds in Costa Rica. Additionally, *Cephalopteris glabricollis* migrated away from breeding areas before food abundance peaked, and temporal patterns of *C. glabricollis* abundance at lower elevations correlated poorly with food abundance (Chaves-Campos et al. 2003). Likewise, Rosselli (1994) found that *Corapipo altera* left breeding elevations during months of peak fruit abundance and returned to breed during months of fruit scarcity. Finally, although Loiselle and Blake (1991) found peaks in the community-level abundance of frugivores that were temporally correlated with peak fruit abundance at each of three elevations, examination of their results show that birds are not migrating from elevations with lower relative fruit abundance to elevations with higher relative fruit abundance. Despite the inconsistencies between predicted and observed relationships between food resources and bird movements, no other hypotheses explaining altitudinal migration have yet been tested. Spatial variation in predation risk is one of the primary alternative explanations for altitudinal migration (Loiselle and Blake 1991).

If variation in predation risk explains altitudinal migration in the manner proposed by Fretwell (1980), the pattern of uphill migration to breeding sites predicts that the risk of predation decreases with increasing elevation. While support for this prediction would not eliminate alternative hypotheses, a pattern of elevational decline in nest predation risk is critical to the predation hypothesis. Thus, testing this prediction is an efficient first step in testing the Fretwell (1980) hypothesis because failure to support this prediction could eliminate nest predation as a factor influencing altitudinal migration.

Support for the prediction of a negative relationship between elevation and nest predation comes from Skutch (1985) who reported a linear decline in nest predation with increasing elevation in the Neotropics (Fig. 1). However, several problems with Skutch's (1985) data make conclusions tenuous. For example, Skutch (1985) calculated the proportion of successful nests based on an average of only 1.7 nests per species and 67 nests per site. Using different species to compare relative nest predation risk across elevational gradients is problematic because species vary widely in risk of nest predation due to differences in nesting substrate and parental behavior (Martin 1993; Conway and Martin 2000). Moreover, Skutch's (1985) six sites, ranging from Panamá to Guatemala, were not adjacent to each other. The lowest elevation site, (Barro Colorado Island, 88 m) was a man-made island in the Panama Canal Zone, whereas all the other sites were mainland. Finally, the six sites varied dramatically in degree of anthropogenic disturbance, ranging from old-growth forest (Montaña Azul, 1687 m) to banana plantations (Motagua Valley, 150 m) and cattle pastures (Los Cartagos, 2132 m). Because of these problems, comparisons in nest predation risk along a contiguous elevational gradient are needed to more adequately test the nest predation hypothesis. Skutch (1985) proposed a mechanism for the pattern of decreasing in nest predation with increasing elevation that he presented, noting that nest predators (in particular, snakes) seemed to be more abundant at low than high elevations. Thus far, no evidence has been published to support Skutch's (1985) claim of decreasing snake abundance with increasing elevation in the tropics. Furthermore, snakes are not the only predators of eggs and nestlings in the Neotropics; both mammals and birds are important predators of tropical bird nests (Robinson and Robinson 2001). Little is known about how the species responsible for nest predation vary along tropical altitudinal gradients.

A meta-analysis might provide one way to test Fretwell's (1980) nest predation hypothesis and validate Skutch's (1985) results. However, insufficient nest predation data are available in the literature with which to examine whether nest predation risk varies with altitude in tropical regions. A more direct approach to testing the nest predation hypothesis involves controlled field experiments. Here I test a critical component of the Fretwell (1980) hypothesis by conducting a nest predation experiment using artificial nests to understand how relative predation risk varies along an altitudinal gradient within the humid tropics. Specifically I asked the following questions: (1) What is the elevational pattern of predation on artificial nests along an elevational gradient in Costa Rica?; (2) Is that pattern consistent with the hypothesis that birds migrate uphill to reduce their risk of nest predation?; and (3) Are elevational patterns of nest predation related to elevational changes in the types of nest predators?

Materials and Methods

I worked on the Atlantic slope of the central volcanic cordillera of Costa Rica on a single, continuous, altitudinal gradient of tropical forest. Protected forest extends from 30 m above sea level at La Selva Biological Station to 2906 m at the summit of Barva volcano in Braulio Carrillo National Park, and includes the private reserves of Rara Avis and Selva Tica (Fig. 2). At approximately 9º 30’ N, seasonal fluctuations in temperature and day length are small. Rainfall peaks geographically in premontane forest between 500 and 800 m, and peaks seasonally from May–August, and again from November–December (meteorological data from Rara Avis, La Selva, Instituto Meteorológico Nacional, and Instituto Costarricense de Electricidad). Mean annual rainfall is very high, ranging from 3000–4000 mm/year (at both highest and lowest elevations) to > 8000 mm/year at Rara Avis. Seasonal patterns of rainfall and temperature are similar over the entire elevational gradient (Gómez and Herrera 1986).

I placed nests over the largest altitudinal range possible, from the base of the mountains to within 130 m of the peak of Barva volcano. All sites were located in “old-growth” forest, defined here as forests not known to have been disturbed by logging activities, and classified as primary forest based on regional satellite imagery and land-use maps. I placed 385 nests at the following eight sites (Fig. 2): two locations at La Selva (40 m elevation and 120 m elevation; lowland forest), Quebrada Gonzalez, Selva Tica, and Rara Avis (500 m, 650 m, and 820 m, respectively; premontane forest), and Puesto Zurquí, Chateau Barva, and Puesto Barva (1650 m, 2050 m, and 2780 m, respectively; montane cloud forest). I placed 50 nests at each site except at 2050 m, where I placed 35 nests. I placed all 385 nests over eight consecutive days, and monitored nests over the subsequent two weeks, returning to each site in the same sequence as nests were originally placed. The experiment ran from 3–24 May 2004. Over 80% of the birds in this region breed during May (Stiles and Skutch 1989).

At each site, I placed nests along two 250 m transect lines that were separated by at least 100 m. I chose the location and direction of these lines based on digital elevation models and GIS land-use coverages to maintain a relatively uniform elevation along each transect line. All transect lines were located > 0.5 km from all roads, and > 20 m from all trails. I placed nests > 5 m from the transect line, alternating to the left and right along the line at 10 m intervals. I then chose the nearest understory tree or shrub that I judged capable of supporting a small open-cup nest.

I constructed artificial nests from small baskets of woven bark strips covered inside and out with moss designed to mimic nests of understory open-cup nesting passerines that breed in this region of Costa Rica (e.g., *Tanagara icterocephala, Chlorothraupis carmioli, Myadestes melanops*). I attached nests to trees 1–2 m above the ground using black wire, then adorned nests with small epiphytes, leaf skeletons, twigs, and rootlets collected from the vicinity of the nest site. I attempted to locate and camouflage the artificial nests to closely resemble real nests, based on photos, descriptions, and personal observations of nests of understory open-cup nesting passerines in tropical wet forest. In each nest, I placed one infertile canary egg and one plasticine (soft modeling clay) egg. Both eggs were the same size and color and were similar in size to eggs of the species listed above (~20 mm long and ~15 mm diameter). I used small canary eggs rather than much larger quail eggs often used in artificial nest experiments because canary eggs may attract a more realistic range of nest predator sizes (Rangen et al. 2000). Baiting nests with both real and plasticine eggs is a useful approach: the real egg may attract olfactory-hunting predators because their odors more closely resemble wild bird eggs than do artificial eggs (Pärt and Wretenberg 2002), and the plasticine egg often retains the tooth, bill, or claw marks of the nest predator.

I checked nests after one week (day 6, 7 or 8) and again after two weeks (day 13, 14, or 15). I considered the nest to have been depredated if either the canary egg, the plasticine egg, or both eggs had been attacked or were missing from the nest. When either egg had disappeared from a nest, I carefully searched the ground in a radius of approximately 3 m surrounding the nest for fragments of eggshell or plasticine. I removed any depredated nests after the first nest check, and removed all nests after the second check. I inspected damaged plasticine eggs for signs of bill or tooth marks to determine the type of predator responsible for attacking the nest. Mammologists and herpetologists at La Selva Biological Station and the University of Arizona confirmed my identification of mammalian and reptile marks. To verify some unusual marks on plasticine eggs found in nests, I presented captive lizards and bullet ants (*Paraponera*) with plasticine eggs and compared resulting marks to marks found on eggs in nests.

I used logistic regression to model the relationship between nest success and elevation, treating elevation as a continuous variable. To test whether the relationship between elevation and risk of nest predation was better described by a polynomial model than a linear model, I used a likelihood ratio test to assess if the quadratic term (elevation^2) better described the patterns in my data than the linear model. To account for slight differences among sites in the number of days between nest checks, I also calculated daily survival probability for each site (Johnson 1979). I constructed linear and polynomial regression models using 1 – daily survival probability (daily predation probability) as the response variable and elevation as the explanatory variable. To compare the relationship between elevation and the proportion of nests depredated in this study with the relationship documented by Skutch (1985), I used daily survival probabilities to standardize the proportion of nests depredated to 14 days. This was the median number of days my nests were exposed and falls within the range of incubation duration for understory passerines in this region. I then combined the standardized proportions with the proportions reported by Skutch (1985) in a single ANOVA model and tested whether the slope of the relationship between predation and elevation differed between the two datasets by including an elevation*dataset interaction term in the model.

To determine if predator type differed by site, I conducted contingency table analyses, grouping predators into taxonomic categories (birds, mammals, snakes, and ants) that also correspond to the sensory modality used in locating prey. Using plasticine eggs to estimate the relative importance of different nest predators undoubtedly underestimates the incidence of predation by snakes (Weatherhead and Bloun-Demers 2004). Because snakes swallow prey whole, nests depredated by snakes will probably result in disappearance of the entire canary egg. If lower elevation sites suffer from proportionately more snake predation as Skutch (1985) proposed, then the number of canary eggs that disappear from nests should decrease with increasing elevation. I evaluated this prediction by plotting the proportion of all nests at each elevation from which the canary egg disappeared completely and around which I found no eggshell fragments.

Results

Overall, predation risk declined with increasing elevation (Fig. 3). I found strong evidence for a linear relationship between likelihood of nest predation and elevation (likelihood ratio test, $\chi^2 = 9.8$, $P = 0.002$) that closely resembled the relationship presented by Skutch (1985). The slope of the linear fit of the proportion of nests depredated at each elevation (standardized to 14 days; –0.057 per 1000 m, SE = 0.018), did not differ statistically from the slope of the linear fit of Skutch's data (–0.089 per 1000 m, SE = 0.037; $t = 0.9$, $P = 0.408$). Although the highest daily probability of predation was at 500 m rather than at the two lowland sites at 30 and 120 m (Fig. 3), the relationship between the likelihood of nest predation and elevation was not well described by a curvilinear fit (likelihood ratio test, $\chi^2 = 1.1$, $P = 0.296$). Both linear ($F_{1, 7} = 4.8$, $P = 0.070$, $R^2 = 0.446$) and polynomial ($F_{2, 6} = 4.5$, $P = 0.075$, $R^2 = 0.645$)

regression models provided comparable fits to the daily predation probability data. However, I found little evidence that the polynomial model improved the fit to these data over the linear model ($t = -1.8$, $P = 0.139$).

Only 9% of nests were not attacked during the two-week experiment. Nest predators marked plasticine eggs in 80% of depredated nests (Table 1). In 14% of nests the canary egg was damaged or taken and the plasticine egg remained intact. The plasticine egg disappeared entirely in 4% of the nests. Birds left more marks in plasticine eggs than any other predator group. Of the nests to which a predator could be assigned ($n = 196$), birds attacked 59%, mammals attacked 36%, and snakes and bullet ants combined attacked 5% of the nests. Mammalian tooth marks included dentition patterns of both marsupials and rodents.

The relative incidence of attack by predator groups differed among elevations for nests to which I could assign a predator type (likelihood ratio test, $\chi^2 = 59.8$, $P < .0001$). Bird attacks were most common at 650 m, whereas mammal attacks were most common at 1650 m (Fig. 4). Canary egg disappearance did not decrease with elevation (linear regression, $t = 0.8$, $P = 0.445$, $R^2 = 0.100$). The highest incidence of canary egg disappearance was at 1650 m. I found no relationship between elevation and incidence of unknown marks (linear regression, $t = -0.4$, $P = 0.681$, $R^2 = 0.030$).

Discussion

The results of this study generally support the prediction of declining nest predation risk with elevation, consistent with the hypothesis that spatial variation in nest predation risk promotes altitudinal migration. Many migrant species (56.5% of those breeding in the region) spend their non-breeding season in forests with higher relative nest predation risk as estimated from this study, moving uphill to breed in safer higher-elevation forests. However, the highest risk of nest predation in this region of Costa Rica seems to be at 500 and 650 m in premontane forests, not in lowland forests. Consequently, species that migrate from forests below 300 m to breed in premontane forests are actually migrating to the elevations of highest predation risk on the entire gradient. Roughly 26% of Costa Rican altitudinal migrant species exhibit such migration patterns, breeding wholly or partly between 400 m and 800 m, and spending their non-breeding season wholly or partly below 300 m (Stiles and Skutch 1989; Loiselle and Blake 1991; W. A. Boyle, unpublished data). Thus, the relative risk of nest predation among elevations is consistent with the migration patterns of much of the avifauna, but additional factors such as temporal and spatial variation in food resources and climate must also contribute to explaining the impetus for altitudinal migration in this region.

I propose a potential explanation for the lower-than-expected nest predation risk I observed at lowland sites. Predation risk in lowland forest may have recently declined due to anthropogenic disturbance. In contrast to forests above 700 m, lower elevations in this region have experienced high levels of deforestation and fragmentation since the mid-1900's (Butterfield 1994; Read et al. 2001). Sigel et al. (2006) provide evidence for losses of understory bird species at La Selva Biological Station over the past 40 years. Potentially, lowland forests have also lost many avian nest predators, implying that 40–50 years ago (before much of the recent land-use change occurred) daily predation probabilities at lowland sites may have equaled or exceeded those of premontane sites.

Because predation is the major cause of nest failure in birds (Ricklefs 1969), natural selection should favor nest locations and parental behavior that minimize the risk of nest predation. Differences in the predominance of bird and mammalian predation among elevations imply that selective pressures imposed by visual vs. olfactory predators probably change along this elevational gradient. The results of this study predict that at lower elevations where visual predators (birds) depredate most nests, there should be stronger selection for nest crypsis and inconspicuous parental behavior. At higher elevations where olfactory nest predators (mammals) predominate, there should be stronger selection for nest placement in sites inaccessible to non-volant vertebrates.

A recent review (Moore and Robinson 2004) critiqued the use of artificial nests based on evidence that artificial nests often fail to reveal the same patterns of relative predation risk among sites as real nests (e.g., Burke et al. 2004). Artificial nests differ in important ways from natural nests, including lacking parents who may provide additional camouflage or defend nests from predators, decreasing the probability of nest depredation (Major and Kendal 1996). Additionally, artificial nest studies estimate relative risk of egg predation; the actual risk of nest predation extends beyond the egg stage through hatching and fledging. Thus, the inferences that can be drawn from studies of nest predation using artificial nests are clearly limited. Yet critics of artificial nests acknowledge that (i) data from artificial nests are better than no data (Faaborg

2004), and (ii) in landscape-scale studies where multiple species are involved, the use of real nests is often impractical (Villard and Pärt 2004).

The results of this study provide valuable information for a number of reasons. First, very few preliminary data are available with which to justify the intensive nest searching and monitoring necessary to conduct such a study of this geographic scale using real bird nests. Second, realistic nest construction, nest placement, and use of appropriately-sized real eggs yield results that may better approximate patterns of predation on real nests than do other artificial nest experiments (Davison and Bollinger 2000). Finally, and most importantly, artificial and real nests may provide different kinds of information about how predation risk varies across biological gradients. Studies monitoring real nests estimate predation risk after local adaptation to the biological landscape has already occurred. However, predation on artificial nests may better estimate the relative risk among sites for naïve species whose nest placement, design, and parental behavior have not already been shaped by local selective pressures (i.e., a population that is becoming migratory). Although the former approach may be preferable for applied studies of nest success across disturbance gradients, the latter may be more appropriate for understanding why traits such as bird migration evolved.

Two approaches will be required to further our understanding of how nest predation risk varies altitudinally. First, we need replication among elevational gradients across the Neotropics to establish the generality of the results presented here and to determine if lower-than-expected predation on lowland nests is attributable to anthropogenic factors. Unfortunately, few forested elevational gradients remain in the

Neotropics that would permit such large-scale replication. Second, we need to corroborate these elevational patterns of relative predation risk using real bird nests. The tremendous difficulties of locating sufficient nests in wet tropical forests and the desirability of controlling for nest characteristics suggest that among-elevation comparisons within a species over smaller elevational ranges will be the best approach to use.

My results suggest that altitudinal variation in predation risk and the migration patterns of many altitudinal migrant species are consistent with Fretwell's (1980) hypothesis explaining how predation risk could influence migration, implying that further predictions of the nest predation hypothesis merit testing. For example, future comparative work could examine nesting correlates of migratory behavior. Because nest types differ in their vulnerability to predation (e.g., open cup nests, cavity nests, etc.), then migrant taxa should be over-represented among lineages whose species construct nests most susceptible to predation. An additional prediction this hypothesis makes is that within migrant species that nest over a range of elevations, those breeding at higher elevations should experience greater nesting success than those at lower elevations. Clearly further tests of this and alternative hypotheses will be necessary to conclude which ecological factors are of greatest importance in explaining why some birds migrate.

My data from a single forested Neotropical altitudinal gradient also generally corroborate the pattern first described by Skutch (1985) based on data from sites located throughout Central America. However, the current relationship between predation risk and elevation may not be strictly linear. To improve our knowledge of how nest predation shapes the behaviors and distributions of tropical birds, we will need more detailed studies of reproductive success of tropical birds across elevational gradients and replication at the landscape scale. To better understand the factors promoting the evolution of altitudinal migration, future studies should acknowledge that a single factor may not explain the patterns of all migrant species, and that species-specific tests of multiple hypotheses will be required to explain migratory behavior.

Acknowledgments

I owe sincere thanks to M. Burke, J. Brokaw, M. Lord, R. Repasky, and J. Wolfe for incredibly hard work in the field. C. Conway, J. Bronstein, B. Enquist, D. Papaj, R. Steidl, K. Borgmann, B. Boyle, K. Hughes, and the Conway and Bronstein lab groups provided valuable suggestions during the planning of this project and criticism of earlier drafts of this manuscript. C. Valldeperas and his canaries donated 500 eggs. Emilia resolved a nest crisis with exceptional good nature. B. Hammel rented me his car cheap, and D. B. and D. A. Clark kept me sane. J. Losos, M. Nachman, and M. Williams helped with imprint ID. The directors and staff of Braulio Carrillo National Park, La Selva Biological Station, Rara Avis, and Selva Tica granted permission to work on their land and provided logistical support. J. Guevara at MINAE processed all permit applications and R. Tenorio granted permission to work in the ACCVC. Grants and fellowships from NSF (DDIG DEB-0410531), NSERC (PGS-B fellowship), the Silliman Award, the Center for Insect Science, and the Dept. of EEB at the University of Arizona helped finance field work.

References

Alerstam T (1990) Bird Migration, English edn. Cambridge University Press, Cambridge

Alerstam T, Enckell PH (1979) Unpredictable habitats and evolution of bird migration. Oikos 33:228-232

Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103:247-260

Berthold P (2001) Bird Migration: A General Survey, Second edn. Oxford University Press, Oxford, UK

Burgess ND, Mlingwa COF (2000) Evidence for altitudinal migration of forest birds between montane Eastern Arc and lowland forests in East Africa. Ostrich 71:184-190

Burke DM et al. (2004) Patterns of nest predation on artificial and natural nests in forests. Conservation Biology 18:381-388

Butterfield RP (1994) The regional context: land colonization and conservation in La Selva. In: McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS (eds) La Selva: Ecology and Natural History of a Neotropical Rain Forest. The University of Chicago Press, Chicago, IL, pp 299-306

Cardoso da Silva JM (1993) The Sharpbill in the Serra dos Carajás, Para, Brazil, with comments on altitudinal migration in the Amazon Region. Journal of Field Ornithology 64:310-315

Chaves-Campos J (2004) Elevational movements of large frugivorous birds and temporal variation in abundance of fruits along an elevational gradient. Ornitología Neotropical 15:433-445

Chaves-Campos J, Arévalo JE, Araya M (2003) Altitudinal movements and conservation of Bare-necked Umbrellabird *Cephalopteris glabricollis* of the Tilarán Mountains, Costa Rica. Bird Conservation International 13:45-58

Chesser RT, Levey DJ (1998) Austral migrants and the evolution of migration in New World birds: diet, habitat and migration revisited. American Naturalist 152:311-319

Conway CJ, Martin TE (2000) Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. Evolution 54:670-685

Davison WB, Bollinger E (2000) Predation rates on real and artificial nests of grassland birds. Auk 117:147-153

Dingle H (1996) Migration: the Biology of Life on the Move. Oxford University Press, NY

Faaborg J (2004) Truly artificial nest studies. Conservation Biology 18:269-370

Fretwell SD (1980) Evolution of migration in relation to factors regulating bird numbers. In: Keast A, Morton ES (eds) Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC, pp 517-527

Gauthreaux SA, Jr. (1996) Bird migration: methodologies and major research trajectories (1945-1995). Condor 98:442-453

Ghalambor CK, Martin TE (2001) Fecundity-survival trade-offs and parental risk-taking in birds. Science 292:494-497

Gómez LD, Herrera W (1986) Vegetación y Clima de Costa Rica, 1st edn. Editorial

Universidad Estatal a Distancia, San José, Costa Rica

Greenberg R (1980) Demographic aspects of long-distance migration. In: Keast A, Morton ES (eds) Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC, pp 493-504

Hensler GL, Nichols JD (1981) The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93:42-53

Johnson DH (1979) Estimating nest success: the Mayfield method and an alternative. Auk 96:651-661

Johnson DN, Maclean GL (1994) Altitudinal migration in Natal. Ostrich 65:86-94

Keast A (1995) The nearctic-neotropical bird migration system. Israel Journal of Zoology 41:455-470

Laymon SA (1989) Altitudinal migration movements of Spotted Owls in the Sierra Nevada, California. Condor 91:837-841

Loiselle BA, Blake JG (1991) Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72:180-193

Major RE, Kendal CE (1996) The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. Ibis 138:298-307

Martin TE (1993) Nest predation among vegetation layers and habitat types: revising the dogmas. American Naturalist 141:897-913

Martin TE, Martin PR, Olson CR, Heidinger BJ, Fontaine JJ (2000) Parental care and clutch sizes in North and South American birds. Science 287:1482-1485

Moore RP, Robinson WD (2004) Artificial bird nests, external validity, and bias in ecological field studies. Ecology 85:1562-1567

Morton ES (1977) Intra-tropical migration in Yellow-green Vireo and Piratic Flycatcher. Auk 94:97-106

Pärt T, Wretenberg J (2002) Do artificial nests reveal relative nest predation risk for real nests? Journal of Avian Biology 33:39-46

Pearson DL (1980) Bird migration in amazonian Ecuador, Peru, and Bolivia. In: Keast A, Morton ES (eds) Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC, pp 273-283

Rabenold KN, Rabenold PP (1985) Variation in altitudinal migration, winter segregation, and site-tenacity in two subspecies of Dark-eyed Juncos in the southern Appalachians. Auk 102:805-819

Ramos-Olmos MA (1983) Seasonal movements of bird populations at a Neotropical study site in Southern Veracruz, Mexico. PhD dissertation, University of Minnesota, Minneapolis, MN.

Rangen SA, Clark RG, Hobson KA (2000) Visual and olfactory attributes of artificial nests. Auk 117:136-146

Read JM, Denslow JS, Guzman SM (2001) Documenting land-cover history of a humid tropical environment in northeastern Costa Rica using time-series remotely sensed data. In: Millington AC, Walsh SJ, Osborne PE (eds) GIS and Remote Sensing Applications in Biogeography and Ecology. Kluwer Academic Publishers, Boston, pp 69-89

Ricklefs RE (1969) An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48

Robinson WD, Robinson TR (2001) Observations of predation events at bird nests in central Panama. Journal of Field Ornithology 72:43-48

Rosselli L (1994) The annual cycle of the White-ruffed Manakin, *Corapipo leucorrhoa*, a tropical frugivorous altitudinal migrant, and its food plants. Bird Conservation International 4:143-160

Sigel BJ, Sherry TW, Young BE (2006) Avian community response to lowland tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. Conservation Biology 20:111-121

Skutch AF (1985) Clutch size, nesting success, and predation on nests of neotropical birds, reviewed. In: Buckley PA, Foster MS, Morton ES, Ridgely RS, Buckley FG (eds) Neotropical Ornithology, vol 36. The American Ornithologists' Union, Washington, DC, pp 575-594

Solórzano S, Castillo S, Valverde T, Avila L (2000) Quetzal abundance in relation to fruit availability in a cloud forest of southeastern Mexico. Biotropica 32:523-532

Stiles FG (1983) Birds. In: Janzen DH (ed) Costa Rican Natural History. University of Chicago Press, Chicago, IL, pp 502-530

Stiles FG, Skutch AF (1989) A Field Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, NY

Villard MA, Pärt T (2004) Don't put all your eggs in real nests: a sequel to Faaborg. Conservation Biology 18:371-372

Weatherhead PJ, Bloun-Demers G (2004) Understanding avian nest predation: why ornithologists should study snakes. Journal of Avian Biology 35:185-190

Tables and Figures

Table 1

Summary of nest fates along an elevational gradient in Costa Rica. I considered a nest to have been depredated if either one or both eggs were damaged or removed. Results are based on 375 nests; nine nests were lost due to flooding and one nest was accidentally destroyed.

Nest fate	Number of nests	% of all nests
Neither egg attacked	35	9.3
Plasticine egg removed	15	4.0
Only canary egg attacked	51	13.6
Avian marks on plasticine egg	115	30.7
Mammalian marks on plasticine egg	71	18.9
Snake marks on plasticine egg	5	1.3
Ant marks on plasticine egg	5	1.3
Unknown marks on plasticine egg	78	20.8

Figure legends

Figure 1 Relationship between elevation and proportion of nests depredated from six Neotropical sites, redrawn from Skutch (1985). Points in the figure represent mean proportion of depredated nests at each site, and sample sizes refer to the number of nests (number of species) used to calculate means. Sites and their elevational ranges include: 25–125 m, Barro Colorado Island (BCI), Panamá; 60–240 m, Motagua Valley (MV), Guatemala; 610–700 m, El General (EG), Costa Rica; 1525–1830 m, Montaña Azul (MA), Costa Rica; 1980–2285 m, Los Cartagos (LC), Costa Rica; 2440–3050 m, Sierra de Tecapán (SDT), Guatemala. Sites are plotted at the median elevation from the range provided in Skutch (1985).

Figure 2 Location and elevation of eight study sites on the Atlantic slope of Costa Rica: 40 m and 120 m, La Selva Biological Station; 500 m, near the Quebrada Gonzalez ranger station in Braulio Carrillo National Park (BCNP); 650 m, Selva Tica reserve; 820 m, Rara Avis reserve; 1650 m, near the Puesto Zurquí ranger station, BCNP; 2050 m, near the Chateau Barva refuge in BCNP; 2780 m, near the peak of Barva volcano, BCNP.

Figure 3 Relationship between elevation and daily probability of nest predation for 375 nests placed at eight sites ranging in elevation from 40 m to 2780 m. Daily probability of nest predation is calculated as 1 – daily survival probability. Error bars represent the SE of the maximum likelihood estimator (Johnson 1979; Hensler and Nichols 1981). The right-hand y-axis represents the proportion of nests depredated standardized to 14 days at each site using daily survival probability to enable direct comparison with Figure 1.

Figure 4 Relationship between elevation and proportion of nests depredated by birds (black circles) and mammals (gray circles). Values represent the proportion of all nests placed at a site where the plasticine egg bore either bill marks or tooth marks.

Figure 1

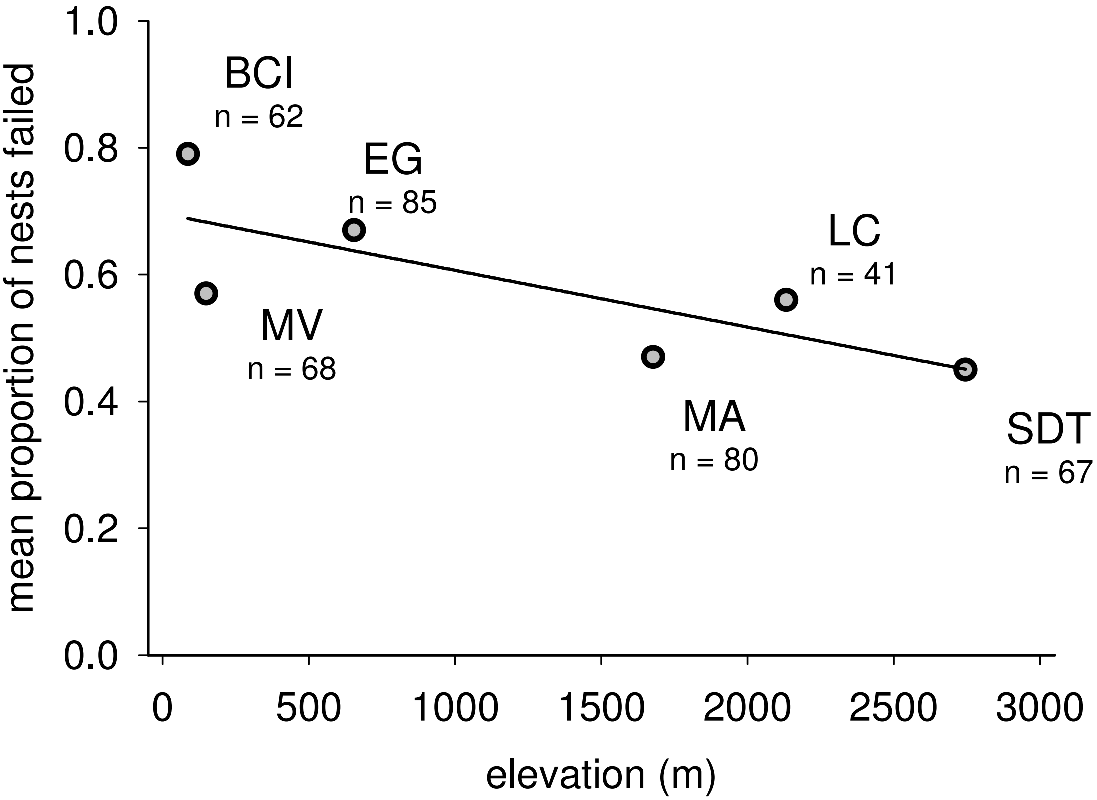

1.0
0.8
0.6
0.4
0.2
0.0
mean proportion of nests failed
0
500
1000
1500
2000
2500
3000
elevation (m)
BCI
n = 62
EG
n = 85
MV
n = 68
MA
n = 80
LC
n = 41
SDT
n = 67

Figure 2

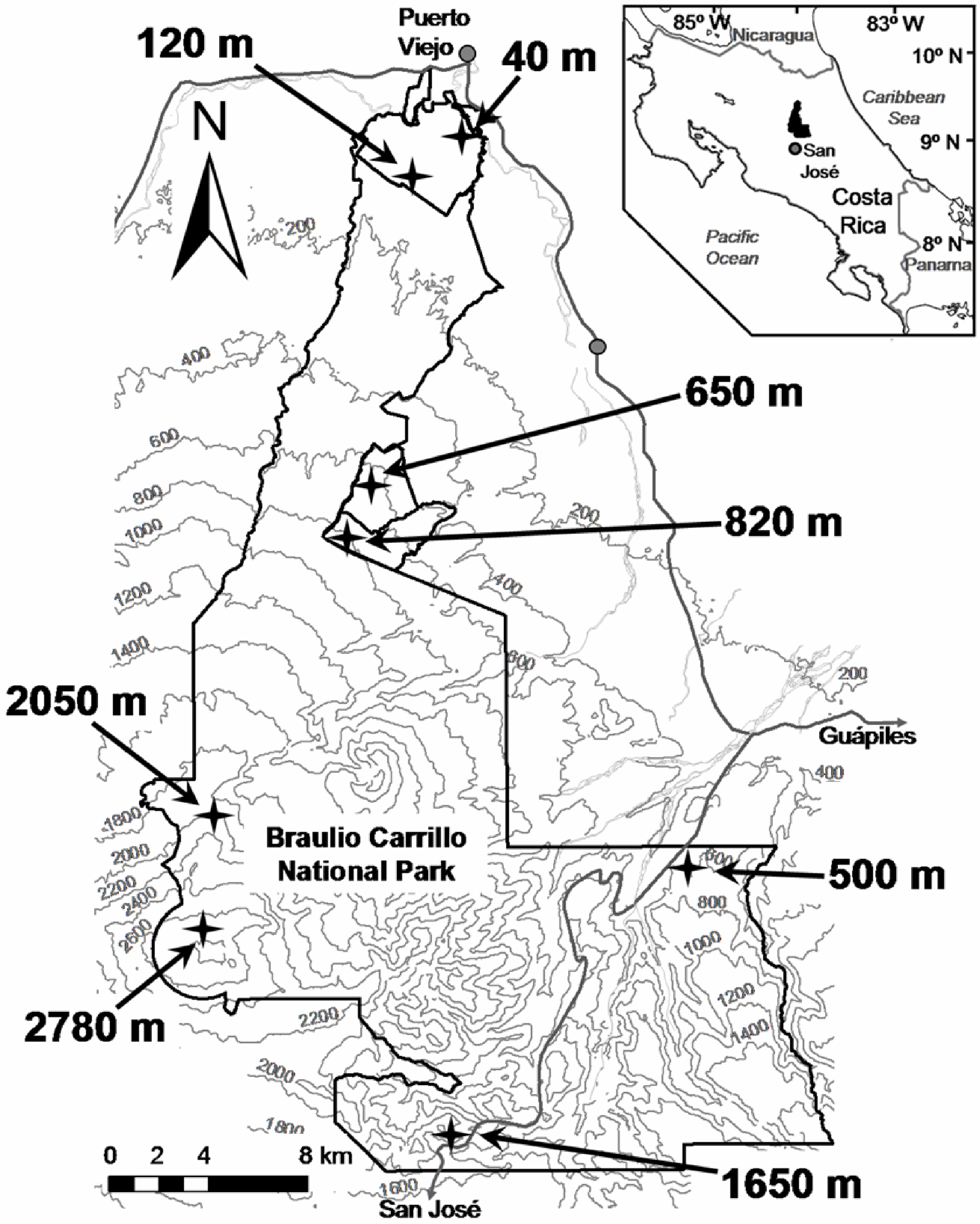

Puerto Viejo
120 m
40 m
N
650 m
820 m
2050 m
Braulio Carrillo National Park
500 m
2780 m
1650 m
Guápiles
San José
0 2 4 8 km
200
400
600
800
1000
1200
1400
1800
2000
2200
2400
2600
1600
85° W
83° W
10° N
9° N
8° N
Nicaragua
Caribbean Sea
San José
Costa Rica
Pacific Ocean
Panama

Figure 3

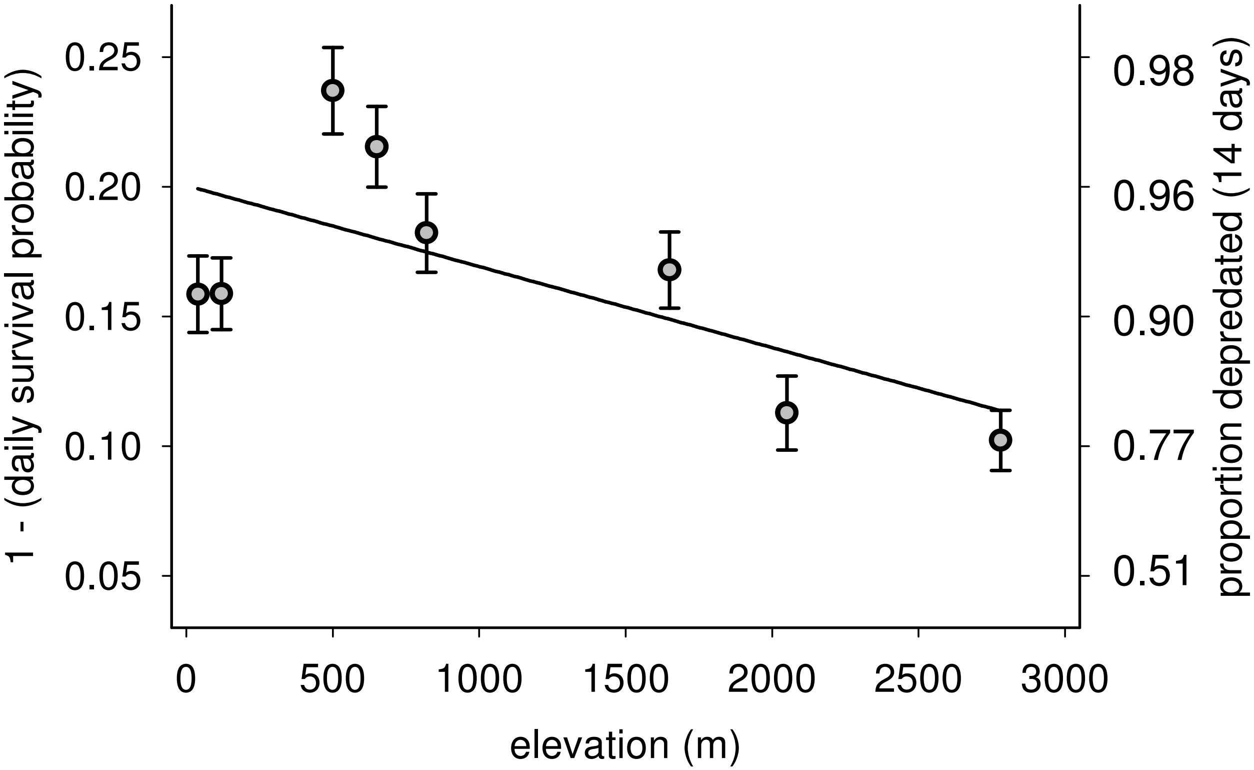
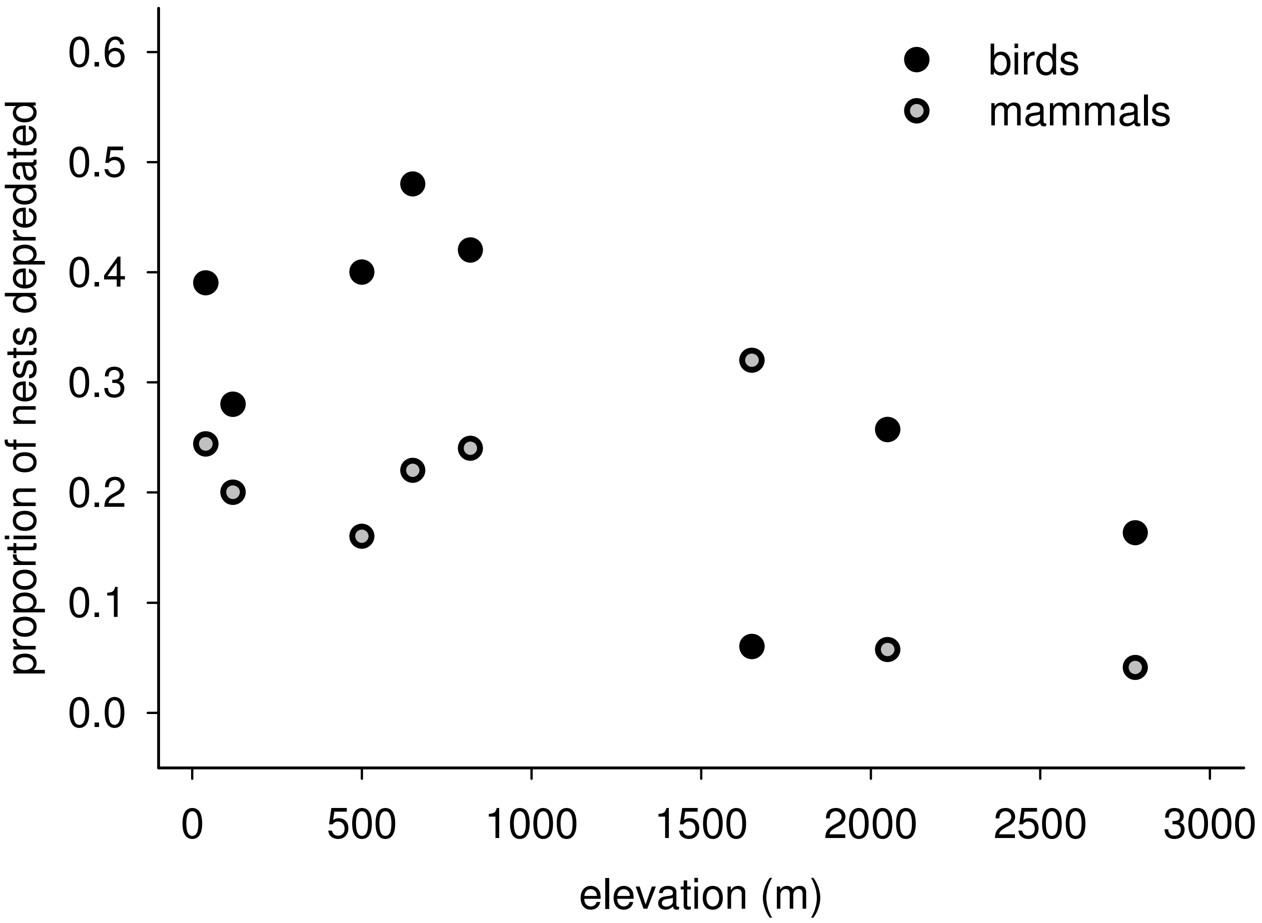

0.25
0.20
0.15
0.10
0.05
1 - (daily survival probability)
0.98
0.96
0.90
0.77
0.51
proportion depredated (14 days)
0
500
1000
1500
2000
2500
3000
elevation (m)

Figure 4


birds
mammals
proportion of nests depredated
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0
500
1000
1500
2000
2500
3000
elevation (m)

APPENDIX D

EXTRINSIC AND INTRINSIC FACTORS EXPLAINING ALTITUDINAL MIGRATION IN A TROPICAL BIRD

Extrinsic and intrinsic factors explaining altitudinal migration in a tropical bird

W. Alice Boyle, Dept. of Ecology and Evolutionary Biology, University of Arizona,
alboyle@email.arizona.edu

Key words: altitudinal migration, arrival time, arthropod availability, body size, *Corapipo altera*, dominance, elevational gradient, evolution of migration, frugivory, fruit productivity, partial migration, Pipridae, sex ratio, standing crop, tropical forest

Abstract

Many animals undergo annual migrations. These movements are well-studied at proximate levels, but their fundamental causes are poorly understood. Among tropical frugivorous birds, annual migration is generally thought to have evolved in the context of exploiting reciprocal peaks in fruit abundance among locations and seasons. Previous tests of this reciprocal fruit abundance hypothesis have yielded equivocal results, but have (1) used inappropriate metrics for comparing fruit production among locations and seasons, (2) failed to adequately explain why some but not all individuals migrate, and (3) not tested alternative hypotheses. In this paper, I tested two hypotheses based on fruit limitation and protein limitation to explain both uphill and downhill migratory movements in a Costa Rican understory frugivorous bird, the White-ruffed Manakin (*Corapipo altera*). I also examined variation in migratory behavior at the individual level by comparing diets, sex ratios, and body conditions of *C. altera* at three different elevations throughout the year. My results are consistent with the hypothesis that *C. altera* migrate uphill (but not downhill) to exploit seasonal and spatial peaks in fruit availability, and are inconsistent with the protein limitation hypothesis. The apparent lack of food limitation during the non-breeding season at breeding elevations, combined with evidence for sex-biased migration, differences between sexes in body condition of migrants and residents, and rainfall patterns suggests that foraging limitation explain could explain the downhill portion of the migratory cycle. This study provides the first empirical test of the protein limitation hypothesis, provides novel data on the degree of temporal and spatial variation in both fruit and arthropods over the

course of the year along an elevational gradient in the tropics, and demonstrates that standing crop is a poor surrogate for fruit production rates when evaluating hypotheses proposed to explain the evolution of migration (or any other behavior). Most importantly, this study is the first to provide a conceptual and empirical link between interspecific and intraspecific explanations for migratory behavior in birds.

Introduction

Many species of animals migrate between breeding and non-breeding areas every year, profoundly affecting the diversity, composition, and biotic interactions of the communities they move between (Keast and Morton 1980, Hagan and Johnston 1992, Dingle 1996, Greenberg and Salewski 2005). Despite the ubiquity of animal migration and a profusion of theory explaining how (Lundberg 1988, Kaitala et al. 1993, Joseph et al. 1999, Loxdale and Lushai 1999, Bell 2000, Zink 2002, Rappole et al. 2003) and why (Cox 1968, Fretwell 1980, Greenberg 1980, Ketterson and Nolan 1983, Cox 1985, Levey and Stiles 1992, Gatehouse 1994, Alerstam et al. 2003) migratory behavior evolved, relatively few empirical studies have tested predictions made by these hypotheses. Consequently, even in relatively well-studied groups such as birds we have a poor understanding of which ecological processes are the most important in influencing whether or not an animal migrates. Within birds, much of the difficulty in studying the ultimate causes of migration stems from our focus on long-distance temperate-tropical migrants. Arguably, long-distance migrants are not the best candidates for assessing the causes of migration because: (1) we know relatively little about where many long-distance migrant populations spend their non-breeding seasons

(Webster et al. 2002); (2) individuals within a species often do not vary in whether or not they migrate; and (3) breeding and non-breeding areas differ in many important respects, any of which could potentially be responsible for migratory behavior. In contrast, short-distance intra-tropical bird migrations provide excellent systems in which to test hypotheses proposed to explain the evolution of migration. Specifically, in short-distance migrants: (1) the short distances involved facilitate linking breeding populations with their non-breeding ranges; (2) most species are partially migratory, permitting us to examine the correlates of migratory behavior at the individual level (Ketterson and Nolan 1983); and (3) the forests between which individuals migrate are similar in many regards, thereby reducing the number of factors that could be responsible for migratory behavior. Additionally, from an applied perspective, the study of short-distance intra-tropical migration is compelling. Like long-distance migrants, the survival of intra-tropical migrants depends on not just a single area, meaning they may be particularly may be particularly susceptible to habitat loss (Powell and Bjork 2004). Yet birds breeding in tropical mountains typically have smaller range sizes than birds breeding in tropical lowland areas or in the temperate zone (Hawkins and Diniz-Filho 2006) and the forests of many neotropical countries continue to be deforested at alarming rates (Sanchez-Azofeifa et al. 2001).

Recently, Levey and Stiles (1992) proposed a why theoretical framework to understand why birds migrate altitudinally along tropical mountain slopes. They observed that many long-distance migrant species are drawn from primarily frugivorous lineages that also contain short-distance altitudinal migrant species. They also observed that migrant birds frequently inhabit “open habitats”. Based on these observations, they proposed the evolutionary precursor hypothesis to explain why some birds have evolved migratory behavior whereas other have not. The evolutionary precursor hypothesis postulates that temporal variation in fruit availability is greater than the temporal variation of insect availability, and temporal variation (presumably of food resources) in non-forested environments is greater than the temporal variation inside forests. As a result, Levey and Stiles (1992) suggest that being frugivorous and living in non-forested environments pre-adapts some birds to evolving long-distance migration. This hypothesis assumes that within the same environments over the same time period temporal variation in fruit availability is greater than temporal variation in arthropod availability. This important assumption has yet to be tested. Surprisingly, few data on patterns of arthropod abundance (rather than diversity) are available from the Neotropics. What little we do know comes from heterogeneous environments at widely scattered locations over multiple years (Janzen 1973). Furthermore, a recent study (Appendix A) questioned the basis of the evolutionary precursor hypothesis by showing that long-distance and short-distance migrations are associated with different suites of ecological traits, suggesting that short-distance migration may evolve in response to a different suite of evolutionary pressures than long-distance migration. Appendix A also revealed that diet and habitat interact in their association with migration, and foraging group size is more consistently associated with migration than either diet or habitat. This suggests that temporal variation in food availability is poorly captured by the surrogates (diet and habitat) proposed by Levey and Stiles (1992). Hence, further work is needed to understand the potential mechanisms by which spatial and temporal variation in food availability might promote migration.

The question of why birds migrate altitudinally on tropical mountain slopes has also been studied empirically. Because altitudinal migrants are primarily frugivorous or nectarivorous (Stiles 1983), most studies have attempted to correlate migratory behavior with some measure of fruit availability (Wheelwright 1983, Loiselle and Blake 1991, Rosselli 1994, Solórzano et al. 2000, Chaves-Campos et al. 2003, Chaves-Campos 2004) or nectar availability (Stiles 1980). However, measured patterns of fruit availability have rarely matched predicted patterns –reciprocal peaks in fruit availability between breeding and non-breeding elevations. At best, fruit limitation can explain uphill (Rosselli 1994, Chaves-Campos et al. 2003) or downhill (Loiselle and Blake 1991) movements but not all of the annual migratory cycle. Second, this “reciprocal fruit abundance” hypothesis relies on variation in production rates of ripe fruits for plant species that are important in birds’ diets, not directly on variation in standing crop of fruits of the whole plant community (the parameter measured in many past studies; Appendix B). Thus, until we know the degree to which standing crop reflects productivity, we don’t know how much confidence we can place in the conclusions based on temporal and spatial patterns in standing crop. However, a recent comparative study does suggest that fruit limitation in some way influences the evolution of altitudinal migration in tropical birds (Appendix B). What we now lack are: (1) explicit mechanistic hypotheses that identify the specific food resources critical in shaping migratory behavior, (2) an integration of explanations for among- and within-species variation in migratory behavior, (3) a direct test of the assumption that fruit resources are more temporally variable than arthropod resources, and (4) estimates of the relative production rates of ripe fruit among elevations across a migrant species' range. In this paper, I address all four of these issues by testing hypotheses explaining the causes of altitudinal migration in a tropical frugivorous bird, the White-ruffed Manakin (*Corapipo altera*).

Hypotheses explaining altitudinal migration at the species level

Explaining altitudinal migration requires accounting for both uphill and downhill migratory movements. Birds may migrate uphill for different reasons that they migrate downhill. Birds may experience temporal variation in their vulnerability to different suites of predators or have different energetic and nutritional requirements due to breeding activities. Thus, failure to find expected relationships between migration patterns of frugivorous birds and abundance of fruit could be due to: (1) alternative factors (i.e., predation) promoting migratory movements, (2) inappropriate metrics of fruit abundance (i.e., measuring standing crop instead of production rates, or counting fruits unimportant in migrant diets), or (3) seasonal changes in the nutritional needs of frugivores (i.e., shifting to arthropods to increase protein and calcium uptake) during the breeding season.

If food explains both uphill and downhill migration patterns, then which foods consumed by understory frugivores should be predicted to vary seasonally and altitudinally? The *fruit limitation hypothesis* postulates that if the production rates of fruits important in the diets of migrant species are greater during the breeding season at breeding elevations, then uphill migration could track the abundance of these specific fruits. The aggregate energetic requirements of the population should be greatest near the end of the nesting period and immediately post-fledging because of the influx of new individuals into the population (Rosselli et al. 2002). Hence, the fruit limitation hypothesis predicts: (1) the production rates of ripe fruits of plant species important in the diets of migrants should be higher at breeding elevations during breeding and fledging periods than at non-breeding (typically lower) elevations, and (2) if prediction #1 is true, then the fruits responsible for the higher production rates at breeding elevations should be particularly common in the diets of recently fledged birds during this period. The fruit limitation hypothesis could also explain downhill migration if (3) fruit availability is relatively *more* abundant at non-breeding elevations compared to breeding elevations during the non-breeding season. Fretwell (1980) proposed that food availability likely limits migrant populations during the non-breeding season, and indeed, few alternative explanations could explain downhill movements.

An alternative to the fruit limitation hypothesis is the *protein limitation hypothesis*. This hypothesis postulates that birds migrate uphill to exploit higher arthropod availability because protein is potentially more limiting than carbohydrates during breeding. Because the morphologies of highly frugivorous species are poorly adapted for the detection, capture, and digestion of arthropod prey (Levey and Martínez del Rio 2001), frugivores may have to locate and time the protein-intensive activities of females (i.e., egg production, nestling feeding, and moult) to exploit the locations and seasons of highest arthropod availability (as suggested by Poulin et al. 1992 and Levey

1988). The protein limitation hypothesis predicts that: (1) arthropod abundance should be higher at breeding elevations than non-breeding elevations during breeding. Furthermore, this hypothesis assumes that: (2) the diets of adult females of migrant species should consist of a greater proportion of arthropods during the breeding season relative to other seasons, (3) adult females should eat more arthropods than adult males and young birds during the breeding season, and (4) diets of both sexes should consist of a greater proportion of arthropods during moult than during other times of year.

Hypotheses explaining migration at the individual level

Explaining altitudinal migration sometimes also involves explaining why some individuals within most intra-tropical migrants do not migrate. Partial migration seems to be common among altitudinal migrants species (Stiles and Skutch 1989), although the movement patterns of few species are detailed enough to estimate the proportion of migrant species that are partially migratory. Although comparative methods provide a powerful tool for identifying traits associated with variation in migratory behavior on evolutionary time scales, partially migratory species provide the opportunity to identify the trade-offs associated with migration on ecological time scales. Migratory behavior could be phenotypically or genotypically fixed at the individual level (Lundberg 1988, Berthold 2001), or be a condition-dependent strategy in which individuals are capable of changing migratory strategy over their life-time (Ketterson and Nolan 1983, Cristol et al. 1999). All hypotheses explaining intraspecific variation in migratory behavior as a conditional strategy (i.e., individuals “decide” whether or not to migrate each year) assume that food availability or physiological tolerance (or both) limit the abilities of individuals to remain at breeding locations during the non-breeding season. While hypotheses relying on fixed phenotypic or genetic differences in migratory strategy (Lundberg 1988) would not predict *a priori* differences in migratory behavior within breeding populations or among age and sex classes, all condition-dependent hypotheses do make such predictions.

Three condition-dependent hypotheses have received the most attention to explain variation in migratory behavior within species. These three hypotheses are based upon interrelated age- and/or sex-dependent trade-offs in reproduction and survival. The *dominance hypothesis* invokes despotic behavior and competition for food (Ketterson and Nolan 1976), akin to Cox's (1968) hypothesis and the competitive exclusion hypothesis of Appendix B for among-species variation in migratory behaviors). Dominant individuals (typically older and/or larger) are able to obtain more of the dwindling resources than subordinate individuals, and are thus able to stay on breeding grounds year-round, while the subordinates migrate to areas with less competition for food. The *arrival time hypothesis* (Ketterson and Nolan 1976) akin to Fretwell (1980) predicts that the sex whose fitness is most limited by intra-sexual competition on the breeding grounds will be more likely to trade off food-related benefits of migrating for reproductive benefits of arriving early or staying. Finally, the *body size hypothesis* (Ketterson and Nolan 1976) depends on inclement weather on the breeding ground making year-round residency a risky strategy. Because larger individuals can fast for longer periods than smaller individuals due to greater reserves relative to their metabolic rate (Calder 1974), only the largest individuals are predicted to trade off the risk of starvation due to bad weather on the breeding grounds against the energetic costs and the survival risks of migrating. Thus, identifying if migratory behavior is sex- or age-biased and if migrant and resident individuals differ in physical condition is critical to determining if individual variation in migratory tendency is a fixed or conditional strategy. This approach can also help distinguish among condition-dependent hypotheses explaining partial migration, and identifying the trade-offs associated with different strategies.

The objectives of this study were to test the fruit availability and protein limitation hypotheses to explain both uphill and downhill movements of an altitudinal migrant species, and to test the dominance, body size, and arrival time hypotheses to explain why some individuals in a partially migratory species do not migrate. Additionally, I aimed to test the assumption of the evolutionary precursor hypothesis (Levey and Stiles 1992) that fruit is a more variable resource than arthropods for tropical birds. I focused on a common forest understory species (*Corapipo altera*) that migrates between lowland and premontane forests in Central America. Previous work in the region suggested that although elevational differences in nest predation risk could explain uphill migrations for many species (Appendix B), birds such as *C. altera* that spend the non-breeding season in lowland forests are unlikely to experience reduced risk of nest predation by migrating to premontane forest to breed. Thus, this paper focuses on hypotheses relying on food limitation to drive migratory behavior of this species.

Methods

Focal species and study sites

White-ruffed Manakins (*C. altera,* Pipridae) are small (10–12 g) understory frugivorous birds that inhabit wet forests of southern Central and northern South America (BirdLife International 2004). Populations on the Atlantic slope of Costa Rican breed between 400–900 m elevation primarily during Apr–Jun, and are partially migratory (some unknown proportion of the individuals descend to lower elevation forests following breeding; Loiselle and Blake 1991, Rosselli 1994). Male *C. altera* display at leks that females visit to choose and copulate with a male (Rosselli et al. 2002). Sexes are dimorphic in both plumage and size (females average 1.5 g heavier then males). Females alone build nests, incubate and feed young (Stiles and Skutch 1989).

I studied *C. altera* at three sites differing in elevation that spanned breeding and non-breeding ranges in the vicinity of the 47,572 ha Braulio Carrillo National Park (BCNP) in northeastern Costa Rica. The highest-elevation site (Rara Avis Reserve, 750 masl, 10°17'3" N, 84°02'47" W) lies in the middle of breeding elevations for *C. altera* in this region. Forests at this site are classified as premontane pluvial (Holdridge 1967), and receive a mean annual rainfall of 8,279 mm (± SE 263 mm; Rara Avis, unpublished data). I also studied *C. altera* at two elevations below the breeding range: (1) La Selva Biological Station (10°24’59” N, 84°01’55” W, ~100 masl), and (2) BCNP near the “Cantarrana” refuge (10° 22’16” N, 84°02’45” W, 300 masl). Forests at La Selva are lowland tropical wet (Holdridge 1967) and receive a mean annual rainfall of 4,260 mm (± SE 100 mm, unpubl. data). Canopies are higher at La Selva than at Rara Avis with larger trees, fewer epiphytes, and a more open understory. The intermediate site at

Cantarrana (300 m) is located roughly equidistant (~7 km straight-line distance) between the La Selva site (100 m) and the Rara Avis site (750 m), and in terms of species composition and forest structure, appears to be transitional between the lower and higher elevation sites. By interpolating daily rainfall data collected during days I worked at 300 m, I estimated 6,845 mm annual rainfall at Cantarrana. Hereafter I refer to these three sites by their elevation.

Temperature is virtually aseasonal in the region, and seasonal patterns of rainfall are similar along the gradient. On average, May–Jul and Dec are the rainiest months at all elevations and Feb–Apr the least rainy, with substantially more precipitation falling during the second half of the year than the first. Total annual rainfall during 2004 was 17–19% higher than average. In particular, the typically drier month of Mar received 171% (at 750 m) and 275% (at 100 m) of the monthly mean precipitation, and the typically wet month of May received 179% (at 750 m) and 269% (at 100 m) of the monthly mean precipitation. The second half of the year was typically wet, with monthly precipitation values similar to their long-term averages.

Manakin capture and dietary data

I spent 5–7 days at each site during each month in 2004. I captured *C. altera* in 6–16 mist nets (12 m wide x 3 m tall, 38-mm mesh) placed in the same locations on successive months in the understory of old-growth forest. I opened mist nets at 0600, and kept them open until noon or until rain began, checking nets every 20 min. I collected fecal samples by placing birds in cages for 30 min and collecting all regurgitated and fecal matter voided during this time. I banded each bird with a numbered aluminum leg band and measured wing chord (mm) and body mass (to the nearest 0.01 g). I also recorded sex (based on plumage, body mass, and/or presence of a brood patch or cloacal protuberance), an index of subcutaneous fat (0–5; Helms and Drury 1960), and presence of body and/or flight feather moult. I immediately released individuals at the net when they had been captured previously on the same day, but resampled individuals recaptured on subsequent days.

I preserved fecal samples in 75% alcohol and subsequently examined contents under a 40 x microscope. I used presence/absence of seed types found in the whole sample to characterize the fruits consumed by *C. altera,* and matched seeds found in fecal samples to seeds in a reference collection from plants collected at the site (Boyle 2003). I visually estimated the relative proportion of fecal matter consisting of arthropod remains (identified to family or order when possible) relative to fruit pulp and seeds in each sample by inspecting the relative amount of arthropod pieces in each quadrant and comparing this to the amount of all fruit pulp and seeds, averaging estimates among quadrants within a sample. Separating all arthropod pieces from fruit matter and weighing arthropod mass was not possible due to the extremely small size of most arthropod fragments. Although this method may not accurately represent the volume or mass of arthropods, it provides a quantitative index of the relative importance of arthropods and fruit in diets and is similar to the methods used in other studies of frugivorous birds (Herrera 1998). I found seeds from 76 plant species in 283 fecal samples of *C. altera* during this study (appendix 1).

Fruit production rates

To test the fruit limitation hypothesis, I monitored phenology and counted fruits each month on 226 individual plants belonging to 35 species in the Melastomataceae and Rubiaceae believed to be important in the diets of *C. altera* based on preliminary fecal sample analyses, previous work on this species (Rosselli 1994), and fruit characteristics. I marked plants with numbered metal tags, measured their diameter at breast (1.3 m) height (dbh), basal diameter, and estimated their height (to the nearest 0.5 m). After analyzing fecal samples, I chose to restrict estimates of fruit production rates to the 18 species of marked plants whose seeds were also found in fecal samples collected from *C. altera* during 2004 (173 individual plants: 73 at 750 m, 43 at 300 m, and 57 at 100 m). These 18 marked species accounted for 44.9 % of the seed records in 283 *C. altera* fecal samples analyzed from 2004. Of the 15 plant species whose seeds most commonly appeared in fecal samples, only four were not species for which I calculated fruit production rates.

I visited each marked plant at the beginning of a week's sampling period and noted if the plant was in bud, flower, had ripe or unripe fruits, and counted the total number of ripe fruits and infructescences on each plant. I selected and marked with green flagging 1–11 infructescences on which to count fruits for all fruiting individuals. The number of infructescences on which I counted fruits varied due to variation in infructescence accessibility, number of infructescences per plant, and number of fruits per infructescence ($\bar{x}$ = 4.1 infructescences/plant). Flagging appeared not to deter avian foraging, as I observed birds consuming fruits from marked infructescences on several occasions. On each marked infructescence, I counted all ripe, unripe, parasitized (unripe fruits attacked by pathogens or seed predators), and rotten (ripened, but attacked by pathogens) fruits, removing parasitized and rotten fruits on each visit. I rechecked marked infructescences at the end of the sampling week ($\bar{x}$ = 4.9 days between checks) and recounted fruits. I estimated the per-infructescence production of ripe fruits as [*n* unripe 1st check] – [*n* unripe 2nd check] – [*n* parasitized 2nd check]. I estimated the daily production rate of ripe fruit for each plant during a given month as the mean per-infructescence production multiplied by the total *n* infructescences bearing fruit that month. These calculations assume that fruits disappearing between checks were eaten by frugivores rather than lost before ripening to pathogens or seed predators.

To calculate monthly rates of fruit production (at the species level) at each of the three elevations, I estimated the density of individual plants per species by surveying 10 (300 m and 750 m) or 15 (100 m) 0.01-ha belt transects (2 m x 50 m) systematically spaced ≥100 m apart surrounding the bird capture locations. In each transect, I identified and measured the dbh, basal diameter, and plant height (to the nearest 0.5 m) of all individuals in the families Melastomataceae and Rubiaceae. Additionally, I recorded whether each individual plant was reproductive. Voucher specimens of each species from each site are deposited at the herbaria of the Museo Nacional de Costa Rica, the Instituto Nacional de Biodiversidad, and the Missouri Botanical Garden. Using individuals in transects as well as individuals marked for fruit estimates, I determined the minimum size at which I found individual plants producing flowers and fruit, and used the number of individuals ≥ this minimum size cut-off in transects to estimate the density of reproductive-sized individuals per ha at each elevation.

To estimate production rates at the level of the site or elevation, I multiplied the mean per-individual estimate of fruit production in a given month by the number of reproductive-sized individuals per ha for each species. In a few cases, marked plant species did not occur in plant transects, yielding estimates of <10 individuals per ha. I assigned these plant species densities of two individuals per ha to estimate fruit production rates by elevation and month for those species. I arbitrarily chose densities of two individuals per ha for these plant species as a conservative estimate of their abundance which apparently is > 0/ha (marked individuals occur within the study area) but < 10/ha (not found in transects). Finally, I summed the monthly fruit production rates for all species at a site to obtain overall fruit productivity estimates per month at each elevation. Because the data from Jan are incomplete, I compared monthly fruit production estimates between sites from Feb–Dec. Appendix 2 provides a summary for all marked plant species of reproductive size cut-offs, densities, and fruit production data by elevation.

Arthropod availability

To test the protein limitation hypothesis, I sampled the abundance of understory arthropods at up to 10 sampling points at each site every month during 2004 ($\bar{x} = 8.1$ samples/site/mo). I used sweep nets to sample foliage-dwelling arthropod abundance between 0.2–2.5 m above the ground. *C. altera* forage by sallying from understory and midstory (1–6 m) perches to snatch fruits and arthropods from foliage (Stiles and Skutch 1989, W. A. Boyle, pers. obs.). Thus, sweep samples are a more appropriate sampling method for this species than methods that either sample arthropods inhabiting other substrates or that are biased toward aerial taxa (Cooper and Whitmore 1990). I located the 10 sampling points ≥100 m apart at the center of a 50-m radius circle, within which I randomly located one 5 x 5 m square of vegetation to sample each month. Thus, I sampled ten 5 x 5 m patches of forest from each site during each month from similar areas, but I avoided sampling the same patches repeatedly. I conducted 4 min sweeps between 11:00 and 17:00 hrs and did not sample when rainfall exceeded a light drizzle.

I examined all surfaces of every piece of leaf and twig to separate arthropods (visible to the naked eye, approx. ≥1 mm) from plant debris. I measured body length (mm) and identified every arthropod to order. I weighed the combined wet mass of arthropods and preserved samples in 75% alcohol. I eliminated ants and termites from analyses because *C. altera* are not known to consume either of these groups of taxa (Rosselli 1989). I also excluded taxa inhabiting rotting wood or soil (Isopoda, Annelida, Zoraptera, Psocoptera), as these taxa likely entered into samples when the net broke open rotting twigs. Finally, I excluded arthropods >30 mm long from analyses because I assumed that prey larger than 30 mm were too difficult for *C. altera* to capture and handle successfully. Appendix 3 summarizes sweep sample contents by site and month.

Analyses

To ensure that plant species for which I estimated fruit production rates represented a similar proportion of the diet of *C. altera* throughout the year, I examined whether the proportion of seeds from marked plant species found in fecal samples differs among seasons using contingency table analyses and likelihood ratio tests. I examined whether fruit production rates and standing crops differed among elevations using 2-factor ANOVA models (site and month) using *ln*-transformed production rates. I used linear regression to explore the degree to which estimates of standing crop reflects daily rates of fruit production for each species using data from any individual that either produced or had a standing crop of ≥ 1 fruit in a given month. I *ln*-transformed estimates of both productivity rates and standing crop before analyses.

I evaluated the protein limitation hypothesis by conducting ANOVA analyses using both the number of arthropods in samples as well as the total mass of arthropods in samples as response variables. I tested for an interaction between site and season using each sample as the unit of replication. To further explore patterns in arthropod abundance, I constructed richer models including weather conditions at the time samples were collected, and interactions between weather, season, and site. To verify the assumption of increased protein consumption during the breeding season for female *C. altera*, and during moult for adults of both sexes, I analyzed the patterns of arthropod remains in fecal samples. I tested for differences between sexes and seasons in the proportion of samples containing any arthropod remains using contingency tables and 1-tailed Fisher's exact tests, and in the mean percent of arthropod remains in those samples using *t*-tests.

To test the assumption underlying the evolutionary precursor hypothesis (Levey and Stiles 1992) that fruits are a more variable resource than arthropods, I calculated the mean and the coefficient of variation in fruit production rates and the number of arthropods in sweep samples for all three sites.

To test the predictions of the three hypotheses explaining partial migration, I examined variation in migratory strategy among individual *C. altera* in relation to sex and age. I compared the proportion of adult (≥2nd year) males relative to adult females captured at lower elevation sites during the non-breeding using contingency table analyses and likelihood ratio tests. I also compared the proportions of first-year birds captured during the non-breeding season at lower elevations (100 m and 300 m combined) with the proportions captured at 750 m. To assess whether migrant and non-migrant individuals differ in body condition, I compared migrant individuals (birds captured at either 100 m or 300 m) with "non-migrant" individuals captured at 750 m between Oct and Feb. Although I am confident that birds captured at the lower-elevation sites had migrated, some of the captured at 750 m may have migrated down to 750 m from slightly higher elevations, or subsequently migrated to lower elevations. I constructed a general linear model including migratory status, sex, age, fat score, month, and the migratory status*sex interaction, and using the mass:wing chord ratio as the response variable.

Results

I captured 252 individual *C. altera,* and recaptured banded individuals 138 times during a total of 13,311 mist-net-hours. From these 390 captures, I collected 371 fecal samples and analyzed the contents of 283 of these samples. Fifty-six individuals were recaptured in more than 1 month (up to 6 different months at Rara Avis). Three individuals were recaptured at different elevations from their initial capture location, thereby documenting movements of individuals: (1) from 100 m to 750 m, (2) from 750 m to 300 m and back to 750 m, and (3) from 750 m to 100 m. Five individuals were recaptured at the same non-breeding site in Nov or Dec as where they were initially captured in Jan or Feb. In all five cases those individuals had not been captured for 6–10 months, suggesting some within-individual predictability in migratory strategy and site-fidelity to non-breeding sites.

The patterns of migration, breeding, and moult in *C. altera* during 2004 were remarkably similar to patterns previously described for this species (Rosselli 1994), reinforcing the evidence that altitudinal migration (summarized in Fig. 1) is a temporally and spatially predictable behavior. Capture rates were roughly equal in Jan at all three sites, with capture rates increasing at 300 m and 750 m and declining at 100 m in Feb. Uphill migration (Feb–Mar) was relatively synchronous, with a dramatic increase in capture rates at 750 m during Mar (Fig. 2). I did not capture any *C. altera* at 100 m between Apr–Oct, nor at 300 m between Mar–Jun, suggesting that individuals rarely (if ever) remain at lower elevations during the breeding season. Most breeding probably occurred Apr–Jun; peak proportions (100%) of females had brood patches in May, and the percent of captures consisting of hatch-year birds increased from 0% in May and 4% in Jun to 61% in Jul. Males initiated moult toward the end of the breeding period (May–Jun), while most females initiated moult ~2 months later (Jul-Aug). Moult was protracted within individuals (lasting up to 5 months) and among individuals, with many birds still completing feather growth in Dec when the study ended. Individuals moved downhill highly asynchronously, from early in the post-breeding period (Jul–Sep) to the non-breeding season (Oct–Jan). Capture rates at 750 m gradually declined during Jul–Dec, and gradually increased at the two lower-elevation sites over this same period. By Dec, capture rates approximately equaled Jan levels at all three sites (Fig. 2).

Fruit limitation hypothesis

The production rate of ripe fruits by 18 plant species important in the diets of *C. altera* varied seasonally, and seasonal patterns differed among sites (Fig. 3A). Fruit production rates varied >100-fold between seasons and sites, ranging from a low of 62 fruits/ha/day produced at 100 m during Apr, to 6,809 and 6,788 fruits/ha/day produced at 750 m in Oct and Jul respectively. The fruit limitation hypothesis predicted that production rates of fruits should be higher at breeding elevations during breeding and fledging periods than at lower elevations. In fact, fruit production rates were not higher at 750 m than at lower elevations early in the breeding season; the only months when less fruit was produced at 750 m than at lower elevations was from Mar–May, during which time *C. altera* migrate up to these elevations to initiate breeding. Consistent with the fruit limitation hypothesis, however, fruit production rates were higher at 750 m than at lower elevations when young manakins fledge. The location and months of maximum fruit production during the whole year was at 750 m during Jul and Oct. The Jul peak in fruit production coincides with the location and timing of fledging, corresponding to an increase in *C. altera* capture rates (61% young birds) at 750 m. During Jul, I estimated daily fruit production rate to be 81% lower (at 100 m) and 91%

lower (at 300 m) than the fruit production rate at 750 m. Overall, elevations differed in mean fruit production rates ($F_{13, 33} = 2.2$, $P = 0.057$), with 750 m producing roughly double the number of fruits (3061 ± 473 fruits) that the 300 m site produced (1715 ± 514 fruits), and triple the number of fruits that the 100 m site produced (949 ± 514 fruits).

In contrast to the predictions of fruit limitation hypothesis to explain downhill migration, fruit production rates were never higher at 300 m or 100 m compared to 750 m during the entire post-breeding and non-breeding seasons. The proportion of seed records from plant species used to calculate fruit production rates that I found in fecal samples differed among seasons (likelihood ratio test, $\chi^2 = 24.8$, $P < 0.001$). However, more of the seed records during the post-breeding and non-breeding seasons corresponded to marked plant species than during the breeding and uphill migration seasons. This result implies that post-breeding and non-breeding estimates of fruit availability are better capturing the resources important to *C. altera* than breeding estimates.

To explore whether my conclusions regarding seasonal and spatial patterns of fruit availability would have been different had I used methods comparable to previous studies, I calculated total standing crop of ripe fruits for each elevation. The seasonal patterns of standing crop resembled the seasonal patterns of fruit production rates in some regards (Fig. 3B). Most importantly, the standing crop of fruits at 750 m was higher than at other sites between Jul–Dec, and standing crop was higher at 300 m during Apr and at 100 m during May–Jun (Fig. 3B). However, the temporal patterns of standing crop were more irregular than the temporal patterns of fruit production rates, ranging from a maximum of 15877 fruits/ha at 100 m in May to a minimum of 70 fruits/ha at 300 m in Feb. Furthermore, the relationship between standing crop and production rate differed among species, implying that some fruits are preferred over others. Hence, the appropriateness of estimating fruit availability using standing crop varies with plant species. For instance, standing crop was highly and positively correlated with production rate in a few species (e.g., *Ossaea robusta*, linear regression on *ln*-transformed values, $R^2 = 0.61$; $P < 0.001$). However, standing crop poorly reflected fruit production rates in most species (e.g., *Henriettea tuberculosa*, $R^2 = 0.08$, $P = 0.242$; *Conostegia micrantha*, $R^2 = 0.39$, $P = 0.097$; *Miconia gracilis*, $R^2 = 0.14$, $P = 0.181$) and in some cases, these two measures of fruit availability appeared to be negatively correlated (e.g., *Psychotria suerrensis*, slope of linear regression = –0.4).

The temporal patterns of fruit production rates at a site appeared to be attributable to the phenological patterns of one or a few plant species within a site. Species level patterns in fruit production were due to a combination of factors: the number of reproductive individuals per ha, the degree of fruiting synchrony within and among individual plants, and variation in crop size on individual plants. Fruiting strategies differed among species and among sites for some species. For example, *Palicourea gomezii* (at 750 m), *Clidemia ombrophila* (at 300 m), and *Psychotria acuminata* (at 100 m) produced low and relatively constant numbers of fruits over most of the year, whereas *Conostegia micrantha* and *Ossaea robusta* (at 750 m), *Conostegia rufescens* and *Ossaea macrophylla* (at 300 m), and *Henriettea tuberculosa* (at 100 m) produced massive fruit crops during 1–3 mo, and then either produced no fruit during the rest of the year, or produced much less fruit. The phenological patterns of some species (such as *Henriettea tuberculosa* and *Miconia gracilis*) differed among elevations, producing marked peaks in fruit at one elevation but not another.

Because the spike in fruit production during the early post-breeding season at 750 m appeared to be primarily attributable to the fruiting of *Conostegia micrantha*, and to a lesser extent *Ossaea robusta*, the fruit limitation hypothesis predicted that fruits of these plant species should be abundant in the diets of *C. altera* during Jul–Aug, and particularly predominate the diets of newly-fledged birds. Consistent with this prediction, all 15 fecal samples I analyzed from Jul contained *C. micrantha*, and only two samples contained seeds from additional species. Both *Ossaea* and *Conostegia* were common in the diets of birds of all ages during Jul–Aug, and newly-fledged birds tended to consume these species in slightly greater proportions that older birds (63% vs. 54% of 68 seed records).

Protein limitation hypothesis

If the protein limitation hypothesis explains uphill movements, then arthropod abundance should be higher at breeding elevations than non-breeding elevations during breeding and the onset of moult. Although the mean number of arthropods varied considerably among sites and months, I found few consistent patterns with respect to either site or season (Fig. 4). The number of arthropods in samples was not related to site ($F_{2, 276} = 0.1$, $P = 0.903$), nor did I find an interaction between site and season ($F_{6, 276} = 0.9$, $P = 0.470$). The number of arthropods in sweep samples differed slightly among samples collected in different seasons (breeding, post-breeding, non-breeding, and uphill migration; $F_{3, 276} = 2.1$, $P = 0.103$). However, the season with the most arthropods was not the breeding season (Apr–Jun) as predicted by the protein limitation hypothesis, but the non-breeding season (Oct–Jan), when frugivore protein requirements are presumably at their lowest. Furthermore, the season with the fewest arthropods was the post-breeding season (Jul–Sep), when many adults are moulting. These results are not qualitatively different if the total mass of arthropods in samples rather than number of arthropods is the response variable. The strongest correlate of arthropod abundance in sweeps was weather condition at the time samples were collected (sunny, overcast, or damp). Samples collected during sunny periods contained more arthropods (23.3 ± 1.3) than those collected under overcast (16.0 ± 1.2) or damp (14.8 ± 1.3) conditions ($F_{2, 251} = 10.6$, $P < 0.001$), and this effect was greater during the breeding season than in other seasons (weather*season interaction, $P = 0.012$). Because of the effect of weather, I plotted adjusted mean arthropod abundance by season and site after accounting for the effects of weather (Fig. 5). I found suggestive evidence for a site*season interaction after accounting for the effects of weather ($F_{6, 262} = 1.8$, $P = 0.103$). However, arthropod abundance was still not higher at the 750 m site during the breeding season relative to the two lower elevation sites (Fig. 5).

Because fecal sample analyses revealed a high incidence of spider parts in *C. altera* diets relative to other arthropod types, I separately calculated the pattern of spider abundance by season and site. Spider abundance differed slightly among seasons ($F_{3, 246} = 2.4$, $P = 0.071$) but not among sites ($F_{2, 246} = 0.7$, $P = 0.514$), and I found no evidence of a season*site interaction. However, mean spider abundance was not higher during breeding or post-breeding seasons at 750 m relative to other times of the year or sites; I found the highest numbers of spiders per sample in non-breeding season samples (Oct–Jan).

Consistent with the assumption of increased protein consumption related to breeding, more fecal samples from adult females (62%) contained arthropod remains than adult males (36%; 1-tailed Fisher's exact test, $P < 0.001$). On average, the percent of fecal matter consisting of arthropods was also higher in samples from adult females (6.2% ± 0.7%) than adult males (2.4% ± 0.6%; 1-tailed *t*-test, $t = 3.9$, df = 189, $P < 0.001$). The proportion of fecal samples containing arthropod remains also increased for females during the breeding season (74%) relative to other seasons (46%; 1-tailed Fisher's exact test, $P = 0.012$). However, dietary data do not support the assumption of increased protein requirements during moult. The mean proportion of arthropod remains in fecal samples of females was not higher during the months when their moult peaked (4.8%; post-breeding season, $F_{2, 41} = 1.1$, $P = 0.333$) relative to non-breeding (7.2%) and migration seasons (3.2%). In fact, the mean proportion of arthropod matter in fecal samples of females tended to be lowest during the months of peak moult. Likewise, adult males did not increase their arthropod consumption during the months of peak moult (breeding and post-breeding seasons; proportion arthropods in fecal samples by season; $F_{3, 121} = 1.2$, $P = 0.326$; proportion of samples with any arthropods, likelihood ratio test, $\chi^2 = 0.7$, $P = 0.870$).

Relative variability of fruits vs. arthropods

Mean fruit production rates were negatively related with elevation when all months were combined (table 1). However, the coefficients of variation (CV) in fruit production rate at 750 m and 300 m were very similar (76.3 vs. 75.7) and roughly half the CV for 100 m (145.8). Mean arthropod abundance (all months combined) varied less among sites and among seasons than did fruits. Mean numbers of potential prey for *C. altera* ranged from a low of 5.9 individuals per sweep sample during Jul at 750 m to 31.7 individuals per sweep sample during Jun at 300 m. The coefficients of variation for the mean number of arthropod individuals/sample among months within a site varied little from 39.6 at 750 m, to 38.6 at 300 m, and 38.9 at 100 m. These data suggest that arthropod availability is less variable, both temporally and spatially, than is fruit availability, consistent with the evolutionary precursor hypothesis (Levey and Stiles 1992). The use of standing crop rather than production rate for fruits amplifies these results; the CVs for standing crop were even higher than the corresponding CVs for fruit production rate within a site (table 1).

Correlates of migratory strategy

Variation in migratory strategy among individual *C. altera* was related to sex and body condition, consistent with migration being a conditional strategy in this species. My data suggest that the proportion of adult ($\geq 2^{nd}$ year) males relative to adult females captured at 100 m and 300 m (0.73) during the non-breeding was greater at 750 m (0.53) but this difference was only marginally significant (likelihood ratio test, $\chi^2 = 2.6$, $P = 0.106$). These data suggest that migratory behavior may be male-biased in this population. However, I found no indication of age-biased migration. The proportion of first-year birds captured during the non-breeding season did not differ between lower-elevation sites (100 m and 300 m; 0.64) and 750 m (0.56; likelihood ratio test, $\chi^2 = 0.4$, $P = 0.527$).

Migrant and non-migrant individuals did not differ in body mass after controlling differences in body size (mass:wing chord ratio). However, in models that accounted for differences among individuals in age, fat, and month, migrant females were 5% lighter for their body size than non-migrant females and migrant males were 4.2% heavier than non-migrant males (effect test for migratory status*sex interaction, $F_{2, 93} = 7.1$, $P = 0.001$).

Discussion

Why do manakins migrate uphill?

The uphill migration patterns of *C. altera* and the patterns of fruit production of plant species that *C. altera* consumes are largely consistent with the fruit limitation hypothesis. Fruit production rates were not higher at breeding elevations at the time when *C. altera* leave lowland forest and migrate up there to breed. However, this result does not refute the fruit limitation hypothesis: the time of maximum caloric requirements is likely to be not at the onset of breeding, but later in the nesting period and when females are feeding nestlings, and immediately post-breeding. Fruit production rates do peak at breeding elevations when most young manakins fledge. This results is consistent with results from some other tropical birds that also seem to time fledging during periods of maximum food availability (Young 1994). Dietary data are also consistent with the fruit limitation hypothesis: the plant species primarily responsible for the tremendous abundance of fruit during the post-breeding period at 750 m dominated diets of all *C. altera* sampled during this period, especially diets of young birds. This result highlights the importance of collecting species-specific fruit estimates rather than grouping estimates of fruit abundance from multiple species in a way that does not permit examination of individual phenological patterns. Furthermore, suggests that migration patterns could be disproportionately influenced by the phenology, distribution, and abundance of just a few plant species in the community.

Consistent with assumptions of the protein limitation hypothesis, nutrient demands of breeding do seem to influence the protein intake by *C. altera*. Females consumed more arthropods than did males, and females increased their arthropod consumption during breeding. However, the patterns of arthropod abundance derived from sweep samples are not consistent with the hypothesis that protein limitation explains migration patterns of *C. altera*. Arthropods were not more abundant in samples collected at breeding elevations relative to lower elevations during the breeding season. Few data on patterns of arthropod abundance (rather than diversity) are available from the Neotropics. The data presented here run contrary to some of the only patterns available from samples collected in heterogeneous environments and widely scattered locations over multiple years (Janzen 1973). An important caveat is that these measures of arthropod abundance are equivalent to “standing crop” of plants. Thus, it is possible that breeding elevation forests are in fact more productive in terms of arthropod prey, but prey are consumed in proportion to their production, resulting in a lack of consistent differences in apparent abundance among sites.

Regardless of these methodological considerations, growth of new feather tissues involved in moulting does not seem to require increased consumption of protein from arthropod prey as seems to be the case among Venezuelan frugivores (Poulin et al. 1992). Fecal samples from both sexes revealed no increase in arthropod intake during moult relative to other seasons which implies that it is unlikely that *C. altera* locate the initiation of moult to coincide with the location of greatest arthropod abundance. In general, adult *C. altera* apparently manage to fill their nutrient requirements almost exclusively with fruit; 54.8% of all fecal samples contained no arthropod remains and an additional 28.9% consisted of ≤5% arthropod parts. Perhaps the protein increases necessary to fuel breeding are obtained easily by females regardless of fluctuations in arthropod availability.

Why do manakins migrate downhill?

In contrast to uphill migration, patterns of fruit production are not consistent with the hypothesis that birds migrate downhill to exploit changes in the relative abundance of fruit resources among elevations and seasons. My data suggest that breeding (higher) elevations produce more fruit than lower elevations for most of the year, including the entire post-breeding and non-breeding seasons when *C. altera* migrate to lower elevations. One possibility is that production rates of the plant species I monitored differed from the production rates of the rest of the fruiting plant species that *C. altera* consume during the non-breeding season, and downhill migration functions to exploit those fruits. However, this possibility is unlikely given that the proportion of seed records from *C. altera* diets representing seeds from marked plant species is actually greater during the time of year when *C. altera* migrate down hill.

Loiselle and Blake (1991) found higher fruit abundance at their lowest elevation site (very close to the 100 m site used in this study) during much of the year. In contrast, I have shown here that fruit abundance at the 100 m site was only higher than the other two sites in May and Jun (Fig. 3). The methods I used to estimate fruit availability cannot account for the discrepancy between the results of these two studies. The spatial and temporal patterns I found in standing crop (comparable to their counts of fruits, although restricted to fruits important to *C. altera*) also fail to support the hypothesis that fruit availability explains downhill migration. One possible explanation for the differences in results between these two studies lies in the plant species used to estimate fruit abundance. Loiselle and Blake (1991) counted fleshy fruits produced by the whole community of fruiting plants at their sites, whereas I restricted my estimates of fruit availability to species known to be important in the diet of my focal species. Potentially, fruits consumed by *C. altera* differ from fruits they do not consume in their phenological patterns. In general, the concordance between fruiting and uphill migration patterns and discordance between fruiting and downhill migration patterns found here echoes the results of other species-specific studies of altitudinal migrants and their food resources (Rosselli 1994, Solórzano et al. 2000, Chaves-Campos et al. 2003). Together, these results suggest that alternative hypotheses are required to explain the downhill portion of the migratory cycle.

Why do some, but not all, manakins migrate?

Because many individuals within altitudinal migrant species do not descend to lower elevations after breeding, a full explanation of the causes of downhill migration requires an explanation of intraspecific variation in migratory behavior. My data suggest that individual *C. altera* make migratory decisions associated with sex-related trade-offs in the costs and benefits of year-round residency. Contrary to the predictions of the dominance hypothesis, I found no differences between age classes in migratory tendency that would be consistent with dominant individuals forcing subordinates to be migratory when food becomes limiting. Furthermore, patterns of fruit production and standing crop (Fig. 3) suggest that competition for food should be *lower* at breeding elevations than in the lowland during the non-breeding season which is the reverse of the pattern predicted by both the dominance and the arrival time hypotheses. I did, however, find evidence that males were more likely to migrate, and that the consequences of migratory behavior differ between sexes. This result also implies that the arrival time hypothesis is unlikely to explain variation in migratory behavior in *C. altera* since males should be less willing to relinquish their status on lek by migrating than females who have little to loose by migrating. To reconcile my results with the arrival time hypothesis, one would have to assume that female fitness is more strongly affected by residency than is male fitness. This assumption is questionable given that male *C. altera*, like most manakins, experience strong male-male competition for mates on display leks (Rosselli et al. 2002).

My results, however, are consistent with the body size hypothesis that states that larger individuals should be more likely than smaller individuals to survive fasting imposed by bad weather. At first glance, wet tropical premontane forests may seem unlikely to present risks of severe weather events that could threaten survival. However, rainstorms lasting three or four days occur regularly between May–Jan. Although all elevations are affected, breeding grounds receive double the precipitation of lowland forest (as much as 292 mm precipitation has been recorded in one day at 750 m, Rara Avis, unpubl. data). Prolonged downpours during such storms could limit foraging opportunities to the point of causing starvation, reducing the likelihood of survival for birds that remain resident year-round. Anecdotal evidence supports this idea; post-breeding birds generally lack any detectable body fat at breeding elevations (W. A. Boyle, pers. obs.), and dead *C. altera* showing no outward signs of disease or attack have been found at lower elevations immediately following severe rainstorms (S. Woltman, pers. comm.).

A *foraging limitation hypothesis* could thus explain downhill migration in a manner consistent with the within- and among-species correlates of altitudinal migration presented here and in previous work (Appendix B). Females (the larger sex) may be less likely to migrate because they have the metabolic capabilities to fast for longer periods than do smaller males. Females that gamble successfully on year-round residency are able to forage on abundant food resources when weather conditions permit. Thus, those that survive are in better condition than those that migrate at the beginning of the next reproductive season. In contrast, males that remain resident may be at the limits of their physiological capabilities due to their smaller body size, and may experience greater risks associated with periodic fasting than do females.

That fasting during heavy downpours could result in death by starvation is plausible given the nutritional composition of the fruits consumed by manakins, and is supported by some anecdotal evidence. Carbohydrate-rich fruits are nutritionally more similar to nectar than they are to lipid- or protein-rich foods such as arthropods, vertebrate prey, and fruits of certain plant taxa such as palms or Lauraceae (Wheelwright et al. 1984). The nutritional requirements of species such as *C. altera* that feed on carbohydrate-rich fruits may thus be similar to nectarivorous birds that must maintain high food consumption rates to maintain energy balance (Martínez del Rio et al. 2001). Indeed, Cedar Waxwings (*Bombycilla cedrorum*) increase their consumption rates when fed carbohydrate-rich fruits relative to lipid-rich fruits (Witmer and Van Soest 1998). In *C. altera*, an individual kept in captivity can consumes its body weight in fruits in <1.5 hr (W. A. Boyle, unpublished data).

Comparative results demonstrating species level increases in the proportion of arthropods in diets of residents relative to migrants and are also consistent with the foraging limitation hypothesis (Appendix B). Under the foraging limitation hypothesis, diet is hypothesized to influence the propensity to migrate, but not necessarily due to simple variation in the abundance of fruit. Although fruit abundance may well explain uphill movements for many species, the ability to obtain those fruits (regardless of the rate at which they are produced) and the ability to fast when foraging is not possible may explain why many birds migrate downhill following the breeding season.

Implications for understanding migratory behavior

Although the inferences from this study are limited to a single migrant species in one region, this study brings together multiple explanations for migratory behavior operating at different levels to explain the whole cycle of altitudinal migration. Additionally, I provide the first evidence in support of a critical assumption of the evolutionary precursor hypothesis (Levey and Stiles 1992) and its offshoot, the resource variability hypothesis (Appendix A); that fruit resources are more variable in their abundance than are arthropod resources at a single site. The results of this study extend the results presented by in Appendix A by providing direct evidence that resource variability explains migration to the breeding grounds, and by identifying a mechanism through which diet could interact with physiology to explain departure from the breeding grounds.

Alternative explanations for altitudinal migration remain to be tested. For some species, variation in risk of nest predation or parasite infection could be more important than food availability in shaping uphill migration patterns and location of breeding areas. Comparative studies of variation in nest placement and parental care could further our understanding of whether elevational differences in nest predation risk have been important in the evolution of this behavior. For downhill migration, few alternative explanations remain however. Potentially, the availability of specific micronutrients in fruits is more limiting to adult frugivorous birds than is the overall quantity of carbohydrates (Levey and Martínez del Rio 2001), and the availability of micronutrients could influence downhill movements. However, such a hypothesis would not predict a sex bias in migration, nor would it necessarily predict sex-related variation in body condition among migrants. Future work should test directly the foraging limitation hypothesis by determining the consequences of variation in migratory behavior for both reproduction and survival in males and females, and by evaluating the conjecture that heavy rainstorms can seriously impede foraging.

If we are able to directly link short-distance migrations of tropical birds to variation in fruit production and weather, then we will come tangibly closer to understanding the consequences of anthropogenic disturbance on the long-term persistence of migratory populations. A scenario emerging from research on global climate change is that tropical storm events are anticipated to increase in frequency and severity (Albritton et al. 2001). In addition to any repercussions this may have on resource abundance, an increase in frequency or duration of severe storms could also adversely affect the costs and benefits associated with year-round residency and migratory behavior. Long-term stability of altitudinal migrant populations would thus depend upon whether or not the proximate cues responsible for initiating migratory behavior also change synchronously with changing weather patterns. Furthermore, with Central American lowland forests continuing to disappear (Sanchez-Azofeifa et al. 2001), fewer and fewer refugia from higher elevation storms are available to altitudinal migrant birds.

This paper tested explicit mechanistic hypotheses and identified the specific food resources critical in shaping migratory behavior and integrated explanations for among- and within-species variation in migratory behavior. The results presented here provide a rare empirical test of alternative hypotheses explaining the evolution of migratory behavior at both the species level and at the individual level. This study provides evidence that food limitation is an important factor shaping the evolution of migratory behavior in birds. However, these results also suggest that food limitation is unlikely to be the only important factor. The availability of food probably interacts with nutritional needs, physiological traits, and climatic factors to shape the diversity of migration patterns among and within species of birds.

Acknowledgments

C. Conway, J. Bronstein, B. Enquist, D. Papaj, and R. Steidl commented on earlier drafts of this manuscript. B. Boyle, J. Brokaw, M. Burke, D. Erickson, W. Goulding, M. Hill, N. Kahn, C. Leumas, I. Manley, K. Meyers, J. Montoya, R. Repasky, A. Weldon, M. Williams, and J. Wolfe helped collect much of the data. S. White sorted many fecal samples. C. Tayor, B. Boyle, B. Hammel, F. Morales, N. Zamora, C. Taylor, R. Kriebel, J. Gonzalez, and O. Vargas helped identify plants. A. Bien and staff of Rara Avis, L. D. Gómez and the staff of OTS and La Selva Biological Station, the ALAS project, the La Selva-Barva TEAM project, MINAE and the ACCVC, J. Guevara, R. Tenorio, and the University of Arizona's IACUC committee assisted with logistics, permits, and support in the field. This material is based upon work supported by the National Science Foundation under Grant No. 0410531, an NSERC PGS-B fellowship, and grants from the Center for Insect Science, the Silliman Memorial research award, the International Arid Lands Consortium, the Department of EEB and the Graduate College at the University of Arizona.

Literature Cited

Albritton, D. L., L. G. Meira Filho, U. Cubash, X. Dai, Y. Ding, G. D. J., B. Hewitson, J. T. Houghton, I. Isaksen, T. Karl, M. McFarland, V. P. Meleshko, J. F. B. Mitchell, and e. al. 2001. Technical summary. Pages 21-83 *in* J. T. H. e. al, editor. Climate change 2001: the scientific basis. Cambridge University Press, Cambridge, UK.

Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. Oikos **103**:247-260.

Bell, C. P. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. Journal of Avian Biology **31**:258-265.

Berthold, P. 2001. Bird migration: a novel theory for the evolution, the control and the adaptability of bird migration. Journal Für Ornithologie **142**:148-159.

BirdLife International. 2004. *Corapipo altera*. In IUCN 2006. 2006 IUCN Red List of Threatened Species. *in*.

Boyle, W. A. 2003. Seed images from the Atlantic Slope of Costa Rica. http://eebweb.arizona.edu/grads/alice/SeedPhotos.html.

Calder, W. A. 1974. Consequences of body size for avian energetics. Pages 86-144 *in* R. A. Paynter, editor. Avian Energetics. Nuttall Ornithol. Club Publ.15, Cambridge, MA.

Chaves-Campos, J. 2004. Elevational movements of large frugivorous birds and temporal variation in abundance of fruits along an elevational gradient. Ornitología Neotropical **15**:433-445.

Chaves-Campos, J., J. E. Arévalo, and M. Araya. 2003. Altitudinal movements and conservation of Bare-necked Umbrellabird *Cephalopteris glabricollis* of the Tilarán Mountains, Costa Rica. Bird Conservation International **13**:45-58.

Cooper, R. J., and R. C. Whitmore. 1990. Arthropod sampling methods in ornithology. Pages 29-37 *in* M. L. Morrison, C. J. Ralph, J. Verner, and J. R. J. Jehl, editors. Avian foraging: theory, methodology, and applications, Studies in Avian Biology. Cooper Ornithological Society, Lawrence, Kansas.

Cox, G. W. 1968. The role of competition in the evolution of migration. Evolution **22**:180-192.

Cox, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. American Naturalist **126**:451-474.

Cristol, D. A., M. C. Baker, and C. Corbone. 1999. Differential migration revisited: latitudinal segregation by age and sex class. Current Ornithology **15**:33-88.

Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, NY.

Fretwell, S. D. 1980. Evolution of migration in relation to factors regulating bird numbers. Pages 517-527 *in* A. Keast and E. S. Morton, editors. Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC.

Gatehouse, A. G. 1994. Insect migration: variability and success in a capricious environment. Researches on Population Ecology **36**:165-171.

Greenberg, R. 1980. Demographic aspects of long-distance migration. Pages 493-504 *in* A. Keast and E. S. Morton, editors. Migrant Birds in the Neotropics. Smithsonian

Institution Press, Washington, DC.

Greenberg, R., and V. Salewski. 2005. Ecological correlates of wintering social systems in New World and Old World migratory passerines. Pages 336-358 *in* R. Greenberg and P. P. Marra, editors. Birds of two worlds: The ecology and evolution of migration. Johns Hopkins University Press, Baltimore, MD.

Hagan, J. M., and D. W. Johnston, editors. 1992. Ecology and Conservation of Neotropical Migrant Landbirds. Smithsonian Institution Press, Washington, DC.

Hawkins, B. A., and J. A. F. Diniz-Filho. 2006. Beyond Rapoport's rule: evaluating range size patterns of New World birds in a two-dimensional framework. Global Ecology and Biogeography **15**:461-469.

Helms, C. W., and W. H. Drury, Jr. 1960. Winter and migratory weight and fat; field studies on some North American buntings. Bird Banding **31**:1-40.

Herrera, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-yr study. Ecological Monographs **68**:511-538.

Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San José, Costa Rica.

Janzen, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology **54**:687-708.

Joseph, L., E. P. Lessa, and L. Christidis. 1999. Phylogeny and biogeography in the evolution of migration: shorebirds of the *Charadrius* complex. Journal of Biogeography **26**:329-342.

Kaitala, A., V. Kaitala, and P. Lundberg. 1993. A theory of partial migration. American

Naturalist **142**:59-81.

Keast, A., and E. S. Morton, editors. 1980. Migrant Birds in the Neotropics. Smithsonian Institution Press, Washington, DC.

Ketterson, E. D., and V. Nolan Jr. 1976. Geographic variation and its climatic correlates in sex-ratio of eastern wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). Ecology **57**:679-693.

Ketterson, E. D., and V. Nolan Jr. 1983. The evolution of differential bird migration. Current Ornithology **1**:357-402.

Levey, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecological Monographs **58**:251-269.

Levey, D. J., and C. Martínez del Rio. 2001. It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. Auk **118**:819-831.

Levey, D. J., and F. G. Stiles. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. American Naturalist **140**:447-476.

Loiselle, B. A., and J. G. Blake. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology **72**:180-193.

Loxdale, H. D., and G. Lushai. 1999. Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences **354**:1479-1495.

Lundberg, P. 1988. The evolution of partial migration in birds. Trends in Ecology &

Evolution **3**:172-175.

Martínez del Rio, C., J. E. Schondube, T. J. McWhorter, and L. G. Herrera. 2001. Intake responses in nectar feeding birds: digestive and metabolic causes, osmoregulatory consequences, and coevolutionary effects. American Zoologist **41**:902-915.

Poulin, B., G. Lefebvre, and R. McNeil. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology **73**:2295-2309.

Powell, G. V. N., and R. D. Bjork. 2004. Habitat linkages and the conservation of tropical Biodiversity as indicated by seasonal migrations of Three-wattled Bellbirds. Conservation Biology **18**:500-509.

Rappole, J. H., H. Helm, and M. A. Ramos-Olmos. 2003. An integrative framework for understanding the origin and evolution of avian migration. Journal of Avian Biology **34**:124-128.

Rosselli, L. 1989. El ciclo anual de un ave frugívora migratoria altitudinal, *Corapipo leucorrhoa* (Pipridae) y los frutos que consume. M.Sc. thesis. Universidad de Costa Rica, San José, Costa Rica.

Rosselli, L. 1994. The annual cycle of the White-ruffed Manakin, *Corapipo leucorrhoa*, a tropical frugivorous altitudinal migrant, and its food plants. Bird Conservation International **4**:143-160.

Rosselli, L., P. Vasquez, and I. Ayub. 2002. The courtship displays and social system of the Whtie-ruffed Manakin in Costa Rica. Wilson Bulletin **114**:165-178.

Sanchez-Azofeifa, G., R. C. Harriss, and D. L. Skole. 2001. Deforestation in Costa Rica: a quantitative analysis using remote sensing imagery. Biotropica **33**:378-384.

Solórzano, S., S. Castillo, T. Valverde, and L. Avila. 2000. Quetzal abundance in relation to fruit availability in a cloud forest of southeastern Mexico. Biotropica **32**:523-532.

Stiles, F. G. 1980. The annual cycle in a tropical wet forest hummingbird community. Ibis **122**:322-343.

Stiles, F. G. 1983. Birds. Pages 502-530 *in* D. H. Janzen, editor. Costa Rican Natural History. University of Chicago Press, Chicago, IL.

Stiles, F. G., and A. F. Skutch. 1989. A Field Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, NY.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology & Evolution **17**:76-83.

Wheelwright, N. T. 1983. Fruits and the ecology of Resplendent Quetzals. Auk **100**:286-301.

Wheelwright, N. T., W. A. Haber, K. G. Murray, and C. Guindon. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. Biotropica **16**:173-192.

Witmer, M. C., and P. J. Van Soest. 1998. Contrasting digestive strategies of fruit-eating birds. Functional Ecology **12**:728-741.

Young, B. E. 1994. The effects of food, nest predation and weather on the timing of breeding in Tropical House Wrens. Condor **96**:341-353.

Zink, R. M. 2002. Towards a framework for understanding the evolution of avian migration. Journal of Avian Biology **33**:433-436.

Tables, Figures, and Appendices

Table 1

Summaries by site of the number of plants species and individuals monitored during 2004, the number of arthropod samples collected, and the coefficients of variation for both fruit and arthropod abundance. Seasonality in fruit production was substantially higher than the seasonality of arthropod abundance at all three sites, and seasonality of fruit was greatest at the lowest elevation site.

site name	elevation	*n*			Coefficient of Variation		
		consumed by *C. altera* (total)					
		marked plant species	marked plant individuals	arthropod samples	fruit production rates	standing crop	arthropod abundance
La Selva	100 m	9 (19)	57 (80)	92	145.8	171.1	38.9
Cantarrana	300 m	12 (22)	43 (72)	90	75.7	78.2	38.6
Rara Avis	750 m	12 (13)	73 (74)	95	76.3	103.5	39.6

Figure legends

Figure 1 Depiction of the timing and movements of White-ruffed Manakins (*C. altera*) between the three study sites during 2004. Although no manakins spent the breeding season at either of the two lower-elevation sites, capture rates of *C. altera* gradually declined post-breeding at 750 m and increased at the two lower-elevation sites until all three sites had roughly equal capture rates at the very beginning and end of the year.

Figure 2 The monthly pattern of capture rate of C. altera per 100 mist net hours (MNH) at each of my three study sites during 2004.

Figure 3 The monthly pattern of daily ripe fruit production rate (panel A) and standing crop of ripe fruits (panel B) per ha for 18 species of plants whose fruits are important in the diet of *C. altera*. I estimated daily production rates and standing crop by monitoring 173 marked plants, and using per-plant values combined with density estimates (the number of reproductive individuals per ha) for each species to calculate production rates and standing crop for each elevation. Appendix 2 provides detailed information on the plants used to derive these patterns. The top bar depicts the annual cycle of *C. altera* movements. During the breeding season (Apr-Jun) all *C. altera* are at higher elevations. During the post-breeding, non-breeding, and uphill migration seasons, *C. altera* are present at all three elevations.

Figure 4 The monthly pattern of arthropod abundance as estimated by sweep samples. Each point is the mean of number of individuals of potential prey for *C. altera* from an average of 8.1 samples/site/month. Error bars represent one standard error of the mean.

The top bar depicts the annual cycle of *C. altera* movements as in Figure 2. Appendix 3 summarizes the contents of samples at each site throughout the year.

Figure 5 The seasonal pattern of the mean number of arthropods in samples after controlling for weather-related variation in abundance.

Figure 1

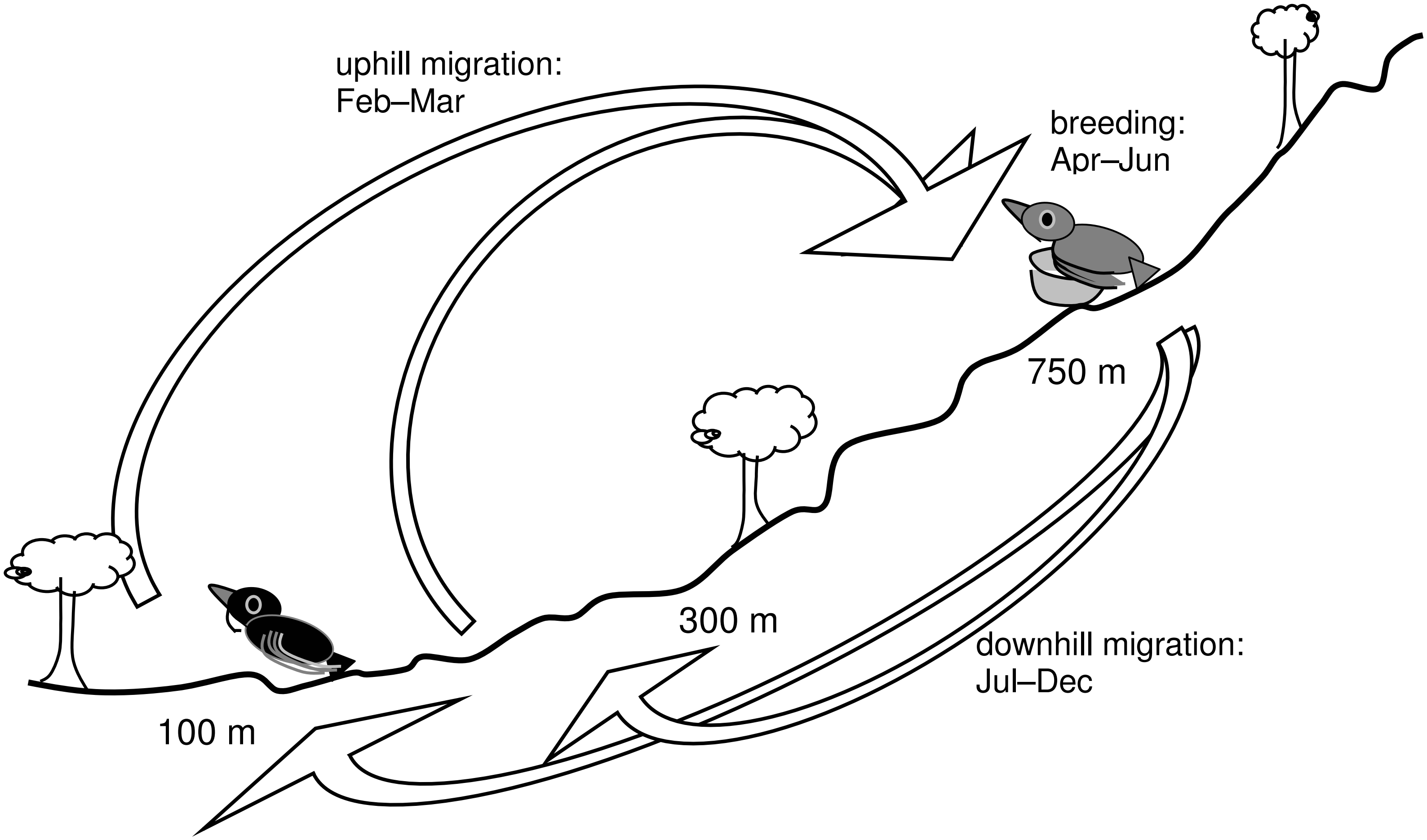

uphill migration:
Feb–Mar
breeding:
Apr–Jun
750 m
300 m
100 m
downhill migration:
Jul–Dec

Figure 2

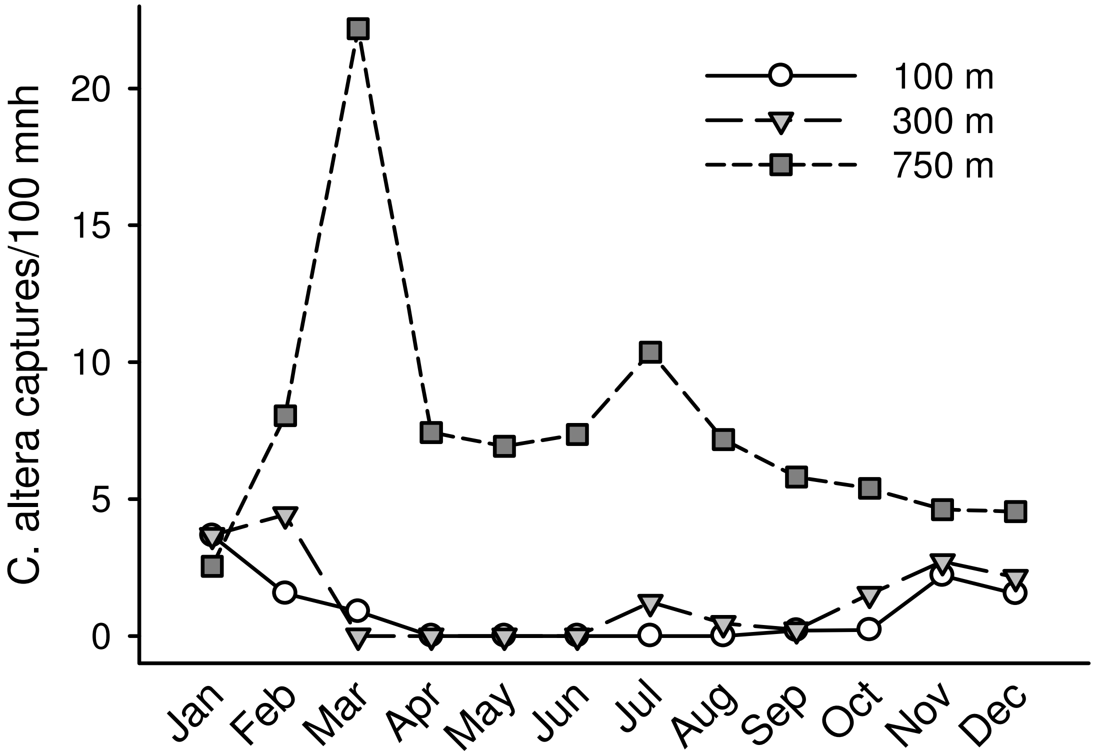

C. altera captures/100 mnh
0
5
10
15
20
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
100 m
300 m
750 m

Figure 3

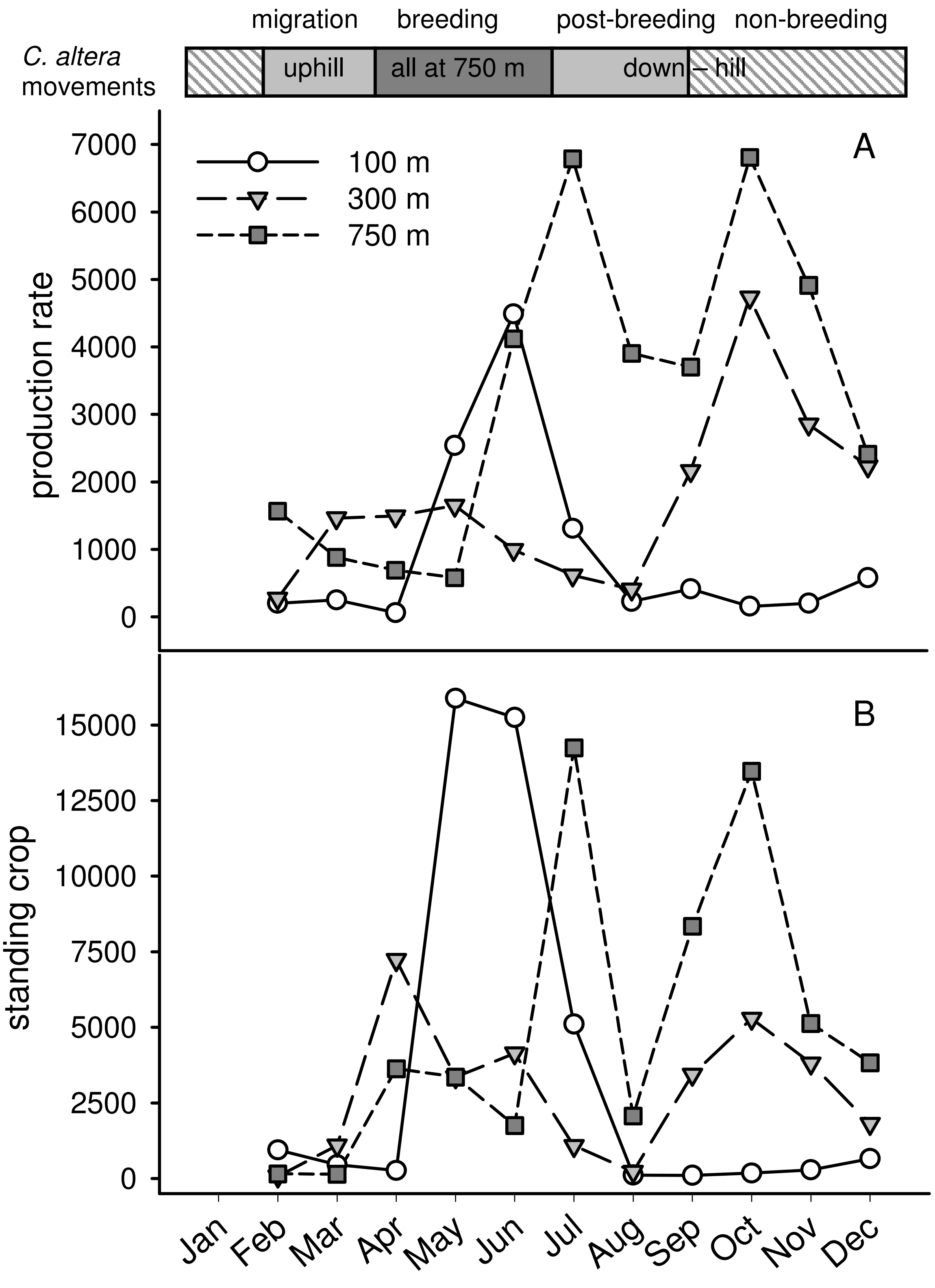

migration
breeding
post-breeding
non-breeding
C. altera movements
uphill
all at 750 m
down – hill
A
100 m
300 m
750 m
production rate
0
1000
2000
3000
4000
5000
6000
7000
B
standing crop
0
2500
5000
7500
10000
12500
15000
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 4

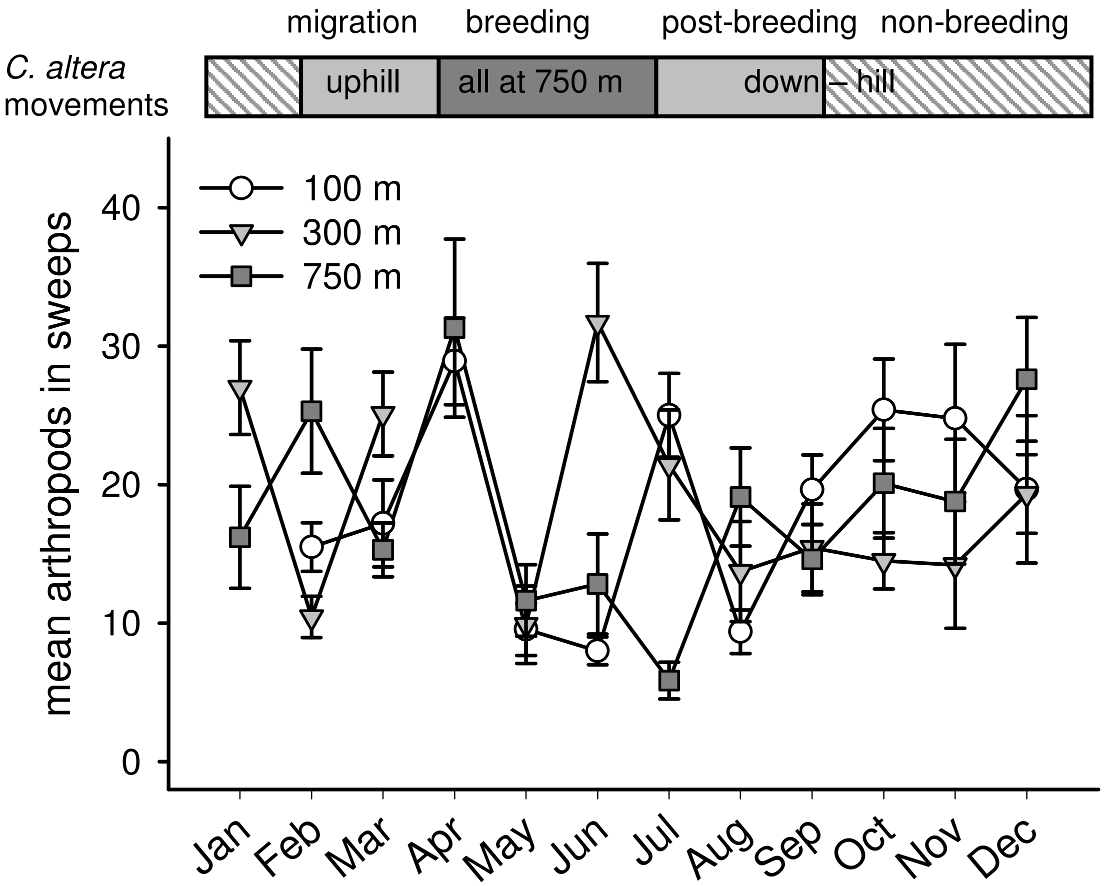
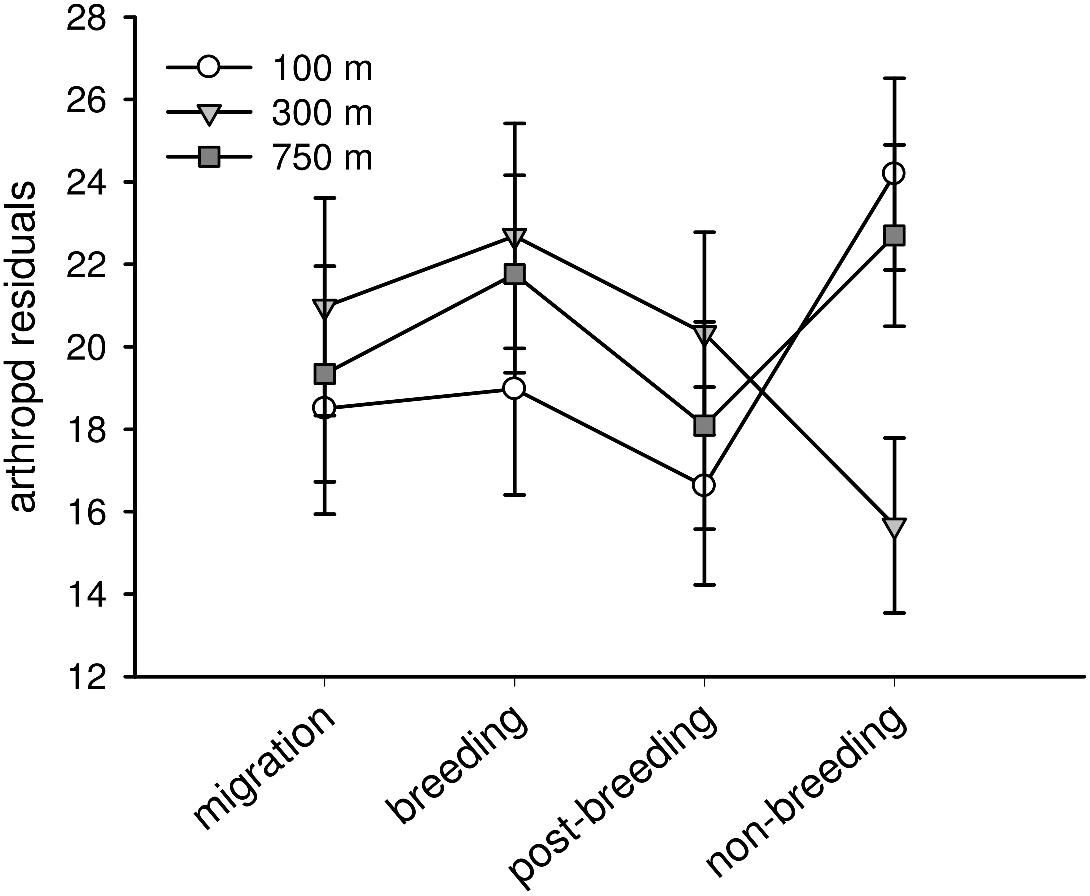

migration
breeding
post-breeding
non-breeding
C. altera
movements
uphill
all at 750 m
down – hill
mean arthropods in sweeps
0
10
20
30
40
100 m
300 m
750 m
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 5


28
26
24
22
20
18
16
14
12
arthropd residuals
100 m
300 m
750 m
migration
breeding
post-breeding
non-breeding

Appendix 1

Plant species whose seeds I found in 283 *C. altera* fecal samples, and their frequency of occurrence. I analyzed all fecal samples from site-month combinations during which I collected 10 or fewer fecal samples. At sites during months in which I collected > 10 samples, I analyzed 10–38 samples, attempting to equally represent different sex and age classes.

Species	**N samples**
AQUIFOLIACEAE	
Ilex maxima W. J. Hahn	6
ARACEAE	
Anthurium bakeri Hook. f.	2
Anthurium clavigerum Poepp.	1
Anthurium obtusilobum N/D	1
Anthurium scherzianum Schott	1
ARALIACEAE	
Schefflera nicaraguensis (Standl.) A. C. Sm.	4
Schefflera systyla (D. J. Smith) Viguier	2
ARECACEAE	
Geonoma ferruginea H. Wendl. ex Spruce	1
CECROPIACEAE	
Coussapoa parviceps Standl.	4
CHLORANTHACEAE	
Hedyosmum bonplandianum Kunth.	2
Hedyosmum costaricense C. Wood	2
Hedyosmum scaberrimum Standl.	20
CLUSIACEAE	
Clusia stenophylla Standl.	1
DILLENIACEAE	
Pinzona coriacea Mart. & Zucc.	3
ERICACEAE	
Cavendishia capitulata Donn. Sm.	1
EUPHORBIACEAE	
Tetrochidium euryphyllum Standl.	6
GESNERIACEAE	

Species	**N samples**
Besleria columnoides Hanst.	4
Besleria robusta Donn. Sm.	1
Besleria aff. solanoides Kunth.	1
MARCGRAVIACEAE	
Marcgravia caudata Triana & Planch.	14
Marcgravia pittieri Gilg.	6
MELASTOMATACEAE	
Blakea tuberculata Donn. Sm.	4
Clidemia clandestina Almeda	7
Clidemia densiflora (Standl.) Gleason	11
Clidemia discolor (Triana) Cogn.	3
Clidemia epiphytica (Triana) Cogn.	9
Clidemia japurensis DC.	7
Clidemia ombrophila Gleason	4
Clidemia sp.1	1
Conostegia micrantha Standl.	48
Conostegia oerstediana O. Berg ex Triana	1
Conostegia rufescens Raudin	5
Conostegia xalapensis (Bonpl.) D. Don	1
Henriettea tuberculosa (Donn. Sm.) L. O. William	39
Leandra longicoma Cogn.	4
Miconia argentea (Sw.) DC.	28
Miconia calocoma Almeda	1
Miconia centrodesma Naudin	2
Miconia gracilis Triana	1
Miconia hammelii (sp. nov.)	1
Miconia impetiolaris (Sw.) D. Don	2
Miconia ligulata Almeda	6
Miconia loreyoides Triana	11
Miconia multiplinervia Cogn.	10
Miconia multispicata Naudin	5
Miconia serrulata (DC.) Naudin	1
Miconia simplex Triana	6
Miconia Indet 59	10
Ossaea brenesii Standl.	6
Ossaea laxivenula Wurdack	3
Ossaea macrophylla (Benth.) Cogn.	17
Ossaea micrantha (Sw.) Macfad.	3

Species	**N samples**
Ossaea robusta (Triana) Cogn.	30
Indet 53	1
MONIMIACEAE	
Siparuna tecaphora (Poepp. & Endl.) A. DC.	1
MORACEAE	
Ficus colubrinae Standl.	7
NYCTAGINACEAE	
Neea amplifolia Donn. Sm.	1
RUBIACEAE	
Guettarda crispiflora Vahl.	1
Hamelia patens Jacq.	1
Palicourea gomezii C. M. Taylor	2
Psychotria cooperi Standl.	13
Psychotria elata (Sw.) Hammel	2
Psychotria hispidula Standl. Ex Steyerm.	2
Psychotria luxurians Rusby	11
Psychotria microbotrys Ruiz ex Standl.	1
Psychotria buchtienii Standl.	10
Sabicea panamensis Wernham	12
Indet 62	2
Indet 63	1
Indet 64	2
SOLANACEAE	
Witheringia solanacea L'Hér	1
ZINGIBERACEAE	
Indet 60	1
Unknown Family	
Indet 36	4
Indet 38	1
Indet 65	1
Indet 66	2

Appendix 2

Summary of fruiting parameters, the number of marked individuals, density/ha for all plant species I marked to monitor phenology and fruit production at each of my three study sites. In this table, sites are represented by the elevation at which they are located; the 100 m site was on the property of the La Selva Biological Station, the 300 m site was in Braulio Carrillo National Park near the “Cantarrana” refuge, and the 750 m site was in the Rara Avis reserve.

species	min. repro. size[1]	in *C. altera* diet?[2]	*n* marked individs.			density/ha[3]			mean (SE) fruit production rate[4]			max mean production rate (month)[5]		
			100 m	300 m	750 m	100 m	300 m	750 m	100 m	300 m	750 m	100 m	300 m	750 m
Melastomataceae														
Clidemia densiflora (Standl.) Gleason	0.7	yes	8	6	0	33	30	0	2.6 (0.7)	7.8 (2.6)		7.2 (Dec)	26.1 (Dec)	
Clidemia hammelii Almeda	1	no	0	3	0	0	70	0		2.0 (1.2)			11.2 (Oct)	
Clidemia ombrophila Gleason	1	yes	2	3	0	2	2	20	14.7 (7.6)	3.8 (1.9)		63.3 (Sep)	20.2 (Mar)	
Conostegia cf bracteata	2	no	6	1	0	2	2	0	1.1 (0.2)	1.3 (0.6)		1.3 (Jul)	5.4 (Oct)	
Conostegia lasciopoda Benth	5.5	no	0	3	0	7	2	0		5.6 (0.2)			5.7 (Aug)	
Conostegia micrantha Standl.	3.5	yes	8	5	14	2	2	80	6.2 (0.8)	9.4 (4.8)	27.5 (16.0)	6.9 (Jun)	17.7 (Jun)	71.8 (Jul)
Conostegia rhodopetala Donn. Sm.		no	0	0	1	0	0	2						
Conostegia rufescens Raudin	1.1	yes	0	4	8	0	90	530		8.5 (2.9)	1.4 (1.1)		12.6 (Dec)	4.7 (Nov)

species	min. repro. size[1]	in *C. altera* diet?[2]	*n* marked individs.			density/ha[3]			mean (SE) fruit production rate[4]			max mean production rate (month)[5]		
			100 m	300 m	750 m	100 m	300 m	750 m	100 m	300 m	750 m	100 m	300 m	750 m
Melastomataceae sp. 1	7.8	no	1	0	0	2	0	0						
Graffenrieda galleotii (Naudin) L. O. Williams	2	no	0	3	0	20	10	0		2.4 (1.3)			5.8 (Nov)	
Henriettea tuberculosa (Donn. Sm.) L. O. William	2.5	yes	14	6	6	47	30	40	20.1 (11.0)	5.8 (3.2)	8.9 (5.9)	94.2 (Jun)	25.3 (May)	38.0 (Jun)
Leandra grandifolia Cogn.	1.6	no	0	1	0	0	2	0		9.5 (4.1)			17.0 (Nov)	
Miconia affinis DC.		no	1	0	0	2	0	0						
Miconia appendiculata Triana		no	3	1	0	2	2	0						
Miconia dorsiloba Gleason	2	no	0	5	0	0	10	0		0.6 (0.4)			2.8 (Oct)	
Miconia gracilis Triana	2	yes	6	5	8	2	10	2	2.3 (1.3)	4.2 (2.7)	0.9 (0.9)	6.6 (Jul)	18.7 (May)	2.7 (May)
Miconia grayumii Alameda	3.9	no	1	0	0	2	0	0	46.2 (16.0)			145.8 (Feb)		
Miconia ligulata Almeda	2	yes	0	2	0	0	40	0						
Miconia loreyoides Triana	2	yes	0	0	1	0	0	20			0.4 (0.2)			1.0 (Apr)
Miconia multispicata Naudin		yes	0	2	0	0	2	0						
Miconia nervosa (J. E. Sm.) Triana	1	no	4	1	0	13	2	0	0.3 (0.1)	3.1 (1.3)		0.4 (Apr)	4.4 (Apr)	
Miconia simplex Triana	1.3	yes	6	3	0	27	40	0	0.8 (0.6)	2.0 (1.5)		3.6 (Dec)	15.0 (Nov)	
Miconia sp. G		no	1	0	0	2	0	0						
Ossaea brenesii Standl.	2.3	yes	0	0	1	0	0	30			0.4 (0.1)			0.9 (Oct)
Ossaea macrophylla (Benth.) Cogn.	0.9	yes	6	5	7	7	210	40	0.4 (0.4)	4.7 (1.4)	1.9 (0.9)	2.1 (Aug)	15.8 (Oct)	5.7 (Dec)

species	min. repro. size[1]	in *C. altera* diet?[2]	*n* marked individs.			density/ha[3]			mean (SE) fruit production rate[4]			max mean production rate (month)[5]		
			100 m	300 m	750 m	100 m	300 m	750 m	100 m	300 m	750 m	100 m	300 m	750 m
Ossaea robusta (Triana) Cogn.	1.5	yes	1	0	8	2	0	150	17.3 (7.9)		10.6 (3.5)	68.4 (Aug)		40.3 (Oct)
Rubiaceae														
Coussarea talamancana Standl.	4.9	no	0	3	0	7	20	0		0.1 (0.1)			0.7 (Jul)	
Palicourea gomezii C. M. Taylor	3.5	yes	0	0	7	0	40	20			1.1 (0.2)			2.7 (Mar)
Psychotria acuminata Benth.	2.2	no	1	0	0	2	0	0	1.0 (0.4)			3.3 (Feb)		
Psychotria buchtienii Standl.	0.7	yes	6	0	10	100	20	280	0.3 (0.2)		0.7 (0.2)	1.9 (Mar)		1.9 (Jul)
Psychotria elata (Sw.) Hammel	1	yes	0	0	2	13	160	270			0.5 (0.4)			0.9 (Oct)
Psychotria hispidula Standl. Ex Steyerm.	1.6	yes	0	1	0	0	10	0		1.5 (1.3)			8.1 (Oct)	
Psychotria microbotrys Ruiz ex Standl.	1.2	yes	0	1	1	7	2	10		16.1	1.5 (1.4)		16.1 (Oct)	7.2 (Nov)
Psychotria suerrensis Donn. Sm.	1	no	4	8	0	67	90	0	0.2 (0.1)	0.1 (0.0)		0.5 (Sep)	0.3 (Nov)	
Rudgea cornifolia (Kunth) Standl.	4.7	no	1	0	0	2	0	0						

[1] I estimated the minimum size at which a species is reproductive by three sets of measurements (basal diameter, diameter at

breast height, and height of tree) for all marked individuals of a species and all individuals entering into plant transects (see text for details). I also noted for each individual if it was in bud, flower, or fruit. I chose the best predictor of reproductive status by conducting three sets of logistic regression analyses. Because basal diameter was more strongly correlated with reproductive status than either dbh or tree height, I used basal diameter (cm) as my measure of minimum reproductive size. I then searched all records of plants from all sites for each species for the smallest individual found flowering or fruiting and used this as my minimum reproductive size for the species as a whole.

[2] I marked individuals of some plant species that I never subsequently found in fecal samples of *C. altera*. I restricted my analyses to those species whose seeds appeared in the 283 fecal samples (Appendix 1) collected during 2004 that I examined.

[3] I calculated density of reproductive-sized individuals per ha for each marked plant species at each of the three sites by conducting 10–15 0.01 ha belt transects. I located transects ≥ 100 m from each other, and noted the species, basal diameter, dbh (if relevant) and height of all individuals ≥ 1 m tall of all species in the families Melastomataceae and Rubiaceae. I used the summed densities in these transects to estimate densities per ha. I arbitrarily assigned values of 2 individuals/ha to species I marked at a site but that occur in such low densities that they did not enter into transects at that site.

[4] Mean production rate represents the average daily production rate of ripe fruits for all individuals bearing fruit in a given month at a site, averaged over all fruiting months for the species.

[5] Maximum production rate is the highest monthly mean production rate (and the month in which that maximum occurred) calculated by taking the average rate of all individuals bearing fruit in a given month.

Appendix 3

Mean mass and sample contents of 276 sweep samples from three sites during 2004. I excluded ants and termites as well as taxa belonging to orders that characteristically inhabit soil and decaying wood (orders on the right side of the table) as these taxa are not potential prey of *C. altera*.

			n individuals of orders included in analyses																						*n* individuals, excluded orders							
	N samples	mean (SE) sample mass	Arachnida (Aranae)	Arachnida (non-Aranae)	Chilopoda	Colembola	Coleoptera	Diptera	Dermaptera	Dictyoptera	Diplopoda	Ephemeroptera	Hemiptera	Homoptera	Hymenoptera (non-Formicidae)	Larvae and eggs	Lepidoptera	Neuroptera	Odonata	Orthoptera	Phasmida	Thysanoptera	Thysanura	unknown	Diplura	Hymenoptera (Formicidae)	Isopoda	Isoptera	Phthiraptera	Psocoptera	Siphonaptera	Zoraptera
La Selva, 100 m																																
Feb	10	0.374 (0.174)	40	3			27	10	2	4			1	13	12	8		1		23	2		2	8		21	1	3				
Mar	10	0.194 (0.079)	17	4	2		45	21	4	10			15	7	7	9	1		3	13	3			11		107	2	2	1			
Apr	10	0.173 (0.031)	48	4	1		46	63	13	13			20	23	19	3	2		3	14				17		30	3					
May	9	0.107 (0.029)	14	8			20	8	2	5			1	3	5	1	1			4				14		19						
Jun	2	0.092 (0.08)	4				4	2					1											5				3				
Jul	10	0.216 (0.057)	29	8	1		67	33	15	4		1	4	22	29	7	5	1		11	1			15		21	2					
Aug	8	0.167 (0.049)	15	4			22	3		3			11	2	2	3				3	2			5		11		15				

			n individuals of orders included in analyses																						*n* individuals, excluded orders							
	N samples	mean (SE) sample mass	Arachnida (Aranae)	Arachnida (non-Aranae)	Chilopoda	Colembola	Coleoptera	Diptera	Dermaptera	Dictyoptera	Diplopoda	Ephemeroptera	Hemiptera	Homoptera	Hymenoptera (non-Formicidae)	Larvae and eggs	Lepidoptera	Neuroptera	Odonata	Orthoptera	Phasmida	Thysanoptera	Thysanura	unknown	Diplura	Hymenoptera (Formicidae)	Isopoda	Isoptera	Phthiraptera	Psocoptera	Siphonaptera	Zoraptera
Sep	8	0.274 (0.126)	23	10			26	22	1	10				21	10	4	4			14	1			13		32	1	4				
Oct	10	0.546 (0.191)	54	11	1		37	49		7			14	13	16	6	3			24	4	1		18		55	7	1				
Nov	9	0.37 (0.148)	39	15	1	1	45	24	1	12			13	10	15	6	5			20	2			16		59	4	10		1	1	1
Dec	6	0.22 (0.087)	20	6			22	19	1	6			6		14	5	2			10	2			5	1	10	5	1				
Cantarrana, 300 m																																
Jan	9	0.190 (0.050)	43	6	1		65	29	12	1			2	28	22	3				27	1			4		18						
Feb	9	0.138 (0.033)	16	1	2	1	23	5	1	3			2	4	7	5	1			20		1		4		7	1					
Mar	10	0.229 (0.065)	52	12			43	27	9	7				21	19	8	7		1	31	5			11		49	1					
May	8	0.075 (0.041)	12	7			13	12	2	2			1	9	5	4	1			9				2		23	1					
Jun	10	0.272 (0.099)	44	15	1		59	46	14	15			17	29	20	12	4			31	1			10		54	4					
Jul	7	0.296 (0.116)	24	4			27	15	6	3	1		6	21	12	10				10				11		45	4					
Aug	7	0.175 (0.061)	17	4	1		26	7	1	4			3	10	2	4	1			11	1			6		2	1					

			n individuals of orders included in analyses																							*n* individuals, excluded orders							
	N samples	mean (SE) sample mass	Arachnida (Aranae)	Arachnida (non-Aranae)	Chilopoda	Colembola	Coleoptera	Diptera	Dermaptera	Dictyoptera	Diplopoda	Ephemeroptera	Hemiptera	Homoptera	Hymenoptera (non-Formicidae)	Larvae and eggs	Lepidoptera	Neuroptera	Odonata	Orthoptera	Phasmida	Thysanoptera	Thysanura	unknown	Diplura	Hymenoptera (Formicidae)	Isopoda	Isoptera	Phthiraptera	Psocoptera	Siphonaptera	Zoraptera
Sep	9	0.304 (0.075)	23	10	1	2	26	15	3	8			1	11	6	9	3			10	1			10		377	4					
Oct	10	0.279 (0.117)	36	2			21	12	1	7			9	10	15	2	2			16	1		3	11		73	1	9				
Nov	5	0.074 (0.031)	15	11			4	3		4				13	5	6	1			2	4			3		144	2					
Dec	6	0.084 (0.018)	16	1			18	16	1	3			2	11	18	8	1			6	1			14		103	1	5				
Rara Avis, 750 m																																
Jan	5	0.096 (0.01)	11	1			21	9	3	1		1	1	5	7	2	1			12			1	5		3	4					
Feb	10	0.187 (0.078)	48	7		2	54	29	7	5			12	37	15	3				28	1			6		10	2					
Mar	10	0.061 (0.012)	36	5			31	11	3	6	1		4	14	9	7	1		3	11	1			11		30	2	1	1			
Apr	10	0.209 (0.031)	37	5			56	50	8	16			12	42	24	7	4			27	2		1	23		22	6					
May	8	0.124 (0.058)	16	8	1		35	3	1	1			1	6	5	2	1			4	1			8		6	2					
Jun	6	0.163 (0.071)	14	5			14	9		3			4	5	1	9	1			7	2			3		85	6					

			n individuals of orders included in analyses																						*n* individuals, excluded orders							
	N samples	mean (SE) sample mass	Arachnida (Aranae)	Arachnida (non-Aranae)	Chilopoda	Colembola	Coleoptera	Diptera	Dermaptera	Dictyoptera	Diplopoda	Ephemeroptera	Hemiptera	Homoptera	Hymenoptera (non-Formicidae)	Larvae and eggs	Lepidoptera	Neuroptera	Odonata	Orthoptera	Phasmida	Thysanoptera	Thysanura	unknown	Diplura	Hymenoptera (Formicidae)	Isopoda	Isoptera	Phthiraptera	Psocoptera	Siphonaptera	Zoraptera
Jul	7	0.040 (0.012)	9				8	3		1			1	7	4	1					1	1		5		20				1		
Aug	10	0.121 (0.022)	32	6			46	30	3	3	1		6	11	22	3				22				6		16	5					
Sep	5	0.079 (0.033)	8	6			22	7	6	3				10	2	3				3				3		5	1	1				
Oct	10	0.278 (0.196)	29	4	2		76	20		6	1		15	6	14	6	2			15	1			6		15	2	4				
Nov	9	0.177 (0.075)	22	9			30	13	3	4			15	11	6	35	4			15	2			1		22	2			1		
Dec	5	0.124 (0.029)	23	1	2		51	10	3	1			9	11	11	1				7				8	1	51	3					