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Linking Avian Life History and Ecological Traits With Environmental Attributes: Investigation of Patterns Across Ecological and Evolutionary Scales

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Evolution, Ecology and Organismal Biology

by

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DEDICATION

I dedicate this dissertation to my loving and supportive parents

ABSTRACT OF THE DISSERTATION

Linking Avian Life History and Ecological Traits With Environmental Attributes: Investigation of Patterns Across Ecological and Evolutionary Scales

by

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Natural selection favors traits that enhance fitness in a species and species occur in habitats for which they have suitable traits. These represent evolutionary and ecological processes respectively. Elucidating the relationships between species life history, ecological traits and environmental attributes is necessary to understand the factors shaping the evolution of traits and to gain a mechanistic understanding of communities so we may be able to predict their responses to environmental change.

In the first chapter, I analyze distribution patterns of a breeding bird community along an elevational gradient to test for distinct associations of traits with environmental variation associated with elevation. Communities in high elevations have species with longer nestling periods and wherein males perform incubation feeding. These patterns are similar to those observed in comparisons across phylogenetically paired taxa and

demonstrate that selection pressures across elevational gradients select for similar traits despite phylogenetic histories.

In the second chapter, I analyze relationships between life history, ecological traits and environmental attributes across multiple spatial scales in a breeding bird community distributed in a vegetation type subjected to rapid anthropogenic disturbance in the form of urbanization, agriculture, exotic grass invasion. Disturbance variables were associated with larger body mass, residents, disturbance tolerance. Foraging behaviors such as probing and bark gleaning responded negatively to disturbance and can serve as indicators for future monitoring. Seed eating, ground foraging, rock nesting and gleaning were related positively to disturbance and native vegetation attributes indicating species with these traits may better cope with environmental change.

In the third chapter, I analyzed life history variation in galliforms along elevational gradients to test the hypothesis that high elevation environments select for a trade-off of reduced fecundity and increased investment in offspring quality. I predicted that lack of parental care constraint would result in clutch size not varying across elevations but number of broods raised would be fewer at high elevations. Investment in offspring quality would reflect as variation in egg mass. As predicted, clutch size did not vary and egg mass increased with elevation providing partial support for the hypothesis.

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GENERAL INTRODUCTION

What are the causes and consequences of variation in species traits? How does a species cope with the environmental conditions found in its habitat? What are the implications for species and communities when environmental conditions change? These are some of the questions that ecologists have been tackling over the past decades. Community ecologists have studied the properties of aggregate populations; for e.g. species richness and diversity of communities (Keddy 1992) and factors that influence community structure and composition. These represent processes arising out of patterns of distribution and abundance of species. Evolutionary ecologists have focused on the causes and consequences of species life history and ecological traits and the factors that drive their evolution (Roff 1992, Martin 1996). An integration of the two approaches can help us understand how selection pressures resulting from environmental variation shape evolution of species traits, and how the association between traits and environmental variables could influence species distribution patterns and consequently affect community structure and composition. Trait based approaches that analyze relationships between species traits and environmental variables have been advanced to help bridge this gap (Mcgill et al. 2006, Webb et al. 2010). Traits refer to biological attributes of organisms that span morphology, physiology, behavior and life history characteristics of species and that affect species' fitness (Webb et al. 2010). Trait based approaches have the advantage of being taxon independent, and since they are not constrained by species identity can be applied across assemblages to produce generalizable results. As these approaches are directly related to the environment, they facilitate a mechanistic understanding of relationships and thus increase our ability to make predictions across environmental gradients and/or change (Webb et al. 2010). Studies of trait-environment relationships allow us to ask questions at ecological and evolutionary scales (Ribera et al. 2001). At an evolutionary scale, it helps us understand the selection pressures resulting from environmental variation that facilitate the evolution of species traits, e.g. life history strategies. At the ecological scale, it helps us understand how such trait-environment associations facilitate species persistence in a habitat and therefore, the influence of such relationships in determining changes in community structure and composition in the face of potential environmental change. For e.g. these approaches have been used to understand community response to urbanization (Meffert and Dziock 2013), land management practices (Ribera et al. 2001), response of species to fire (Azeria et al. 2011).

A useful way to understand how species traits and consequently their distribution patterns are affected by environmental variation is to investigate such trends along environmental gradients (McGill et al. 2006). Life history traits and strategies represent a set of co-adapted traits evolved in response to ecological conditions (Stearns 1976). Avian life history variation along environmental gradients such as latitude is well known. As we move from the tropics to the poles, clutch sizes increase, egg masses decrease, incubation and nestling periods decrease, adult mortality increases (Lack 1947, 1948, Martin 1996). Moreau (1944) first discussed the pattern of increasing clutch size with latitude. Subsequently, Lack (1947, 1948) , Skutch (1949), Ashmole (1963) outlined factors including daylength, food availability, nest predation risk and resource seasonality as possible mechanisms of selection driving such variation. Over time, emphasis has shifted from analyzing patterns in single traits to considering the overall life history strategy of species across these gradients (Martin 2004). In doing so, the ways by which different life history traits influence one another and the trade-offs between life history traits has become clear (Nur 1984, Roff 1992, Ghalambor and Martin 2001). Thus, the ultimate factors shaping latitudinal gradient in avian life history variation can be better understood as a trade-off between reproductive effort and adult mortality, where tropical species trade-off higher adult survival for lower fecundity (Ghalambor and Martin 2001, Martin 2002). This is achieved by the effect of proximate environmental factors on individual or correlated traits. For instance, shorter breeding seasons and increasing daylength in temperate latitudes has been shown to allow for larger clutch sizes due to greater time available for foraging (Rose and Lyon 2013). Increasing temperature and resource seasonality towards higher latitudes also selects for greater clutch size through density dependent effects of adult mortality (Ashmole 1963, Jetz et al. 2008). Nest predation influences juvenile mortality risk such that high levels of nest predation may constrain parental effort and may select for smaller clutch size and shorter developmental periods (Skutch 1949, Ghalambor and Martin 2001). Food availability can also influence investment in reproduction (Lack 1947, 1948, Martin 1987 for review). Studies of life history variation along latitudinal gradients have been instrumental in helping understand latitudinal gradients in species richness and diversity (Cardillo 2002).

An analogous environmental gradient that has received far less attention is elevational gradients. Elevational gradients show considerable environmental variation although over shorter spatial scales. Such environmental zonation allows mountains to support high species richness and diversity (Körner and Spehn 2002). Across elevational gradients, high elevations have colder temperatures, shorter breeding seasons, invariant daylength, lower atmospheric pressure, greater snow cover duration and greater environmental stochasticity. This consistent environmental variation offers unique selection pressures that influence life history evolution (Badyaev and Ghalambor 2001). Studies of avian life history variation across elevational gradients have shown that species and populations at high elevations lay smaller clutches, raise fewer broods, have longer incubation and developmental periods, have longer duration of parental care, have higher adult survival and fledge offspring in better condition (Badyaev 1997, Badyaev and Ghalambor 2001, Bears et al. 2009, Martin et al. 2009, Lu et al. 2010). Overall, high elevation species and population demonstrate a strategy where reduced fecundity trades-off with increase in adult and juvenile survival and/or offspring quality. Studies in other taxa have also showed that high elevation environments favor increased investment in offspring as a means to increase offspring quality and survival (Berven 1982, Baur and Raboud 1988). In birds, however, the focus has remained overwhelmingly towards studying patterns in altricial passerines. Given the limited number of studies investigating such patterns, focusing on a narrow group of species can preclude us from understanding if the trade-off between fecundity and offspring quality is indeed general. Additionally, it is vital to investigate such patterns not only across populations of a species but across multiple taxa with phylogenetically diverse histories to reveal if these strategies are evolutionary adaptations resulting through natural selection as a response to environmental and ecological constraints.

At an ecological scale, the evolution of such traits by species has consequences for species presence in a habitat and can translate into changes in community structure and composition. Keddy (1992) noted that the processes by which species are sorted into communities resembles processes of evolution by natural selection and is determined by the match between environmental conditions and species traits (Ribera et al. 2001). Southwood (1977) articulated this as the habitat templet theory; that environmental attributes act as a filter and select for certain traits; species possessing those traits pass through the filter and are able to persist in the environment. Research has shown that some of the primary factors influencing avian communities are habitat structure and composition (Wiens and Rotenberry 1981, Rotenberry 1985) and that the influence of these factors can vary with spatial scale (Wiens and Rotenberry 1981). Across large spatial scales, habitat structure and configuration appear to determine species distributions whereas within smaller spatial scales, floristic composition may determine species presence/absence (Wiens and Rotenberry 1981). Habitat disturbance can modify these relationships across all spatial scales (Brawn et al. 2001). Disturbance affects species through habitat loss, habitat degradation rendering existing habitat unsuitable, affecting breeding success to name a few. Depending on the nature of disturbance, different sets of species may be affected due to the differential effects of disturbance on traits. For example, in a study looking at the effects of logging in Borneo, terrestrial insectivores and canopy bark-gleaning insectivores were most adversely affected (Cleary et al. 2007). Urbanization is a common disturbance factor. Common effects of urbanization are known to be a decline in species richness and diversity (Chace and Walsh 2006) and biotic homogenization (McKinney 2006) wherein urbanization acts as an environmental filter allowing few species with urban-adapted traits to dominate and exploit urban conditions. Urban adapted species tend to be generalists, resident , omnivorous with a larger geographic distribution (Croci et al. 2008, Lizée et al. 2011). However, although certain traits are known to be influenced positively by urbanization, there is variation in which traits are favored depending on the urban context (Meffert and Dziock 2013). Exotic plant species can decrease habitat suitability and alter species richness and abundance of bird species (Flanders et al. 2006). Earlier efforts to understand the impacts of anthropogenic disturbance focused on identifying changes in species richness and abundance, identifying indicator groups for monitoring (Canterbury et al. 2000). However, in order to fully understand how disturbance impacts a community, we need information on how functional traits relate to disturbance variables as well as habitat variables across different spatial scales, so that we can better understand which factors influence the persistence of species and thus potentially predict responses of communities to environmental change (Moretti and Legg 2009, Davies et al. 2010).

Dissertation structure

In this dissertation, I explore trait environment relationships at both ecological and evolutionary scales. Chapter 1 and 2 investigates questions at an ecological scale and chapter 3 tests hypotheses across evolutionary scales.

In Chapter 1, I examine trait-environment relationships in a breeding bird community along an elevational gradient. Considerable environmental variation exists along elevational gradients and this environmental variation acts as a filter on species distribution patterns by selecting for species that have traits suited to specific environmental conditions found along the gradient. Analysis of life history variation along elevational gradients have focused on single species or a group of related species. However, if environmental conditions along elevational gradients act as filters, they must select for similar traits irrespective of species relatedness. I test the hypothesis that bird communities distributed across the elevational gradient would reveal distinct associations between traits and environmental variables associated with elevation and that these patterns would resemble those observed in studies of intraspecific and interspecific trait variation seen across elevational gradients.

In chapter 2, I analyze relationships between species ecological and life history traits and environmental variables across multiple spatial scales in a bird community distributed within the highly heterogeneous coastal sage scrub vegetation type. Coastal sage scrub is a rapidly disappearing vegetation type subjected to intense anthropogenic disturbance, namely urbanization and exotic species invasion. Past studies on bird community dynamics have shown that habitat structure and composition are influential factors and that their effects are mediated by spatial scale. Additionally, it is know that disturbance affects these relationships from local to regional scales. However, we know little about how species traits are related to disturbance variables and what consequences such relationships have for community composition and structure in the face of continued disturbance and environmental change. We hypothesized that we would find distinct trait associations with disturbance versus native vegetation variables across both local and landscape scales. We then discussed the implications for these associations to future community composition.

In chapter 3, I looked at patterns of life history variation in precocial species along elevational gradients and test the hypothesis that environmental variation across elevational gradients select for select for investment in offspring quality at a cost of reduced fecundity. These patterns have previously been shown predominantly using altricial species where investment in offspring quality and survival is achieved through increase in parental care. I hypothesize that precocial species that lack the intensive parental care found in altricial species would show similar patterns despite intrinsic differences such as developmental mode and this would be achieved through investments in egg mass. I test this hypothesis through comparative analyses on life history traits of Galliformes species after controlling for potential confounding factors such as phylogeny, latitude and body mass. Comparative analyses such as these are necessary as a first step to establish the generality of these patterns and to help elucidate the selection pressures that facilitate the evolution of such trade-offs.

REFERENCES

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103:458–473.

Azeria, E. T., J. Ibarzabal, C. Hébert, J. Boucher, L. Imbeau, and J.-P. L. Savard. 2011. Differential response of bird functional traits to post-fire salvage logging in a boreal forest ecosystem. Acta Oecologica 37:220–229.

Badyaev, A. V. 1997. Avian life history variation along altitudinal gradients: an example with cardueline finches. Oecologia 111:365–374.

Badyaev, A. V., and C. K. Ghalambor. 2001. Evolution of life histories along elevational gradients: Trade-off between parental care and fecundity. Ecology 82:2948–2960.

Baur, B., and C. Raboud. 1988. Life history of the land snail *Arianta arbustorum* along an altitudinal gradient. Journal of Animal Ecology 57:71–87.

Bears, H., K. Martin, and G. C. White. 2009. Breeding in high-elevation habitat results in shift to slower life-history strategy within a single species. Journal of Animal Ecology 78:365–375.

Berven, K. A. 1982. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica* II. An experimental analysis of larval development. Oecologia 52:360–369.

Brawn, J. D., S. K. Robinson, and F. R. Thompson III. 2001. The role of disturbance in the ecology and conservation of birds. Annual Review of Ecology and Systematics 32:251–276.

Canterbury, G., E., T. E. Martin., D. R. Petit, L. J. Petit, and D. F. Bradford. 2000. Bird communities and habitat as ecological indicators of forest condition in regional monitoring. Conservation Biology 14:544–558.

Cardillo, M. 2002. The life-history basis of latitudinal diversity gradients: How do species traits vary from the poles to the equator? Journal of Animal Ecology 71:79–87.

Chace, J. F., and J. J. Walsh. 2006. Urban effects on native avifauna: A review. Landscape and urban planning 74:46–69.

Cleary, D. F., T. J. Boyle, T. Setyawati, C. D. Anggraeni, E. E. Loon, and S. B. . Menken. 2007. Bird species and traits associated with logged and unlogged forest in Borneo. Ecological Applications 17:1184–1197.

Croci, S., A. Butet, and P. Clergeau. 2008. Does urbanization filter birds on the basis of their biological traits? Condor 110:223–240.

Davies, K. F., B. A. Melbourne, C. D. James, and R. B. Cunningham. 2010. Using traits of species to understand responses to land use change: Birds and livestock grazing in the Australian arid zone. Biological Conservation 143:78–85.

Flanders, A. A., W. P. Kuvlesky Jr, D. C. Ruthven III, R. E. Zaiglin, R. L. Bingham, T. E. Fulbright, F. Hernández, L. A. Brennan, and J. H. Vega Rivera. 2006. Effects of invasive exotic grasses on South Texas rangeland breeding birds. Auk 123:171–182.

Ghalambor, C. K., and C. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292:494–497.

Jetz, W., C. H. Sekercioglu, and K. Böhning-Gaese. 2008. The worldwide variation in avian clutch size across species and space. PLoS biology 6:e303.

Keddy, P., A. 1992. Assembly and response rules: Two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.

Körner, C., and E. M. Spehn (Eds.). 2002. Mountain biodiversity: A global assessment. The Parthenon Publishing Group, London, UK.

Lack, D. 1947. The significance of clutch-size. Ibis 89:302–352.

Lack, D. 1948. The significance of clutch-size. Part III.—Some interspecific comparisons. Ibis 90:25–45.

Lizée, M.-H., J.-F. Mauffrey, T. Tatoni, and M. Deschamps-Cottin. 2011. Monitoring urban environments on the basis of biological traits. Ecological Indicators 11:353–361.

Lu, X., T. Yu, W. Liang, and C. Yang. 2010. Comparative breeding ecology of two white-bellied redstart populations at different altitudes. Journal of Field Ornithology 81:167–175.

Martin, M., A. F. Camfield, and K. Martin. 2009. Demography of an alpine population of savannah sparrows. Journal of Field Ornithology 80:253–264.

Martin, T. E. 1987. Food as a limit on breeding birds: A life-history perspective. Annual Review of Ecology and Systematics:453–487.

Martin, T., E. 1996. Life history evolution in tropical and south temperate birds: What do we really know? Journal of Avian Biology 27:263–272.

Martin, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. Proceedings of the Royal Society B: Biological Sciences 269:309–316.

Martin, T. E. 2004. Avian life-history evolution has an eminent past: Does it have a bright future? Auk 121:289–301.

Mcgill, B., B. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. Trends in Ecology & Evolution 21:178–185.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247–260.

Meffert, P. J., and F. Dziock. 2013. The influence of urbanisation on diversity and trait composition of birds. Landscape Ecology 28:943–957.

Moreau, R. E. 1944. Clutch-size: A comparative study, with special reference to African birds. Ibis 86:286–347.

Moretti, M., and C. Legg. 2009. Combining plant and animal traits to assess community functional responses to disturbance. Ecography 32:299–309.

Nur, N. 1984. The consequences of brood size for breeding blue tits II. Nestling weight, offspring survival and optimal brood size. Journal of Animal Ecology 53:497–517.

Ribera, I., S. Dolédec, I. S. Downie, and G. N. Foster. 2001. Effect of land disturbance and stress on species traits of ground beetle assemblages. Ecology 82:1112–1129.

Roff, D. A. 1992. Evolution of life histories: Theory and analysis. Routledge, Chapman and Hall, New York.

Rose, A. P., and B. E. Lyon. 2013. Day length, reproductive effort and the avian latitudinal clutch size gradient. Ecology 94:1327–1337.

Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? Oecologia 67:213–217.

Skutch, A. 1949. Do tropical birds rear as many young as they can nourish. Ibis 91:430–458.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46:337–365.

Stearns, S. C. 1976. Life-history tactics: A review of the ideas. Quarterly review of biology:3–47.

Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. LeRoy Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecology Letters 13:267–283.

Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological monographs:21–41.

Chapter 1： Life history correlates of environmental variation in a breeding bird community across an arid elevational gradient

ABSTRACT

Patterns of life history variation along elevational gradients have been explored using comparisons between phylogenetically paired taxa. However, selection pressures resulting from environmental variation must select for similar traits irrespective of species phylogenetic histories. I tested the hypothesis that distribution patterns of a breeding bird community along an elevational gradient should reveal distinct trait associations with environmental attributes associated with elevation, similar to that observed in comparisons of phylogenetically paired taxa. I analyzed patterns of covariation between life history and ecological traits, and environmental variables such as temperature, precipitation, vegetation structure and composition along an elevational gradient. Results showed that across the elevational gradient, high elevation communities were comprised of species with longer nestling periods, and had males that fed females during incubation. These traits were associated with change in temperature, precipitation and vegetation composition along the elevational gradient. As hypothesized, these patterns resemble those observed in comparisons of phylogenetically paired taxa and suggest that variation in temperature could influence on these traits. Energetic constraints of breeding at colder temperatures in high elevations may influence nestling period duration and incubation feeding by males may serve to alleviate that constraint.

INTRODUCTION

Patterns of avian life history variation have been investigated mainly through studying correlations between species traits and environmental variation such as seasonality in resources and temperature (Ashmole 1963, Ricklefs 1980, Jetz et al. 2008), ambient temperature (Cooper et al. 2005), daylength (Rose and Lyon 2013) and nest predation (Martin 1996), usually across large geographic scales such as latitudinal gradients. Prominent amongst these patterns are a reduction in clutch size as we move from temperate areas towards the tropics, accompanied by an increase in egg size, adult survival and increase in incubation and nestling periods (Lack 1947, 1948, Martin 1996, 2008, Ghalambor and Martin 2001). These patterns have been established at both intra- and inter-specific levels.

An analogous environmental gradient that has received less attention is elevation, even though elevation has been considered a significant influence on life histories due to the selection pressures individuals face as environments vary substantially and systematically with altitude (Badyaev 1997, Johnson et al. 2006, Bears et al. 2009). Mountains occupy 25% of the earth's land surface and are characterized by steep environmental gradients (Körner 2007). Facilitated by the physical changes that occur across short spatial scales, elevational gradients can encompass substantial environmental heterogeneity, and are thus useful for investigating a wide variety of ecological phenomena. Elevational gradients share common characteristics with latitudinal gradients (e.g. higher elevations have shorter breeding seasons, colder temperatures, more variable and less predictable weather, and greater seasonality as do higher latitudes) yet differ in other important respects such as day length, which is invariant across elevations at the same latitude, and atmospheric pressure and oxygen concentration, which decrease towards higher elevations.

Much of the research on breeding biology of birds deals with the trade-offs involved in balancing the energy needs of the adult and the young (Yom-Tov and Hilborn 1981, Conway and Martin 2000), and considerable work has dealt with the physiological constraints of reproduction at high elevations (Carey 1980, 2002). As we go from low to high elevations, the gradient in environmental conditions also creates a gradient of environmental stress as high elevation habitats are typically much more variable and harsh (Järvinen 1986), necessitating trade-offs between energy required for self-maintenance and that devoted to reproduction (Martin 2001, Martin and Wiebe 2004). In addition, colder temperatures and hypoxic conditions at higher elevations may require longer developmental periods (Wangensteen et al. 1974, Martin 2001), thus requiring higher levels of parental care and increased male participation in parental care (Clutton-Brock 1991, Badyaev and Ghalambor 2001, Johnson et al. 2007), further suggesting that individuals and species in such environments may be trading fewer offspring against higher offspring quality (Badyaev and Ghalambor 2001, Bears et al. 2009). Thus, elevational gradients are exemplary systems to study how environmental conditions such as temperature and rainfall influence life history and ecological attributes of species whilst controlling for factors such as day length and geographical location.

The diversity of birds along elevational gradients means that we can ask questions about the relationship between avian traits and the environment at a number of levels;

how traits and environmental attributes are related within species, across species within a taxonomic group, and across entire species assemblages. However, most research so far has investigated how species traits vary across elevational gradients at the population or sub-specific level (Badyaev and Ghalambor 2001, Johnson et al. 2006, Bears et al. 2009, Martin et al. 2009, Camfield et al. 2010, Li and Lu 2012). Whereas a few studies have looked at interspecific variation within a taxonomic group (Badyaev 1997), or closely related pairs of species (Badyaev and Ghalambor 2001), none have explored how traits vary within an assemblage of species.

The occurrence of species in a habitat depends upon the fit between the suite of traits it possesses and the environmental conditions of its habitat (Southwood 1977, Ribera et al. 2001). Thus, species distributed along elevational gradients may be expected to evolve traits to suit environmental variation along such gradients, and the influence of such selection pressures should apply to species comprising communities as it does to phylogenetically related groups of taxa. Indeed, community assembly along elevational gradients has been shown to be influenced by the filtering effect of environmental variation on species traits (Graham et al. 2009).

Considering life history and ecological traits of multiple species along the same elevational gradient will help us understand how the environment shapes the selection of traits. Focusing on traits rather than individual species also allows us to look for general patterns that can be found in other systems with very different taxonomy (Dray and Legendre 2008). Additionally, unlike latitudinal gradients, elevational gradients can be investigated over relatively short spatial scales, and thus, patterns arising are likely influenced by the environmental gradient itself rather than historical contingency (Malhi et al. 2010).

This study aims to analyze assemblage-level variation in life history and ecological traits in a community of birds distributed along an arid elevational gradient. I hypothesized that distribution patterns of species in a breeding bird community along an elevational gradient would reveal trait-environment associations that are similar to those observed in comparisons of phylogenetically related groups of species. I then discuss potential environmental drivers that may influence these patterns.

MATERIALS AND METHODS

Study area

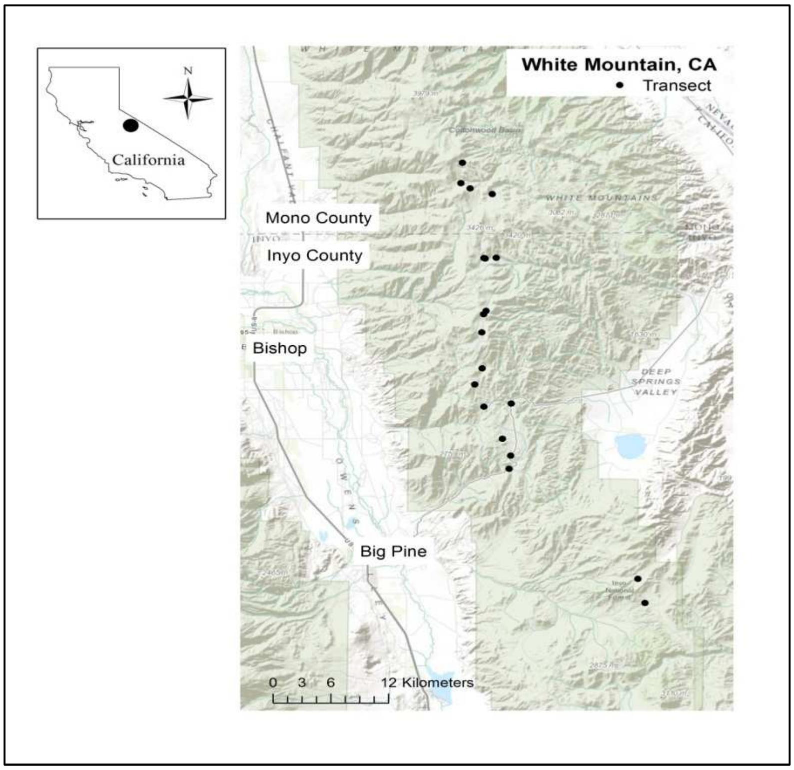


Figure 1.1. The study area within the White Mountains, CA

I used data collected in the White Mountains, CA (37°34′N 118°16′W) between 1989-1991 (Morrison et al. 1993). The White Mountains are located in Inyo County, CA, east of the Sierra Nevada, and separated from the Sierras by the Owens Valley (Fig.1.1). The mountains run approximately 80km north-south (Morrison et al. 1993), and span an elevational range of >3,000m (1,200-4,342m). Lying in the rain shadow of the Sierra Nevada, the White Mountains are relatively arid. Desert scrub dominates from 1,219-1,981m. The primary shrub species at this elevation are shadscale (*Atriplex confertifolia),* creosote bush (*Larrea tridentate),* Nevada ephedra (*Ephedra nevadensis),* rabbitbrush (*Chrysothamnus nauseosus)* and spiny hopsage (*Grayia spinosa).* The middle elevations (1,981-2,896m) are covered by pinyon-juniper woodland dominated by pinyon pine (*Pinus monophylla)* and Utah juniper (*Juniperus osteosperma)* in the overstory, and bitterbrush, rabbitbrush and Great Basin sagebrush (*Artemisia tridentata*) in the understory. The sub-alpine zone is found between 2,896-3,505m and is a patchwork of sagebrushes (*Artemisia* spp.*)* and open forest dominated by limber pine (*Pinus flexibilis)* and bristlecone pine (*Pinus longaeva).* The alpine zone which was not sampled is found above 3,505-4,342m; (Spira 1991).

Birds

Surveys

Ten transects each were laid within woodland habitat covering pinyon-juniper and bristlecone pine, between 2,183-3,518m elevation. Transects were at least 1km apart in each vegetation zone. Transects were U-shaped, with each arm 1800m long and connected by a 600m-long perpendicular strip. Thus, each transect was 4.2km long, collectively surveying a total of 42 km in each vegetation type. Birds were surveyed on each transect between May and July, using point counts spaced 300m apart. Fifteen points were placed on each transect, totaling 150 points in each woodland vegetation type. Three observers conducted the counts every year, yielding 3 surveys per transect per year. Point counts were started at sunrise and lasted for four hours; each point was surveyed for 10 min during which, all birds seen or heard were recorded. The direction of point counts on the transects was reversed each time, so as to avoid any temporal bias in sampling sections of the transect (Morrison et al. 1993).

Life history and ecological traits data

Information on 19 life history and ecological traits was obtained from the Birds of North America Online (Table 1.1; Poole 2005). Nine variables were quantitative: clutch size, egg volume, number of broods per year, incubation and nestling periods, bill length, wing length, and body mass of males and females. Species were marked as single-brooded if less than 25% of the individuals attempted second broods. Ten qualitative variables included sex of incubating parent, presence of incubation feeding by male, migration distance, nest type, nest substrate, basic diet, most common foraging behavior, most common foraging substrate, and the presence of sexual dichromatism and sexual size dimorphism. Migration was categorized as short, medium, long. Short distance migrants were species that migrated no further than the southern boundary of Texas and northern Mexico. Medium distance migrants were species that migrated no further than the Isthmus of Tehuantepec, whereas long distance migrants were those that migrated beyond. Species were coded such that they could occupy multiple categories for qualitative variables (e.g., a species could have foraging behaviors that included both flycatching and sallying). Sexual size dimorphism was categorized as a categorical variable, with either none, female larger, or male larger based on measurements of wing length. If there was no overlap in measurements between the males and females, and the males measured more than females, then the species was coded as “male larger”. If there was overlap in male and female measurements, then the species was coded as non-dimorphic. Species were marked as sexually dichromatic if there were diagnostic plumage differences between males and females as seen in a field guide (Sibley 2003). As far as possible, data were recorded for the subspecies found in the White Mountains. I excluded traits that had categories represented only by one species. Thus, the number of species-by-traits combinations differed for some analyses; 16 traits were represented by 42 species and 2 traits were represented by 43.

Environmental Variables

Vegetation surveys

Vegetation measurements were made once at each point count site during 1989 and1991 (Table 1.2). From one to three 30m-diameter circular vegetation plots, was established at each point count station. One plot was centered on the point, and if a second one was measured it was centered 50-100m away in a random direction from the point center, and if there were a third plot it was centered 100-150m away in another random direction. In each plot, all pinyon pine, Utah juniper, limber pine and bristlecone pine trees present were counted. The height of each tree was placed into one of four height categories (1.5-3m, 3-6m, 6-10m and >10m). For each species, the mid-value of each height category was multiplied by the number of trees of that species found in the height category, summed across all height categories and the total divided by the total number of individuals of the species, to get the average height of that species. All cut stumps, natural stumps and snags were counted in each plot. Crown cover of shrubs was measured using a meter stick spread across the widest area of the crown. Height of shrubs in the plot was also measured. Percent ground cover of shrubs, litter, and other ground substrate was measured using a point intercept method (Bonham 1989). Points were placed at 1-m intervals across the 30-m diameter of the plot. The percent cover of each variable was estimated as the number of hits of that variable along the point intercept transect divided by the total number of intercept points on the transect. All variables measured were averaged across the 1-3 vegetation plots per bird survey point for the final analysis.

Abiotic environmental variables

Weather and elevation data for each transect were obtained from the PRISM Group (www.prism.oregonstate.edu). Latitude and longitude were measured at the beginning of each transect and were entered into PRISM to obtain elevation for each transect. Monthly minimum and maximum temperatures and precipitation were obtained for the breeding season (Feb-Aug) for 1989-1991 for each transect. Temperature and precipitation were averaged across months and years to obtain an average value for each transect. The abiotic environmental variables were recorded only at the transect level, hence, all points belonging to a transect had the same values for a variable (Table 1.2).

However, this “pseudoreplication” is accounted for in a permutation process and does not affect the determination of statistical significance (see below).

I used principal components analysis of all environmental variables to summarize independent patterns of their covariation, and then used the resulting factor scores in the 4th corner analysis described below.

Analysis

I used the 4th corner method developed by Legendre et al. (1997) as modified by Dray and Legendre (2008) to analyze bivariate environment-trait linkages. The fourth corner method was designed to directly relate variation in the biological attributes of an assemblage of species to characteristics of the environments over which that assemblage is distributed. It tests the null hypothesis that there is no statistically significant association between environmental variables and species traits (Legendre et al. 1997). The method links a matrix of the scores of environmental variables recorded at each point site (**R**) to a matrix of the ecological and life history traits scored for each species (**Q**) via a matrix containing the species presence/absence at each site (**L**), resulting in the production of a fourth matrix, which contains the associations between each environmental variable and each species trait variable (Fig.1.2). Different measures of association are calculated depending upon the types of variables involved. Associations between quantitative environmental variables and multi-category qualitative trait variables are evaluated through a pseudo F-statistic, whereas relationships between quantitative environmental and quantitative trait variables are described using Pearson correlation coefficients. Ordinary significance testing is not feasible as multiple observations of a trait with the same value but associated with different species from the same sampling station creates non-independent data. Instead statistical significance is evaluated using permutation tests. To reject the null hypothesis that there is no association between an environmental variable and a trait variable, two null hypotheses must be rejected (Dray and Legendre 2008): H_o1: $\mathbf{R} \neq \mathbf{L}$, that species are randomly distributed and are not associated with the environments in which they are found. This test is achieved by permuting entire rows of matrix **L**. (ii). H_o2: $\mathbf{L} \neq \mathbf{Q}$, that species have random ecological and life history traits. This test is achieved by permuting entire columns of matrix **L**. When both null hypotheses are rejected, we can conclude that there is indeed an association between an environment variable and a trait. Significance testing of associations is achieved by comparing an observed environment-trait association to the distribution of those associations generated by 9999 permutations for each null hypothesis. Following ter Braak et al. (2012), an alpha of 0.05 was used, and only tests that had a p-value < 0.05 after Holm's correction for multiple testing were retained. I excluded qualitative trait variables that had categories represented only by one species. The fourth-corner correlation coefficient cannot be directly compared with the Pearson's r obtained in traditional bi-variate correlations as it is calculated using two matrices (traits and environmental variables) that were sampled on different units (species and sites). Therefore, the distribution of the fourth-corner correlation statistic is unknown and empirical studies have demonstrated that statistically significant correlations are much lower than traditional correlations (Dray and Legendre 2008, Brind'Amour et al. 2011).

The three matrices: **R** (points x environment), **L** (points x species) and **Q** (trait x species) are given below.

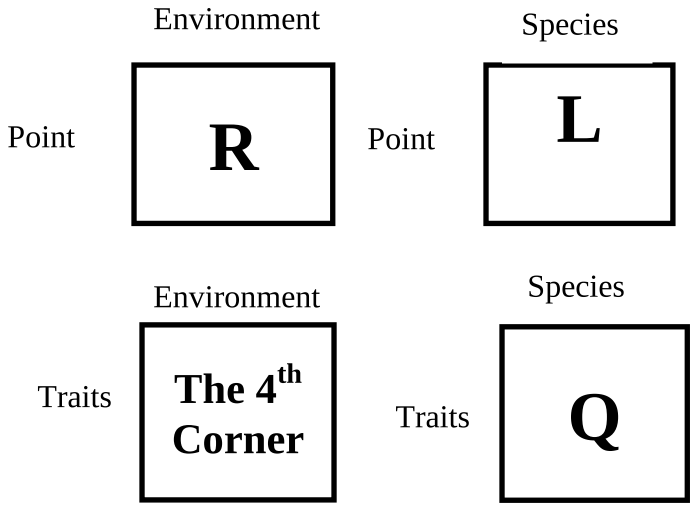


Figure 1.2. Diagrammatic representation of the fourth-corner method

Matrix R: Point x Environment

This matrix initially contained the 23 environmental attributes (abiotic and vegetation variables; Table 1.2) recorded at 300 point count sites. Because of strong inter- correlations among many of the environmental variables, Principal Component Analysis was used to summarize the main patterns of covariation and used the resultant factor scores of the point count sites on the components.

Matrix L: Point x Species

This matrix contains the presence/absence of 43 bird species found across 300 points (Table 1.3). Only species that were detected at more than 2% of the point counts in each of the two vegetation types (pinyon-juniper and bristlecone pine woodland) were included in the analysis.

Matrix Q: Species x Traits

The third matrix contains 19 life history and ecological traits for each of the 43 bird species. Wing length, body mass and bill length were log transformed prior to analysis.

The PCA of environmental variables was performed in SPSS version 20.0 (IBM Corp 2011). The fourth corner analysis was performed in R version 2.15.1 (R Development Core Team 2012) using the ade4 package (Dray and Dufour 2007).

RESULTS

Environmental variables PCA

The PCA produced 6 principal components with eigenvalues greater than 1, which explained 72.7% of the total variance (Table 1.4). PC 1 (38.9% of total variation) was a gradient defined by increasing elevation; with increasing elevation, maximum and minimum temperature decreased, and precipitation increased. Corresponding vegetation variables that increased were the average number of snags, average number and height of bristlecone pine and percent ground covered by litter, whereas the average number and height of pinyon pine and juniper decreased along with the percent ground covered by dead shrubs and the average number of stumps. Thus, PC1 captures the abiotic gradient defined by change in elevation and associated changes in vegetation structure and composition. PC2 and PC 4 (10.04% and 6.4% of total variation respectively) were defined mainly by shrub cover. PC3 (7.5% of total variation) was defined by abundance and height of limber pine, PC5 (5.2% of total variation) mainly captured variation in percent ground covered by substrate. PC6 (4.7% of total variation) is defined by the abundance of mountain mahogany and percent ground covered by vegetation. Because over 90% of the variation in elevation was associated with the first component, the second and subsequent components essentially describe components of habitat variation independent of elevation. As our objective is to examine trait variation in the context of an elevational gradient, we focus on traits related to PC1.

Trait x environment relationships

As noted, 43 bird species occurred at > 2% of the points in each vegetation type and were retained in the analysis. Of the 19 traits examined, two remained statistically significantly ($p < 0.05$) associated with the elevational gradient after correction for multiple tests. Nestling period had a significant positive relationship with PC1 ($r = 0.034$, $p = 0.049$) as did presence of incubation feeding by the male ($r = 0.051$, $p = 0.018$).

DISCUSSION

In accordance with my hypothesis, I demonstrate that patterns detected by whole-community analysis of species trait-by-environment relationships along elevational gradients mirrored several of those observed in phylogenetically paired comparisons. In an analysis of twenty-four pairs of closely related passerine species, Badyaev and Ghalambor (2001) observed that species breeding at higher elevations had longer incubation and nestling periods compared to lower elevation counterparts. They also found that high elevation species had lower clutch sizes, raised fewer broods and had greater parental care. They reasoned that high elevation species were shifting investment away from greater numbers of offspring to higher quality offspring. Intraspecific comparisons of Grey-backed Shrike (*Lanius tephronotus;* Lu et al. 2010a), Blackbird (*Turdus merula maximus;* Lu 2005), Rock Sparrow (*Petronia petronia;* Li and Lu 2012) and White-bellied Redstart (*Hodgsonius phoenicuroides*; Lu et al. 2010b) have reported longer nestling periods in higher elevation populations. Likewise, inter-specific comparisons between congeners have shown that species breeding at higher elevations have longer developmental periods (Lu 2007, Lu et al. 2008, Mu et al. 2008, Li and Lu 2012).

Mu et al. (2008) concluded that longer nestling periods in the Black Redstart (*Phoenicurus ochruros*) were required to increase offspring quality; which they postulated as an effect of low temperature and reduced oxygen availability. Montane populations of White-crowned sparrows (*Zonotrichia leucophrys*) have 24% higher daily energy expenditures than sea-level populations during the incubation and nestling period phase (Weathers et al. 2002). In this study, species in high elevation bird communities had longer nestling periods. One of the variables associated with this was lower temperature. Although it is not possible to tease out the independent effects of environmental variables in this study, research shows that low temperatures may play a role in the longer developmental periods due to the higher energetic costs faced by breeding females (Carey 1980, Conway and Martin 2000, Martin 2001). Higher energetic costs at higher elevations are also supported by the increasing number of species that show incubation feeding by the male. It has been established that incubation feeding by males is an important nutritional contribution to the females (Lifjeld and Slagsvold 1986, Nilsson and Smith 1988, Smith et al. 1989) and increases with decrease in temperature (Nilsson and Smith 1988, Pearse et al. 2004).

Alternatively, longer nestling periods could also result from slower growth rates as a result of lower food availability (Martin 1996, Badyaev and Ghalambor 2001, Stodola et al. 2010) or from lower nest predation rates (Martin 1995, Remeŝ and Martin 2002) at higher elevations. It is as yet unclear if nest predation is consistently lower at higher elevations; some studies have found it to be so (Skutch 1985), others have found no difference (Badyaev and Ghalambor 2001), and yet others have found increased predation on alpine species (Martin 2001). Food availability estimates and nest predation levels are not feasible to obtain for a community analysis and were not considered in this study.

Badyaev and Ghalambor (2001) interpreted the longer duration of incubation and nestling periods, and post fledgling care by high elevation birds to signify a trade-off between reduced fecundity and higher offspring quality. Higher energetic costs of breeding at higher elevations may result in breeding adults having reduced fecundity and lengthening developmental periods to provide sufficient parental care so as to result in high quality offspring. I cannot evaluate this explanation directly in this study because I could not examine offspring quality; however I do note that I did not find statistically significant variation in clutch size, a measure of fecundity, with elevation.

Although I did find two significant relationships of traits with elevation, I might have expected more (e.g., body size, clutch size). One reason for this could be that although a large part of the elevation gradient was sampled (> 1300m), birds in alpine vegetation

>3,500m and in desert scrub <2,100m were not. Also, sagebrush and other shrubby vegetation types adjacent to bristlecone pine woodland were not sampled; however, these do not extend the length of the elevational gradient. Finally, although the White Mountains harbor a diversity of bird species (Morrison et al. 1993), due to their arid nature species often do not occur in high abundances. Thus many species that were detected during sampling were removed from the analysis as they occurred at less than 2% of the sites in either vegetation type. Additionally, the species included in the analysis have wide elevational distributions and are not segregated into low and high elevation species. Such wide elevational distributions may mask other variation in life history patterns with elevation.

In conclusion, I have demonstrated patterns of life history variation and underscored its environmental drivers in a breeding bird community. That life history traits vary in the same direction across species with varied evolutionary histories highlights a strong environmental signal, influencing selection of traits. This study does not explore causal mechanisms; however, it aims to establish a baseline pattern, so that we may better understand the link between primary environmental drivers such as temperature and its influence on life history traits. Understanding how temperature influences life history traits is especially relevant as we seek to understand the potential impacts of climate change on birds, the first step towards which is to establish such baseline patterns. More data from mountain systems distributed across different latitudes and longitudes, will be necessary to explore the generality of these patterns.

REFERENCES

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103:458–473.

Badyaev, A. V. 1997. Avian life history variation along altitudinal gradients: An example with cardueline finches. Oecologia 111:365–374.

Badyaev, A. V., and C. K. Ghalambor. 2001. Evolution of life histories along elevational gradients: Trade-off between parental care and fecundity. Ecology 82:2948–2960.

Bears, H., K. Martin, and G. C. White. 2009. Breeding in high-elevation habitat results in shift to slower life-history strategy within a single species. Journal of Animal Ecology 78:365–375.

Bonham, C. D. 1989. Measurements for terrestrial vegetation. Wiley Intersciences, New York.

Brind'Amour, A., D. Boisclair, S. Dray and P. Legendre . 2011. Relationships between species feeding traits and environmental conditions in fish communities: A three-matrix approach. Ecological Applications 21: 363-37

Camfield, A. F., S. F. Pearson, and K. Martin. 2010. Life history variation between high and low elevation subspecies of horned larks *Eremophila* spp. Journal of Avian Biology 41:273–281.

Carey, C. 1980. Adaptation of the avian egg to high altitude. American Zoologist 20:449–459.

Carey, C. 2002. Incubation in extreme environments. Pages 238–241 *in* D. C. Deeming, editor. Avian incubation: Behavior, environment and evolution. Oxford University Press, Oxford.

Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey.

Conway, C., J., and T. Martin E. 2000. Effects of ambient temperature on avian incubation behavior. Behavioral Ecology 11:178–188.

Cooper, C. B., W. M. Hochachka, G. Butcher, and A. A. Dhondt. 2005. Seasonal and latitudinal trends in clutch size: Thermal constraints during laying and incubation. Ecology 86:2018–2031.

Dray, S., and A. B. Dufour. 2007. The ade4 package: Implementing the duality diagram for ecologists. Journal of statistical software 22:1–20.

Dray, S., and P. Legendre. 2008. Testing the species traits-environment relationships: The fourth-corner problem revisited. Ecology 89:3400–3412.

Ghalambor, C. K., and C. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292:494–497.

Graham, C. H., J. L. Parra, C. Rahbek and J. A. McGuire. 2009. Phylogenetic structure in tropical hummingbird communities. Proceedings of the National Academy of Sciences 106: 19673-19678

IBM Corp. 2011. IBM SPSS statistics for Windows. IBM Corp., Armonk, NY.

Järvinen, A. 1986. Clutch size of passerines in harsh environments. Oikos 46:365–371.

Jetz, W., C. H. Sekercioglu, and K. Böhning-Gaese. 2008. The worldwide variation in avian clutch size across species and space. PLoS biology 6:e303.

Johnson, L. S., J. L. Brubaker, E. Ostlind, and S. L. Balenger. 2007. Effect of altitude on male parental expenditure in Mountain Bluebirds (*Sialia currucoides*): Are higher-altitude males more attentive fathers? Journal of Ornithology 148:9–16.

Johnson, S., L., E. Ostlind, J. Brubaker L., S. Balenger L., B., G. P. Johnson, and H. Golden. 2006. Changes in egg size and clutch size with elevation in a Wyoming population of mountain bluebirds. Condor 108:591–600.

Körner, C. 2007. The use of “altitude”in ecological research. Trends in Ecology & Evolution 22:569–574.

Lack, D. 1947. The significance of clutch-size. Ibis 89:302–352.

Lack, D. 1948. The significance of clutch-size. Part III.—Some Interspecific Comparisons. Ibis 90:25–45.

Legendre, P., R. Galzin, and M. L. Harmelin-Vivien. 1997. Relating behavior to habitat: Solutions to the fourth-corner problem. Ecology 78:547–562.

Li, S., and X. Lu. 2012. Breeding biology of rock sparrows *Petronia petronia* in the Tibetan plateau, with special reference to life history variation across altitudes. Acta Ornithologica 47:19–25.

Lifjeld, J. T., and T. Slagsvold. 1986. The function of courtship feeding during incubation in the pied flycatcher *Ficedula hypoleuca*. Animal Behaviour 34:1441–1453.

Lu, X. 2005. Reproductive ecology of blackbirds (*Turdus merula maximus*) in a high-altitude location, Tibet. Journal of Ornithology 146:72–78.

Lu, X. 2007. Breeding ecology of an old world high-altitude warbler, *Phylloscopus affinis*. Journal of Ornithology 149:41–47.

Lu, X., G. Gong, and X. Zeng. 2008. Reproductive ecology of brown-cheeked laughing thrushes (*Garrulax henrici*) in Tibet. Journal of Field Ornithology 79:152–158.

Lu, X., C. Wang, and T. Yu. 2010a. Nesting ecology of the grey-backed shrike (*Lanius tephronotus*) in south Tibet. The Wilson Journal of Ornithology 122:395–398.

Lu, X., T. Yu, W. Liang, and C. Yang. 2010b. Comparative breeding ecology of two white-bellied redstart populations at different altitudes. Journal of Field Ornithology 81:167–175.

Malhi, Y., M. Silman, N. Salinas, M. Bush, P. Meir, and S. Saatchi. 2010. Elevation gradients in the tropics: Laboratories for ecosystem ecology and global change research. Global Change Biology 16:3171–3175.

Martin, K. 2001. Wildlife in alpine and sub-alpine habitats. Pages 239–260 *in* D. H. Johnson and T. A. O’Neil, editors. Wildlife habitats and relationships in Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Martin, K., and K. L. Wiebe. 2004. Coping mechanisms of alpine and arctic breeding birds: Extreme weather and limitations to reproductive resilience. Integrative and Comparative Biology 44:177–185.

Martin, M., A. F. Camfield, and K. Martin. 2009. Demography of an alpine population of savannah sparrows. Journal of Field Ornithology 80:253–264.

Martin, T., E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65:101–127.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: What do we really know? Journal of Avian Biology 27:263–272.

Martin, T. E. 2008. Egg size variation among tropical and temperate songbirds: An embryonic temperature hypothesis. Proceedings of the National Academy of Sciences 105:9268.

Morrison, M. L., L. S. Hall, J. J. Keane, A. J. Kuenzi, and J. Verner. 1993. Distribution and abundance of birds in the White Mountains, California. Western North American Naturalist 53:246–258.

Mu, H.-Y., N.-F. Liu and M. Yang. 2008. Breeding of the black redstart *Phoenicurus ochruros rufiventris* in the southeastern Qingzang (Qinghai-Tibetan) Plateau. Acta Zoologica Sinica 54:201–208.

Nilsson, J.-Å., and H. G. Smith. 1988. Incubation feeding as a male tactic for early hatching. Animal Behaviour 36:641–647.

Pearse, A. T., J. F. Cavitt, and J. F. Cully Jr. 2004. Effects of food supplementation on female nest attentiveness and incubation mate feeding in two sympatric wren species. The Wilson Bulletin 116:23–30.

Poole, A. 2005. The birds of North America online: http://bna.birds.cornell.edu/BNA/. Cornell Laboratory of Ornithology, Ithaca, NY.

R Development Core Team. 2012. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.

Remeŝ, V., and T. E. Martin. 2002. Environmental influences on the evolution of growth and developmental rates in passerines. Evolution 56:2505–2518.

Ribera, I., S. Dolédec, I. S. Downie, and G. N. Foster. 2001. Effect of land disturbance and stress on species traits of ground beetle assemblages. Ecology 82:1112–1129.

Ricklefs, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk 97: 38–49.

Rose, A. P., and B. E. Lyon. 2013. Day length, reproductive effort and the avian latitudinal clutch size gradient. Ecology 94: 1327-1337

Sibley, D. A. 2003. The Sibley field guide to birds of western North America. Alfred A. Knopf, Inc., New York.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithological Monographs: 575–594.

Smith, H. G., H. Källander, J. Hultman, and B. Sanzen. 1989. Female nutritional state affects the rate of male incubation feeding in the pied flycatcher *Ficedula hypoleuca*. Behavioral Ecology and Sociobiology 24:417–420.

Spira, T., P. 1991. Plant zones. Pages 77–87 *in* C. Hall, Jr. A., editor. Natural history of the White-Inyo range, Eastern California. University of California Press, Berkeley.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46:337-365

Stodola, K. W., D. A. Buehler, D. H. Kim, K. E. Franzreb, and E. T. Linder. 2010. Biotic and abiotic factors governing nestling-period length in the ovenbird (*Seiurus aurocapilla*). Auk 127:204–211.

Ter Braak, C. J. F., A. Cormont, and S. Dray. 2012. Improved testing of species traits–environment relationships in the fourth-corner problem. Ecology 93:1525–1526.

Wangensteen, O. D., H. Rahn, R. R. Burton and A. H. Smith. 1974. Respiratory gas exchange of high altitude adapted chick embryos. Respiration Physiology 21:61-70

Weathers, W. W., C. L. Davidson, C. R. Olson, M. L. Morton, N. Nur, and T. R. Famula. 2002. Altitudinal variation in parental energy expenditure by white-crowned sparrows. Journal of Experimental Biology 205:2915–2924.

Yom-Tov, Y., and R. Hilborn. 1981. Energetic constraints on clutch size and time of breeding in temperate zone birds. Oecologia 48:234–243.

Table 1.1 Life history and ecological traits used in the analysis

Variable	Code	Categories
Clutch Size	Clu.Siz	
No. Broods	No.br	
Egg Volume (cm^3)	Egg.vol	
Incubation Period (Days)	Inc.Per	
Nestling Period (Days)	Nest.Per	
Female bill length (mm)	Bill.Len.F	
Female wing length (mm)	Wing.Len.F	
Female body mass (gm.)	Bod.Ms.F	
Male body mass (gm.)	Bod.Ms.M	
Incubation Feeding by male	Inc.Fd	Y-Yes N-No U-Unknown
Incubating Parent	Inc.P	B- Both F-Female U-Unknown
Migration	Migr	R-Resident S-Short M-Medium L-Long

Variable	Code	Categories
Nest Type	Nest.Typ	O-Open
		C-Cavity
		SC-Secondary Cavity
		P-Pendulous
		U-Unknown
Sexual Dichromatism	Sex.Dichr	Y-Yes
		N-No
Sexual Dimorphism	Sex.Dimor	M-Male is larger
		N-No
Diet	Diet	IN-Insects
		VG-Vegetative matter
		NE-Nectar
		OM-Omnivore
Foraging Strata	For.Strata	T-Terrestrial
		FL-Foliage
		B-Bark
		A-Aerial
		I- Indiscriminate
Foraging Behavior	For.Beh	F-Flycatching
		GL-Gleaning
		SL- Sallying

Variable	Code	Categories
		PR-Probing
		GR- Ground
		H-Hawking
		PCK-Picking seeds and fruit
		MSC-Miscellaneous
Nest Substrate	Nest.Sub	TR-Tree
		SH-Shrub
		STR-Structure
		I- Indiscriminate
		GR- Ground

Table 1.2 Environmental variables and units

Variable	Variable code
Mean monthly max temperature (Feb-Aug) averaged over 1989-1991	ATmax (^{o}C)
Mean monthly min temperature (Feb-Aug) averaged over 1989-1991	ATmin (^{o}C)
Mean monthly precipitation (Feb-Aug) averaged over 1989-1991	APpt (in)
Elevation of transect estimated by PRISM	Elevation (m)
Average number of stumps per plot	Ast
Average number of snags per plot	Asn
Average number of pinyon pine per plot	APm
Average number of Utah juniper per plot	AJo
Average number of limber pine per plot	APf
Average number of bristlecone pine per plot	APl
Average number of mountain mahogany per plot	ACl
Average height of pinyon pine per plot	AhPm (m)
Average height of Utah juniper per plot	AhJo (m)
Average height of limber pine per plot	AhPf (m)
Average height of bristlecone pine per plot	AhPl (m)
Average height of mountain mahogany per plot	AhCl (m)
Average height of shrub species per plot	AhSh (m)
Average crown width of shrubs per plot	AcSh (m)

Variable	Variable code
Mean percentage ground cover of substrate per plot	PcGSub
Mean percentage ground cover of litter per plot	PcLt
Mean percentage ground cover of vegetation per plot	PcGVg
Mean percentage ground cover of live shrubs per plot	PcLSh
Mean percentage ground cover of dead shrubs per plot	PcDSh

Table 1.3 Bird species used in the analysis

Code	Common Name	Scientific Name
AMRO	American Robin	*Turdus migratorius*
ATFL	Ash-Throated Flycatcher	*Myiarchus cinerascens*
BEWR	Bewick's Wren	*Thryomanes bewickii*
BGGN	Blue-Gray Gnatcatcher	*Polioptila caerulea*
BHCO	Brown-Headed Cowbird	*Molothrus ater*
BHGR	Black-Headed Grosbeak	*Pheucticus melanocephalus*
BRCR	Brown Creeper	*Certhia americana*
BRSP	Brewer's Sparrow	*Spizella breweri*
BTYW	Black-Throated Gray Warbler	*Setophaga nigrescens*
BTAH	Broad-Tailed Hummingbird	*Selasphorous platycercus*
BTSP	Black-Throated Sparrow	*Amphispiza bilineata*
BUSH	Bushtit	*Psaltriparus minimus*
CAFI	Cassin's Finch	*Haemorhous cassinii*
CHSP	Chipping Sparrow	*Spizella passerina*
CLNU	Clark's Nutcracker	*Nucifraga columbiana*
CORA	Common Raven	*Corvus corax*
DEJU	Dark-Eyed Junco	*Junco hyemalis*
DUFL	Dusky Flycatcher	*Empidonax oberholseri*
FOSP	Fox Sparrow	*Passerella iliaca*
GRFL	Gray Flycatcher	*Empidonax wrightii*

Code	Common Name	Scientific Name
GTTO	Green-Tailed Towhee	*Piplio chlorurus*
HAWO	Hairy Woodpecker	*Picoides villosus*
HETH	Hermit Thrush	*Catharus guttatus*
HOFI	House Finch	*Haemorhous mexicanus*
HOWR	House Wren	*Troglodytes aedon*
MOBL	Mountain Bluebird	*Sialia currucoides*
MOCH	Mountain Chickadee	*Poecile gambeli*
NOFL	Northern Flicker	*Colaptes auratus*
PIJA	Pinyon Jay	*Gymnorhinus cyanocephalus*
PLTI	Juniper titmouse	*Baeolophus ridgwayi*
PYNU	Pygmy Nuthatch	*Sitta pygmaea*
RCKI	Ruby-Crowned Kinglet	*Regulus calendula*
RECR	Red Crossbill	*Loxia curvirostra*
ROWR	Rock Wren	*Salpinctes obsoletus*
RSTO	Spotted Towhee	*Piplio maculatus*
WESJ	Scrub Jay	*Aphelocoma californica*
SCOR	Scott's Oriole	*Icterus parisorum*
SOVI	Solitary Vireo	*vireo plumbeus*
TOSO	Townsend's Solitaire	*Myadestes townsendi*
VGSW	Violet-Green Swallow	*Tachycineta thalassina*
WBNU	White-Breasted Nuthatch	*Sitta carolinensis*

Code	Common Name	Scientific Name
WETA	Western Tanager	*Piranga ludoviciana*
YRWA	Yellow-Rumped Warbler	*Setophaga coronata*

Table 1.4 Summary of Principal Components Analysis of the **R** (environmental) matrix. Main entries are factor loadings. See Table 1.2 for variable codes. Bold denotes factor loadings > 0.5

Variable	Component					
	Fac_1	Fac_2	Fac_3	Fac_4	Fac_5	Fac_6
ATmax	**-0.94**	-0.08	0.04	-0.02	0.00	0.11
ATmin	**-0.94**	-0.10	0.03	-0.01	-0.01	0.10
APpt	**0.91**	0.09	-0.13	0.01	-0.06	-0.07
Elevation	**0.96**	0.09	-0.06	0.02	0.00	-0.10
Ast	**-0.58**	-0.33	0.10	-0.02	0.28	-0.03
Asn	**0.65**	-0.27	0.16	-0.24	0.02	0.17
APm	**-0.72**	-0.11	0.06	-0.01	-0.27	0.20
AJo	**-0.60**	-0.27	0.05	0.07	0.53	-0.08
APl	**0.71**	-0.36	0.12	-0.25	0.08	0.24
AhPm	**-0.84**	-0.12	0.08	-0.05	-0.10	0.10
AhJo	**-0.72**	-0.22	0.05	0.08	0.27	0.00
AhPl	**0.81**	-0.20	0.00	-0.10	0.08	0.18
PcLt	**0.61**	0.08	0.14	-0.11	0.10	0.18
PcDSh	**-0.55**	0.26	0.05	0.27	-0.01	0.01
AhCl	0.29	**0.65**	0.08	0.29	0.25	0.29
AcSh	-0.40	**0.56**	0.36	-0.47	-0.10	-0.13
PcLSh	-0.27	**0.63**	-0.20	0.27	-0.04	-0.31

Variable	Component					
	Fac_1	Fac_2	Fac_3	Fac_4	Fac_5	Fac_6
APf	0.29	-0.10	**0.76**	0.44	-0.06	-0.11
AhPf	0.34	-0.11	**0.77**	0.38	-0.02	-0.09
AhSh	-0.12	0.56	0.40	**-0.57**	0.06	-0.11
PcGSub	0.14	0.03	0.04	-0.23	**0.68**	-0.31
ACl	0.17	0.44	-0.21	0.33	0.34	**0.46**
PcGVg	0.39	-0.21	-0.26	0.20	-0.03	**-0.55**
Eigenvalue	8.94	2.31	1.71	1.48	1.19	1.08
% variation explained	38.88	10.04	7.46	6.43	5.19	4.71
Cumulative % variation explained	38.88	48.92	56.38	62.82	68.02	72.73

Chapter 2 : Relationships among environmental attributes, life history and ecological traits of birds across multiple spatial scales in a human-modified landscape

ABSTRACT

The occurrence of a species in a habitat is determined by the fit between its traits and environmental conditions. Thus, the relationships between species traits and environmental attributes can help us understand how community structure and composition may respond to environmental change. I investigated trait-environment relationships of a breeding bird community across multiple spatial scales in a vegetation type subjected to intense anthropogenic disturbance. I hypothesized that disturbance and native vegetation variables would have distinct trait associations that would be similar across spatial scales. Disturbance variables were associated with larger body masses, disturbance tolerance and non-migratory behavior. Bark gleaning and probing behaviors were negatively associated with disturbance and species with those attributes may thus be sensitive to it. Rock nesting, rock gleaning, seed eating and ground foraging were positively related to disturbance and native vegetation variables suggesting that species with these traits may not be adversely impacted by disturbance. Clutch size was positively related to rainfall; species associated with native vegetation had fewer broods probably indicating an adaptation to aridity. Life history traits were related to variables at landscape scales whereas ecological traits were influenced by variables at local scale too. Disturbance related traits varied similarly at local and landscape scales. Continued

environmental change may affect community composition and structure as species with traits that are related to disturbance may either be favored or decrease in the landscape.

INTRODUCTION

A central question of evolutionary ecology is: how are the ecological and life history traits of species linked to particular environmental attributes? Southwood (1977) clearly articulated this link by suggesting that habitat is the templet upon which selection forges species' characteristic traits, and that such traits are the result of a long process of adaptation to environmental conditions. Traits refer to biological attributes of species including morphological, physiological, life history and behavioral characteristics that influence species' survival and reproductive success (Webb et al. 2010). Thus, species have specific life history and ecological traits that reflect adaptations to particular environmental conditions, and environmental conditions act as filters that allow only species with certain life history and ecological traits suited to a particular place to persist there (Keddy 1992, Ribera et al. 2001, Díaz et al. 2008). Communities, then, are not random assemblages of species and traits.

Current research focus follows this trend and has emphasized a shift from studying species-environment relationships to elucidating trait- environment linkages. Understanding functional relationships between traits and environmental attributes enables us to move beyond a taxon dependent approach to habitat relationships and uncover basic environmental drivers that shape species responses to their environment, thus allowing for a better understanding of how traits and consequently species may be affected by environmental change. Knowing which traits are sensitive to particular environmental attributes can help us predict community response to environmental changes such as land management (Ribera et al. 2001), exotic species invasion (Thuiller et al. 2006), and habitat alteration (Hausner et al. 2003) and fragmentation (Cleary et al. 2007). For instance, Cleary et al. (2007) demonstrated that logging in Bornean rainforests negatively impacted terrestrial insectivores and canopy bark gleaning insectivores whereas undergrowth insectivores were positively affected. Thus, species loss may be asymmetrical with habitat change and species with susceptible traits may be more affected than others.

Past attempts to link species' ecological and life history traits to environmental attributes have sought to elucidate patterns evident across large spatial scales. For example, avian clutch size increases with latitude; this relationship has been correlated with increasing seasonality in the higher latitudes (Cody 1966, Ricklefs 1980). Likewise, Allen's Rule and Bergman's Rule link increasing appendage length (Allen 1877, Symonds and Tattersall 2010) and body size (Bergmann 1847, Olson et al. 2009), respectively, with increasing latitude. Large scale patterns in plant leaf traits (Reich and Oleksyn 2004) and overall form (e.g., plant height; Moles et al. 2009) have been associated with particular biomes. At the landscape level, life history traits have been shown to predict bird and mammal species' sensitivity to landscape change (Hansen and Urban 1992, Vásquez and Simonetti 1999). While proposed mechanisms underlying these patterns are often contentious (Olson et al. 2009) the patterns themselves are fairly robust. Most studies seeking to link species' ecological and life history traits with environmental attributes examine distributions along a relatively long environmental gradient usually containing a variety of different habitats; presumably a longer gradient allows easier detection of a possibly faint ecological signal. However, environmental filters (habitat features that select for certain traits that allow species to persist) act across multiple spatial scales (Poff 1997). In heterogeneous habitats, particularly those facing multiple anthropogenic pressures and subject to rapid change, the environment can be dynamic, and species distributions based on trait-environment relationships may be affected much more by within-habitat type processes than those operating at larger spatial scales.

The coastal sage scrub vegetation type in southern California is an example of a heterogeneous community with a rich assemblage of birds and plants that is affected by intense anthropogenic disturbance. These include both direct and indirect impacts, due to increasing regional human population size, expanding urbanization, and accelerating land cover conversion due to agriculture and exotic plant species invasion. Over the past 60 years, this has resulted in the reduction of coastal sage scrub habitat to 10-30% of its former extent (Westman 1981, O'Leary 1990, Atwood 1993, McCaull 1994). Previous research in this landscape shows that increasing disturbance such as urbanization has negative consequences for bird richness and abundance, and can alter community composition as it alters habitat structure and composition (Bolger et al. 1997, Crooks et al. 2004). However, while species richness and diversity are useful metrics to understand community change, they do not capture the underlying associations between species traits and the environment that influence such change. Therefore, we focused our investigation on elucidating trait-environment associations in breeding bird communities in coastal sage scrub. I hypothesized that given the pervasive and intense anthropogenic disturbance, there would be distinct associations among ecological and life history traits of species and disturbance variables as well as native vegetation variables and that such associations would be consistent across spatial scales. I then consider the implications of these relationships to community structure and composition in the face of continued environmental change.

METHODS

Study system- Coastal sage scrub

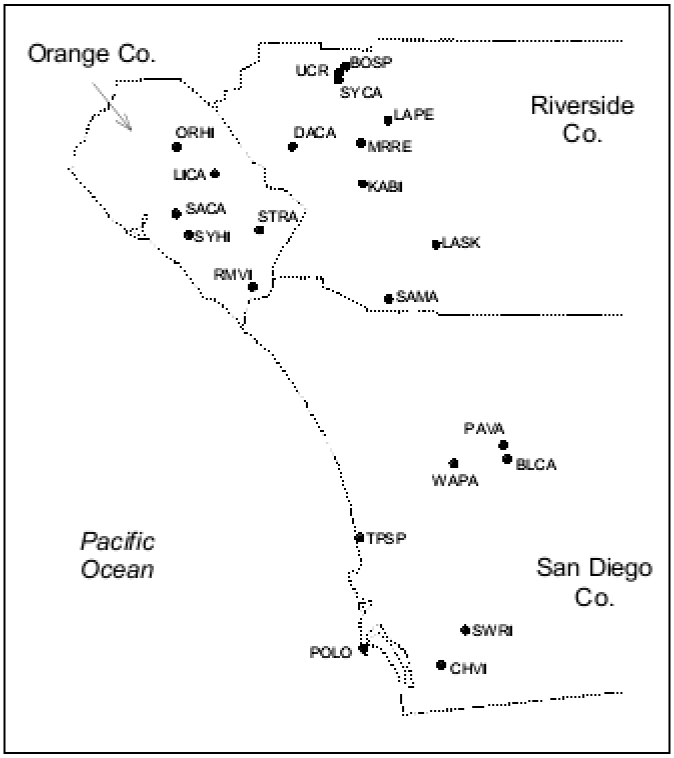


Figure 2.1. Study site location. See Appendix 1 for site codes

I used data collected throughout southern California coastal sage scrub (CSS) vegetation type in Riverside, Orange, and San Diego counties in 1996-1997 as part of the CSS Natural Communities Conservation Planning Program (Fig 2.1; http://www.dfg.ca.gov/habcon/nccp/; Rotenberry et al. 1999). Coastal sage scrub is a drought-deciduous shrubland habitat found in cismontane southern California and Baja California dominated by shrubs of 0.5 to 2.0 m in height (Westman 1981). The dominant shrubs include California sagebrush (*Artemisia californica*), black sage (*Salvia mellifera*), white sage (*Salvia apiana*), California encelia (*Encelia californica),* brittlebush (*Encelia farinosa*), and California buckwheat (*Eriogonum fasciculatum*; (Westman 1981, 1983, O'Leary et al. 1992). Within this vegetation type, defined by a few main shrub species, there is considerable heterogeneity as one moves from the coast to inland sites, and from lower elevation to higher sites. In addition, CSS supports 100 animal and plant species that are considered threatened, rare or sensitive by California or federal wildlife agencies (Atwood 1993, McCaull 1994). Conservation efforts have focused both on focal threatened species (e.g.;, Sage Sparrow, California gnatcatcher Chase and Geupel 2005; see Table 2.1 for scientific names) as well as creating reserves to conserve multiple species (McCaull 1994; http://www.dfg.ca.gov/habcon/nccp/).

Bird surveys

Point count surveys were conducted for breeding resident and migrant birds in the springs of 1996-1997. Two 5-minute unlimited radius counts were conducted at each point (Ralph et al. 1995). A total of 213 points across 22 coastal sage scrub sites were surveyed (Appendix 1). Points were selected in areas dominated by shrub species characteristic of CSS, and placed at least 200m from each other and 50m from other ecotones; counts were conducted between sunrise and 5 hours after sunrise on mornings with no rain or strong wind. All birds detected were included, except for those not using the CSS habitat type and species for which point counts are not an appropriate sampling method. Counts began in mid-late March and concluded by late-April or early-May. Second counts were conducted shortly after the first counts and concluded by late-May or early June. This facilitated the detection of early breeders and late arriving species (as suggested by Ralph et al. 1995). In each site, second counts were made in the same order as the first, to ensure that each site was sampled in early and late spring. Each point was sampled by different observers at each visit to avoid observer bias. The order in which points were sampled was reversed between the first and second visit to avoid potential bias due to time of day. For our analysis, we considered a species present if it occurred on at least one of the four counts, and included only species occurring on at least 5% of the points, for a total of 55 bird species (Table 2.1).

Environmental data

Environmental data fell into four categories: abiotic (climate) variables, vegetation composition (local scale) and habitat structure (local scale), and landscape composition (Table 2.2). I enumerated compositional and structural variables, as a number of studies have looked at bird distributional relationships with regard to vegetation structure, composition (Wiens and Rotenberry 1981, Rotenberry 1985), and climate (Forsman and Mönkkönen 2003, Tingley et al. 2009) across local and landscape scales (Wiens et al. 1987). Climate variables such as temperature and rainfall are known to influence breeding parameters in birds (Tieleman 2004). Details of environmental data sampling are provided in Rotenberry et al. (1999); below we summarize the basic techniques.

Abiotic variables

Abiotic variables included average annual precipitation, mean minimum January temperature, and mean maximum July temperature. Digital temperature and precipitation data were interpolated from normalized 1971-2000 averages from weather stations, 4.6 km resolution, obtained from the PRISM group at Oregon State University (http://www.prism.oregonstate.edu).

Vegetation composition and habitat structure

Vegetation structure and composition were measured using a combination of line-intercept and pin-drop methods (modified from Wiens and Rotenberry 1981). Two perpendicular 50-m transects were laid out in an L-shape with their intersection placed at a bird survey point. To estimate percent coverage for each of several structural types of vegetation (e.g., bunchgrasses, shrubs; Table 2.2a) the length of transect intercepted by each class divided by the total length of the transect (100m) was used. The degree of horizontal patchiness of vegetation was assessed by recording the number of transitions between different vegetation cover types along the transects. Pin drops were conducted at a random point within each 2-m interval along the transects, for a total of 50 sampling points. At each pin drop the nature of the ground cover or substrate (e.g., bare ground, litter; Table 2.2a), and the species identity of each plant that touched the pin was recorded. The number of vegetation contacts (“hits”) occurring in three height classes (1-3 dm, 3-5 dm, and >5 dm) above the substrate surface was recorded and litter depth to the nearest 1cm at the point was measured. Contact data were converted to percent cover by dividing the number of pin drops on which each substrate category or plant species occurred by the total number of pin drops (50). Litter depth and number of species was averaged over the 50 points. Visual assessments for the presence of rock outcrops and trees within a 50-m radius of each survey point were conducted. Most of the measurements were made in 1996 and a few in spring, 1997.

Landscape variables

Information on landscape level variables was collected from digital maps obtained from San Diego, Riverside, and Orange counties as part of each county’s natural community conservation planning (http://www.dfg.ca.gov/habcon/nccp/). Vegetation classification used in county maps followed the state of California’s Natural Diversity Database (Holland 1986). Maps were standardized to follow a similar classification system resulting in a common set of 9 habitat or land cover classes (Table 2.2b). Co-ordinates of each survey point were measured using a Trimble® global positioning system and differentially corrected to a circular error of <5 m. Coordinates were mapped onto the vegetation maps using ARC/INFO in a geographical information system. The area of each of the nine vegetation classes was calculated around a 500-m radius of each point. The perimeter/area ratio for coastal sage scrub, and the perimeter of shrubland (usually chaparral) and coastal sage scrub within the polygons was also calculated. The distance of each point to the edge of the vegetation polygon it was in was measured along with the distance of the point to the edge of the closest urban polygon.

Species' ecological and life history traits

I used the Birds of North America Online (BNA; Poole 2005) to obtain trait information on each of the 55 species; when available, I used information specific to our local subspecies. Traits that described only one species in our sample were dropped, leaving a total of 31 traits (Table 2.3). Three variables are continuous: body mass, clutch size, and number of broods per season. The remaining variables are categorical and coded as either 1 or 0. Unlike other studies, I classified species into more than one category within a general class if it was appropriate to do so (e.g., under foraging substrate/behavior, a species could be classified as both "hawking insects" and "ground-foraging"). Body mass was specific to females if the information was available; otherwise, male body mass was used. If number of broods per season varied between one and two, those species in which fewer than 25% of individuals were double-brooded were classified as single-brooded. Migratory status was denoted as resident or not. "Disturbance tolerance" referred to a subjective assessment of tolerance to urbanization as discussed in a species' BNA account. For cowbird susceptibility, birds were considered either acceptors or rejecters.

Analysis

Variable reduction

The sampling resulted in a total of 59 environmental variables: 17 local-scale habitat structural variables, 24 plant species coverage variables, 14 landscape-level variables and three abiotic variables (Table 2.2). As many of the environmental variables were intercorrelated within their group, two common variable reduction techniques were used to produce fewer new, synthetic variables that still accounted for major, interpretable patterns of covariation among the original variables: detrended correspondence analysis (DCA; Gauch 1982, Pielou 1984) for plant species, and principal components analyses (PCA; Pielou 1984) for landscape variables and for habitat structural variables: Detrended correspondence analysis is a community ordination technique that quantifies the relationship among a set of samples based on the similarity of their species composition. Samples and species are ordered on axes so that samples with similar species composition will have similar axis scores, and species with similar patterns of distribution will also have similar scores. The score of a sample on a DCA axis is a weighted average of the abundance of the species that occur there, and thus the scores of samples on ordination axes can be used as an index of the species composition at those samples. Principal components analysis extracts and summarizes the independent patterns of covariation among a set of variables based on their intercorrelations. Each component accounts for some proportion of the variation within the entire set of variables, and components are conventionally ordered by their eigenvalues, or variances. Components, which are uncorrelated with each other, are interpreted by their correlations with each of the original variables (factor loadings). The position of each sample on a component (its factor score) is a function of its values on each of the original variables and those variables' relationship to each component.

Following DCA and PCA, I used scores from plant community DCA axis1, habitat structure PCs 1-4, and landscape scale PCs 1-5 as the environmental variables data set (see **RESULTS** for interpretations of DCA and PCAs). Because several variables did not contribute substantially to the principal components (presence/absence of rock outcrop or tree within 50m of sampling point, distance of the point to the nearest urban polygon), I included them separately. Likewise, I included the three abiotic variables separately in the environmental variables data set (Table 2.4).

Fourth corner analysis

I used the 4th corner method developed by Legendre et al. (1997) as modified by Dray and Legendre (2008) to analyze bivariate environment-trait linkages. The method uses three matrices: **R** (points x environment), **L** (points x species), and **Q** (traits x species). The fourth corner method was designed to directly relate the biological attributes of species to the characteristics of the environments in which they occur. It tests the null hypothesis that there is no association between variation in a trait and an individual environmental variable (Legendre et al. 1997). The method links the environmental variables matrix to the species trait matrix via the species presence/absence matrix, resulting in the production of a fourth matrix that comprises measures of associations between each environmental and species trait variable (Fig.1.2). Different measures of association are calculated depending upon the types of variables involved. Associations between quantitative environmental variables and multi-category qualitative trait variables are evaluated in an ANOVA-like analysis through a pseudo F statistic, relationships between quantitative environmental and quantitative trait variables are described using Pearson correlation coefficients, and relationships between qualitative environmental variables and qualitative species trait variables are described using a Pearson's chi-square and G statistic. For many reasons, these F, r, and G statistics do not follow their conventional distributions, and instead are evaluated for statistical significance using permutation tests. To do this, specific matrix rows or columns are randomly permuted many times and a statistic calculated for each permutation, thereby generating a distribution of the expected value of the statistic under a null hypothesis of no relationship. The observed statistic is then compared to the generated distribution, and its statistical significance (probability of arising if sampled from a distribution representing the null hypothesis) is estimated. To reject the null hypothesis that there is no association between an environmental variable and a trait variable two null hypotheses must be rejected (Dray and Legendre 2008). H_o1: $\mathbf{R} \neq \mathbf{L}$, there is no association between **R** and **L**; that is, species assemblages are randomly distributed and are not associated with the environments in which they are found. This test is achieved by permuting entire rows of matrix **L**. H_o2: $\mathbf{L} \neq \mathbf{Q}$, there is no association between **L** and **Q**; that is, species have random ecological and life history traits. This test is achieved by permuting entire columns of matrix **L**. When both null hypotheses are rejected, we can conclude that there is indeed an association between an environmental variable and a trait. In both cases, I used 9999 permutations. Following ter Braak et al. (2012), I used an alpha of 0.05 to determine statistical significance and considered only tests that had $p \leq 0.05$ after Holm's (1979) correction for multiple testing. Holm's correction controls the family-wise error rate with less loss of statistical power than the more conservative Bonferroni test (Holm

1979). The RLQ method (Dolédec et al. 1996, Ribera et al. 2001) is similar to the fourth corner method and uses a similar three table approach to relate environmental variables to species traits. Whereas, the RLQ method assesses statistical significance of only the overall relationship of traits and environmental variables, the fourth-corner method allows us to test for statistical significance of single traits and environmental variables. The 4th-corner correlation coefficient cannot be directly compared with the Pearson's r correlation coefficient obtained in traditional bi-variate correlations as it is calculated using two matrices (traits and environmental variables) that were sampled on different units (species and sites). Therefore, the distribution of the fourth-corner correlation statistic is unknown and empirical studies have demonstrated that statistically significant correlations are much lower than traditional correlations (Dray and Legendre 2008, Brind'Amour et al. 2011). The 4th corner analysis was conducted using the ade4 package (Dray and Dufour 2007) in R version 2.15.1 (R Development Core Team 2012).

Matrix R: points x environment

This matrix was comprised of 17 environmental variables scored at 213 survey points. The environmental variables comprised the factor scores from the principal component analyses of the landscape (5 PCs) and habitat structural variables (4 PCs), scores of points on axis 1 of the detrended correspondence analysis of plant species, mean annual precipitation, mean minimum January temperature, mean maximum July temperature, Dist.ed, Dist.urb, Rock and Tree (Table 2.4).

Matrix L: points x species

This matrix contained the presence/absence of 55 species of birds observed across 213 survey points (Table 2.1). Only species that occurred at more than 5% of the points were included in the analysis.

Matrix Q: traits x species

The **Q** matrix described 31 life history and ecological traits for each of the 55 bird species (Table 2.3).

RESULTS

Environmental variables

Detrended correspondence analysis of vegetation variables

I retained the first DCA axis to represent variation in survey points' plant species composition (Table 2.5). This axis had an eigenvalue of 0.85 (maximum possible = 1.0) and a length of 4.46, and thus captured most of the variation in the plant community. The first axis represented a gradient transitioning from points with numerous chaparral-associated species (high negative scores) to those point dominated by inland Riversidian coastal sage scrub (high positive scores).

Principal Component Analysis of local scale habitat structural variables

Principal component analysis of 15 local scale habitat structural variables resulted in 4 components with eigenvalues > 1, which accounted for 67.1% of the total variation (Table 2.6). Factor 1 (shrub vs. grass) accounted for 31.6% of the total variance and contrasted shrub-dominated vs. grass-dominated survey points. Points that had low positive scores along this axis had lower shrub cover, fewer shrub species, less litter cover and depth, fewer vegetation hits in all three height categories and were dominated by grasses signifying greater disturbance. Points that had high positive scores along this axis had greater shrub cover, greater number of shrub species, greater litter cover and depth, and more vegetation hits in all three height categories. Factor 2 (bare ground vs. litter cover) accounted for 12.5% of the total variance and described a gradient from bare ground to increasing litter and woody ground cover around points. Factor 3 (forbs/patchy) accounted for 8.6% of the total variance and described a gradient of increasing forb and rock cover along with increasing horizontal heterogeneity reflected in the number of transitions among vegetation categories per transect. Factor 4 (disturbed) accounted for 7.2% of the total variance and described a gradient of increasing exotic species cover and standing dead material.

Principal Component Analysis of landscape scale variables

Principal components analysis of 12 landscape-scale variables yielded 5 components with eigenvalues > 1 that explained 74.8% of the total variation (Table 2.7). Factor 1 (chaparral vs. CSS) accounted for 25% of the total variance and described a gradient from points embedded in landscapes dominated by chaparral and riparian habitat types (high positive scores) to those principally covered by CSS (high negative scores). Factor 2 (increasing native mosaic) accounted for 15.5% of the total variance and described a gradient of increasing native grassland, woodland and CSS. Factor 3 (aquatic/riparian) accounted for 11.5% of the total variance and described a gradient of increasing aquatic and riparian woodland habitats. Factor 4 (agriculture/exotic) accounted for 10.5% of the total variance and described a gradient of increasing agricultural and exotic grassland habitat. Factor 5 (urban) accounted for 10.4% of the total variance and described a gradient of decreasing urban habitats (high negative scores). In the results and discussion, these factors will be referred to using their names (e.g., “urban” refers to landscape factor 5; Table 2.7).

Trait-environment relationships: 4th corner analysis

The analysis resulted in 57 trait-environment relationships (out of 527 tested) that were significant at $p \leq 0.05$ after correcting for multiple tests (Table 2.8). I found some relationships that were expected (e.g., rock gleaning increasing with presence of rock outcrops), some that are specific to coastal sage scrub and others that are likely to be more broadly relevant. In the following section, I focus on a subset of those relationships associated with the native vegetation and those unique to CSS, along with those related to disturbance and land use change, and to climatic variables.

Associations with native vegetation – coastal sage scrub, chaparral, woodlands and native grasslands (DCA1, LF.1, LF.2, SF.2)

Ten traits were associated with variation in native vegetation types via their association with DCA 1, (coastal sage scrub) LF.1 (coastal sage scrub vs. chaparral), LF.2 (native mosaic) and SF.2 (bare ground vs. litter cover) (see Tables 2.6-2.8). Of these, 5 traits were specifically related to CSS.

As both plant species composition and the surrounding landscape became more dominated by CSS, I found that rock gleaning and ground foraging increased due to their positive and negative associations with DCA1 and LF.1 respectively (r = 0.18, *p* = 0.001; r = -0.06, *p*= 0.025 respectively), whereas foliage gleaning decreased due to its negative association with DCA1 (r = -0.07, *p* = 0.050). Seed eating increased with CSS due to its negative association with LF.1 (r = -0.05, *p* = 0.040) as did the use of rocks as nesting substrates, due to its positive association with DCA 1 (r = 0.12, *p* = 0.004). Increase in chaparral in the landscape was associated with increased probing, bark gleaning, and cavity and tree nesting due to their positive associations with LF.1 (r = 0.09, *p* = 0.009; r = 0.11, *p* = 0.000; r = 0.10, *p* = 0.001; r = 0.06, *p* = 0.030 respectively). Number of broods declined as the native mosaic of woodlands, grasslands and CSS increased in the landscape, due to its negative association with LF.2 (r = -0.05, *p* = 0.050) whereas probing and bark gleaning increased due to their positive association with LF.2 (r = 0.08, *p = 0*.039; r = 0.09, *p* = 0.026). As the amount of bare ground increased and litter coverage decreased, ground foraging and rock gleaning increased as evident by their negative associations with SF.2 (r = -0.05, *p* = 0.040; r = -0.10, *p* = 0.001 respectively).

Associations with disturbance variables (LF.4, LF. 5, SF.1, SF.4 and Dist.Urb)

Ten species traits were associated with increasing local and landscape scale disturbance characterized by increasing urbanization (LF.5, Dist.urb), increasing agriculture and exotic species invasion (LF.4), and local scale habitat structural gradients (SF.1, SF.4).

As the amount of agriculture and exotic grasslands increased in the landscape, so did female body mass, use of rocks as nesting substrates, and rock gleaning due to their positive associations with LF.4 (r = 0.03, *p* = 0.050; r = 0.05, *p* = 0.002; r = 0.04, *p* =

0.049 respectively). However, foliage gleaning and probing decreased due to their negative associations with LF.4 (r = -0.04, p = 0.008; r = -0.04, p = 0.015 respectively). Increase in the amount of urban area in the landscape was positively related to increase in residents and disturbance tolerance in species due to their negative associations with LF.5 (r = -0.06, p = 0.010; r = -0.05, p = 0.032 respectively). As the distance to urban areas increased, rock nesting decreased (r = -0.05, p = 0.001). Seed eating and ground foraging increased as points were more exotic grass dominated due to their negative associations with SF.1 (r = -0.09, p = 0.004; r = -0.08, p = 0.004 respectively). As the coverage by exotic forbs and standing dead material increased, rock nesting, rock gleaning and disturbance tolerance increased due to their positive associations with SF.4 (r = 0.06, p = 0.001; r = 0.08, p = 0.000; r = 0.04, p = 0.043 respectively), whereas probing and bark gleaning behaviors decreased due to their negative association with SF.4 (r = -0.05, p = 0.020; r = -0.04, p = 0.053 respectively).

Associations with climatic variables (Ttl.Ppt, Tmin.Jan and Tmax.Jul)

Four traits were significantly related to temperature and precipitation (Table 2.8a). Clutch size was positively related to total precipitation (r = 0.05, p = 0.029), seed diet was positively related to maximum July temperature (r = 0.11, p = 0.015), and ground foraging and rock gleaning were positively related to maximum July temperature (r = 0.11, p = 0.013; r = 0.16, p = 0.003 respectively).

I found no relationships between fourteen ecological traits and any environmental variable. These included categories pertaining to nest location (shrub, structure, and ground nesting), diet (insects and invertebrates, vegetation, omnivore, and fruit), foraging behaviors (nectar, aerial flycatching, hawking, ground sallying, foliage sallying, picking seeds and fruit) and cowbird acceptor/rejecter. Amongst the environmental variables, the presence/absence of trees within 50-m of the survey point was not related to any trait. The absence of significant associations for a trait implies that variance in the trait is distributed across all environmental features considered. For example, species feeding on insects and invertebrates were found widely distributed along each of the "gradients" we tested them over.

DISCUSSION

Environmental filters are typically thought to operate across steep and long environmental gradients (Willis et al. 2010). However, I found evidence of environmental filters at the landscape and local scale within a vegetation type, albeit one with substantial compositional, structural, landscape, and abiotic heterogeneity. I was able to identify traits that were associated with CSS and those that varied with disturbance as per the hypothesis. Furthermore, observed trait-environment associations with disturbance and native vegetation variables were consistent across spatial scales. The principal native habitat types in southern California include coastal sage scrub, chaparral, oak woodland, riparian woodland, native grasslands and wetlands. Coastal sage scrub is also subjected to increasing disturbance caused by urbanization, agricultural conversion and exotic species invasion (Westman 1981, O'Leary 1990, Atwood 1993, McCaull 1994). This varied mix of vegetation types, along with their inherent heterogeneity, and increasing human disturbance serves to filter species traits to suit the environmental conditions found in this system.

Trait associations with native vegetation

Some patterns were simple and expected, such as the association of rock gleaning with the presence of rocks. However, I also found some unexpected relationships. Across landscape and local scales most trait associations with CSS were as expected. The sparse, often rocky ground cover and low vegetation height in coastal sage scrub favors ground foragers, rock gleaners, and seed eating species (Guthrie 1974). The presence of large rocky outcrops in CSS also selects species that use rock as nesting substrate. I found that foliage gleaning was positively associated with chaparral but negatively associated with CSS at the local scale. Perhaps the greater vertical development in chaparral vegetation as compared to CSS favors foliage gleaners. In a study on the effect of bush thickening on savannah bird species of the southern Kalahari, Seymour and Dean (2010) found that increase in woody species density was associated with an increase in gleaners. At the landscape scale, increase in chaparral, woodlands and native grassland areas favored probing and bark gleaning behaviors due to the greater development of woody vegetation in this habitat type as bark foraging species are typically associated with trees (Seymour and Dean 2010). The use of cavities and trees for nests was also positively associated with chaparral, perhaps due to the proximity of chaparral with woodlands at the landscape level.

Trait associations with disturbance

Although the survey point locations focused on coastal sage scrub, because of large scale and long term human activities in the region the samples also included an urbanization/ disturbance gradient. At the landscape scale, increase in proportions of surrounding area dominated by exotic grasslands/agriculture and urbanization were associated with resident, disturbance-tolerant species with larger body masses. Presence of agricultural areas may ensure food availability throughout the year, thus supporting species with larger body sizes. Species with larger body masses may also be more insulated from disturbance and able to sustain themselves. Studies have shown that urban-adapted species were more sedentary (Croci et al. 2008). Additionally, residents are thought to have had greater time to adjust and adapt to altered environmental conditions encountered in urban settings. Disturbance tolerance also increased in sites dominated by exotic forbs at the local scale. This was expected too as tolerance to exotic plant species at the landscape level should allow for tolerance at the local scale too.

At the landscape scale, increase in sites dominated by agriculture/exotic grasslands, negatively correlated with foraging behaviors such as foliage gleaning and probing. These traits also showed consistent responses at the local scale as they were also negatively associated with disturbance at the local scale too, as seen by their negative relationship with sites dominated by exotic forbs. Sites dominated by exotic forbs and grassland in coastal sage scrub and chaparral areas have been shown to have reduced arthropod abundance and diversity and this may negatively affect foliage and bark gleaners (Lambrinos 2000, Longcore 2003) in addition to lacking much foliage and bark to support probing and bark gleaning behaviors. Additionally, increased use of pesticides and insecticides in agriculture areas may further reduce insect prey for birds.

Rock nesting and rock gleaning were also positively related to disturbance variables at both landscape and local scales. They were positively related to sites dominated by agriculture and with exotic forb coverage. Sites that scored high on exotic forb coverage also had rocky outcrops, making them attractive to species that used rocks. However, rock nesting decreased as distance to urban areas increased. This result was not expected, especially since rock nesting was also positively correlated to DCA1 and therefore to increasing CSS.

Ground foraging and seed eating were influenced by local scale disturbance variables and were associated positively with exotic grass-dominated sites. Large areas of CSS have been converted to exotic grasslands due to invasion by brome grasses (Minnich and Dezzani 1998) and this may facilitate a seed diet and ground foraging species.

I also found some patterns contrary to previous studies. For instance, urbanization is thought to favor granivorous, non-migratory, cavity nesting species (Chace and Walsh 2006). However, cavity nesting species were not associated with urbanization variables and were instead primarily associated with the amount of native vegetation such as woodlands, aquatic and riparian in the landscape whereas a seed-based diet was positively associated with CSS.

Life history traits such as body mass, clutch size and number of broods were primarily influenced by environmental variables at the landscape scale. Clutch size increased with rainfall and the number of broods declined with increase in woodlands, CSS and grassland in the landscape. These patterns are similar to other arid zone studies where clutch size and number of broods were lower in arid habitats as compared to mesic ones (Tieleman 2004, Seymour and Dean 2010). Additionally, in drought-prone arid systems, productivity can be limited via reduction in clutch size and/or the number of broods, by reduced precipitation which limits primary productivity and thus affects food availability for birds (Patten and Rotenberry 1999, Coe and Rotenberry 2003). A study on rufous-crowned sparrows in coastal sage scrub demonstrated that rainfall and its effect on food availability could interact with nest predation to affect productivity in coastal sage scrub (Morrison and Bolger 2002).

Implications of trait-environment relationships in a changing landscape

I found that certain traits such as rock gleaning, rock nesting, seed eating, ground foraging were influenced by variation across landscape and local scales and were positively associated with sites dominated by native vegetation as well as by disturbance.

Additionally, ground foragers, seed eaters and rock gleaners were associated with higher July temperatures. Given the rapid pace of urbanization and human development in this landscape, in addition to rising temperatures due to climate change, species with these traits might be more likely to increase with disturbance happening across larger spatial scales as well as localized disturbance. On the other hand, traits such as probing, bark gleaning were influenced by the landscape context and responded negatively to disturbance. These traits may be sensitive to landscape change and increasing human disturbance, and species with these traits may be more vulnerable. Larger bodied species may be at an advantage as more land is diverted to agriculture and invaded by exotic grasslands. As breeding productivity of birds associated with native vegetation is low and clutch size is influenced by rainfall, future changes to temperature and precipitation patterns in this drought-prone landscape may reduce productivity even further.

Conclusions

The Mediterranean ecosystem in southern California is under severe anthropogenic pressure and has been subjected to varied threats that include habitat loss, fragmentation, invasion by exotic annual plant species, and urbanization to name a few. As the landscape changes further, species composition can change as different traits are favored. Establishing trait associations with native and non-native habitats can help us track changes in bird species composition over time and understand how bird species respond to environmental change. I have demonstrated ecological and life history trait associations with disturbance variables and native vegetation for birds in a coastal sage scrub landscape across different spatial scales. Furthermore, I show that trait associations with disturbance variables are consistent across both spatial scales signifying that structural and compositional changes resulting from disturbance significantly influences traits of species and therefore can impact species composition in the future. Species with foraging behavior traits such as probing and bark gleaning are sensitive to disturbance and occur more frequently only in native vegetation types. Bird species occupying native vegetation raise few broods; along with clutch size, this is an important component of productivity and decreases with increasing aridity. In a drought-prone landscape such as coastal sage scrub, future changes in temperature and precipitation patterns may negatively impact bird productivity. Species that are large bodied, utilizing a seed-based diet, and ground foraging habit along with the use of rocks to forage and nest in, are likely to be at an advantage in both modified and native landscapes. Tests of other Mediterranean shrubland ecosystems should yield comparable results.

REFERENCES

Allen, J. A. 1877. The influence of physical conditions in the genesis of species. Radical Review 1:108–140.

Atwood, J. L. 1993. California gnatcatchers and coastal sage scrub: The biological basis for endangered species listing. Interface between ecology and land development in California. Southern California Academy of Sciences, Los Angeles, CA:149–166.

Bergmann, C. 1847. Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Gottinger studien 3:595–708.

Bolger, D. T., T. A. Scott and J. T. Rotenberry. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. Conservation Biology 11: 406-421.

Brind' Amour, A., D. Boisclair, S. Dray and P. Legendre. 2011. Relationships between species feeding traits and environmental conditions in fish communities: A three-matrix approach. Ecological Applications 21:363-377.

Ter Braak, C. J. F., A. Cormont, and S. Dray. 2012. Improved testing of species traits–environment relationships in the fourth-corner problem. Ecology 93:1525–1526.

Chase, M. K., and G. R. Geupel. 2005. The use of avian focal species for conservation planning in California. Pages 130–142 *in* C. J. Ralph and T. D. Rich, editors. Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference. General Technical Report PSW-GTR-191, USDA Forest Service, Albany, CA.

Cleary, D. F. R., T. J. B. Boyle, T. Setyawati, C. D. Anggraeni, E. E. V. Loon, and S. B. J. Menken. 2007. Bird species and traits associated with logged and unlogged forest in Borneo. Ecological Applications 17:1184–1197.

Cody, M. L. 1966. A general theory of clutch size. Evolution:174–184.

Coe, S. J., and J. T. Rotenberry. 2003. Water availability affects clutch size in a desert sparrow. Ecology 84:3240–3249.

Crooks, K. R., A. V. Suarez and D. T. Bolger. 2004. Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biological Conservation 115: 451-462.

Díaz, A. M., M. L. S. Alonso, and M. R. V. A. Gutiérrez. 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: Patterns along complex environmental gradients. Freshwater Biology 53:1–21.

Doledec, S., D. Chessel, C. J. F. Ter Braak and S. Champely. 1996. Matching species traits to environmental variables: A new three-table ordination method. Environmental and Ecological Statistics 3: 143-166.

Dray, S., and A.-B. Dufour. 2007. The ade4 package: Implementing the duality diagram for ecologists. Journal of statistical software 22:1–20.

Dray, S., and P. Legendre. 2008. Testing the species traits-environment relationships: The fourth-corner problem revisited. Ecology 89:3400–3412.

Forsman, J. T., and M. Mönkkönen. 2003. The role of climate in limiting European resident bird populations. Journal of Biogeography 30:55–70.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press.

Guthrie, D. A. 1974. Suburban bird populations in southern California. American Midland Naturalist 92:461–466.

Hansen, A. J., and D. L. Urban. 1992. Avian response to landscape pattern: The role of species' life histories. Landscape Ecology 7:163–180.

Hausner, V. H., N. G. Yoccoz, and R. A. Ims. 2003. Selecting indicator traits for monitoring land use impacts: Birds in northern coastal birch forests. Ecological Applications 13:999–1012.

Holland, R. F. 1986. Preliminary descriptions of the terrestrial natural communities of California. Unpubl. Report, State of California, The Resources Agency, Department of Fish and Game, 1416, 9th St., Sacramento, CA, 95814.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6:65–70.

Keddy, P., A. 1992. Assembly and response rules: Two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.

Legendre, P., R. Galzin, and M. L. Harmelin-Vivien. 1997. Relating behavior to habitat: Solutions to the fourth-corner problem. Ecology 78:547–562.

McCaull, J. 1994. The natural community conservation planning program and the coastal sage scrub ecosystem of southern California. Pages 281–292 *in* R. E. Grumbine, editor. Environmental Policy and Biodiversity. Island Press, Washington, D. C.

Moles, A. T., D. I. Warton, L. Warman, N. G. Swenson, S. W. Laffan, A. E. Zanne, A. Pitman, F. A. Hemmings, and M. R. Leishman. 2009. Global patterns in plant height. Journal of Ecology 97:923–932.

Morrison, S. A., and D. T. Bolger. 2002. Variation in a sparrow's reproductive success with rainfall: Food and predator-mediated processes. Oecologia 133:315–324.

O'Leary, J. F. 1990. California coastal sage scrub: General characteristics and considerations for biological conservation. Endangered Plant Communities of Southern California. Southern California Botanists Special Publication: 24–41.

O'Leary, J. F., D. Murphy, and P. Brussard. 1992. An NCCP special report: The coastal sage scrub community conservation planning region. California Natural Community Conservation Planning Special Report.

Olson, V. A., R. G. Davies, C. D. L. Orme, G. H. Thomas, S. Meiri, T. M. Blackburn, K. J. Gaston, I. P. F. Owens, and P. M. Bennett. 2009. Global biogeography and ecology of body size in birds. Ecology Letters 12:249–259.

Patten, M. A., and J. T. Rotenberry. 1999. The proximate effects of rainfall on clutch size of the California gnatcatcher. Condor:876–880.

Pielou, E. C. 1984. The interpretation of ecological data: A primer on classification and ordination. John Wiley and Sons, New York, NY.

Poff, N. L. 1997. Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological society: 391–409.

Poole, A. 2005. The birds of North America online. Ithaca: Cornell Lab of Ornithology.

R Development Core Team. 2012. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.

Ralph, C. J., J. R. Sauer, and S. Droege. 1995. Monitoring bird populations by point counts. Gen. Tech. Rep., Pacific Research Station, Forest Service, U. S. Department of Agriculture, Albany, CA.

Reich, P. B., and J. Oleksyn. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. Proceedings of the National Academy of Sciences of the United States of America 101:11001–11006.

Ribera, I., S. Dolédec, I. S. Downie, and G. N. Foster. 2001. Effect of land disturbance and stress on species traits of ground beetle assemblages. Ecology 82:1112–1129.

Ricklefs, R. E. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. Auk: Ornithological Advances 97:38–49.

Rotenberry, J. T. 1985. The role of habitat in avian community composition: Physiognomy or floristics? Oecologia 67:213–217.

Rotenberry, J. T., M. Price V., and W., B. III Kristan. 1999. Autecology of coastal sage scrub birds and mammals. Page 219. Final report, U. S. Geological Survey, Biological Resources Division, Sacramento, CA. http://www.escholarship.org/uc/item/2rj451t2.

Seymour, C. L., and W. R. J. Dean. 2010. The influence of changes in habitat structure on the species composition of bird assemblages in the southern Kalahari. Austral Ecology 35:581–592.

Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46:337–365.

Symonds, M. R. E., and G. J. Tattersall. 2010. Geographical variation in bill size across bird species provides evidence for Allen's rule. The American Naturalist 176:188–197.

Thuiller, W., D. M. Richardson, M. Rouget, S. Proches, and J. R.Wilson. 2006. Interactions between environment, species traits, and human uses describe patterns of plant invasions. Ecology 87:1755–1769.

Tingley, M. W., W. B. Monahan, S. R. Beissinger, and C. Moritz. 2009. Colloquium Papers: Birds track their Grinnellian niche through a century of climate change. Proceedings of the National Academy of Sciences 106:19637–19643.

Vásquez, R. A., and J. A. Simonetti. 1999. Life history traits and sensitivity to landscape change: The case of birds and mammals of Mediterranean Chile. Revista Chilena de Historia Natural 72:517–525.

Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. L. Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. Ecology Letter 13:267-283.

Westman, W. E. 1981a. Diversity relations and succession in Californian coastal sage scrub. Ecology 62:170–184.

Westman, W. E. 1981b. Factors influencing the distribution of species of Californian coastal sage scrub. Ecology 62:439–455.

Westman, W. E. 1983. Xerie Mediterranean-type shrubland associations of Alta and Baja California and the community/continuum debate. Vegetatio 52:3–19.

Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological monographs: 21–41.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: The effects of spatial scale. Oikos: 132–147.

Willis, C. G., M. Halina, C. Lehman, P. B. Reich, A. Keen, S. McCarthy, and J. Cavender-Bares. 2010. Phylogenetic community structure in Minnesota oak savanna is influenced by spatial extent and environmental variation. Ecography 33:565–577.

Table 2.1 Codes, common names, and scientific names of all birds detected at >5% of 213 coastal sage scrub sampling points

Code	Common Name	Scientific Name
CAQU	California Quail	*Callipepla californica*
KILL	Killdeer	*Charadrius vociferus*
MODO	Mourning Dove	*Zenaida macroura*
GRRO	Greater Roadrunner	*Geococcyx californianus*
ANHU	Anna's Hummingbird	*Calypte anna*
COHU	Costa's Hummingbird	*Calypte costae*
ACWO	Acorn Woodpecker	*Melanerpes formicivorus*
NUWO	Nuttall's Woodpecker	*Picoides nuttallii*
NOFL	Northern Flicker	*Colaptes auratus*
BLPH	Black Phoebe	*Sayornis nigricans*
ATFL	Ash-throated Flycatcher	*Myiarchus cinerascens*
WEKI	Western Kingbird	*Tyrannus verticalis*
HUVI	Hutton's Vireo	*Vireo huttoni*
WESJ	Western Scrub-Jay	*Aphelocoma californica*
AMCR	American Crow	*Corvus brachyrhynchos*
CORA	Common Raven	*Corvus corax*
CLSW	Cliff Swallow	*Petrochelidon pyrrhonota*
OATI	Oak Titmouse	*Baeolophus inornatus*
BUSH	Bushtit	*Psaltriparus minimus*
ROWR	Rock Wren	*Salpinctes obsoletus*
CANW	Canyon Wren	*Catherpes mexicanus*
HOWR	House Wren	*Troglodytes aedon*
BEWR	Bewick's Wren	*Thryomanes bewickii*
CACW	Cactus Wren	*Campylorhynchus brunneicapillus*
BGGN	Blue-gray Gnatcatcher	*Polioptila caerulea*

Code	Common Name	Scientific Name
CAGN	California Gnatcatcher	*Polioptila californica*
WREN	Wrentit	*Chamaea fasciata*
HETH	Hermit Thrush	*Catharus guttatus*
CATH	California Thrasher	*Toxostoma redivivum*
NOMO	Northern Mockingbird	*Mimus polyglottos*
EUST	European Starling	*Sturnus vulgaris*
PHAI	Phainopepla	*Phainopepla nitens*
OCWA	Orange-crowned Warbler	*Oreothlypis celata*
COYE	Common Yellowthroat	*Geothlypis trichas*
YRWA	Yellow-rumped Warbler	*Setophaga coronata*
WIWA	Wilson's Warbler	*Cardellina pusilla*
YBCH	Yellow-breasted Chat	*Icteria virens*
SPTO	Spotted Towhee	*Pipilo maculatus*
RCSP	Rufous-crowned Sparrow	*Aimophila ruficeps*
CALT	California Towhee	*Melozone crissalis*
BCSP	Black-chinned Sparrow	*Spizella atrogularis*
LASP	Lark Sparrow	*Chondestes grammacus*
SAGS	Sage Sparrow	*Artemisiospiza belli*
GRSP	Grasshopper Sparrow	*Ammodramus savannarum*
SOSP	Song Sparrow	*Melospiza melodia*
LISP	Lincoln's Sparrow	*Melospiza lincolnii*
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*
BHGR	Black-headed Grosbeak	*Pheucticus melanocephalus*
BLGR	Blue Grosbeak	*Passerina caerulea*
LAZB	Lazuli Bunting	*Passerina amoena*
WEME	Western Meadowlark	*Sturnella neglecta*
BHCO	Brown-headed Cowbird	*Molothrus ater*
BUOR	Bullock's Oriole	*Icterus bullockii*

Code	Common Name	Scientific Name
HOFI	House Finch	*Haemorhous mexicanus*
LEGO	Lesser Goldfinch	*Spinus psaltria*

Table 2.2. Environmental variables

a. Habitat structural variables measured at each sample point

Type	Code	Description
Pin drop measures		Substrates (percent cover)
	Hits.1-3	average number of hits 1-3 dm per pin drop
	Hits.3-5	average number of hits 3-5dm per pin drop
	Hit.>5	average number of hits >5 dm per pin drop
	No.Sp	average number of species at each pin drop
	GC.Lit	fine litter (grass and small forbs)
	Lit.Dep	average litter depth (cm)
	GC.Bare	bare ground
	GC.Wood	coarse litter (woody debris)
	GC.Rock	rock
Line intercept measures		Canopy vegetation (percent cover)
	PC.Grass	bunch grass
	PC.Sh	shrub
	Num.Chng	number of changes between cover classes along the length of transects
	PC.Forb	native forb
	PC.Bras	exotic forb (mainly the mustards *Brassica* and *Hirschfeldia)*
	PC.Sn	standing dead (woody)
Visual assessment		Presence within 50m radius of point
	Rock	large (>2-m diameter) outcrops of rock
	Tree	tree

b. Landscape level variables calculated for each sample point.

Type of Measurement	Code	Description
Total area (ha) within 500-m of point:		
	Ag.A5	Agriculture (fields and orchards)
	Aqat.A5	Aquatic (mainly lakes)
	CSS.A5	Coastal sage scrub
	Ntgr.A5	Native grassland
	Exgr.A5	Exotic grassland
	Wood_A5	Woodland (including forest)
	Urb.A5	Urban
	Shrb.A5	Shrublands (e.g., chaparral; excluding CSS)
	Rip.A5	Riparian
Total perimeter (m) of polygons within 500-m of point:		
	CSS.P5	Coastal sage scrub
	Shrb.P5	Shrublands (excluding CSS)
Perimeter/Area ratio within 500-m of point:		
	CSS.PA5	Coastal sage scrub
Distance (m) from point to other features:		
	Dist.ed	to edge of polygon containing point
	Dist.urb	to nearest urban polygon

Table 2.3. Life history and ecological traits used in the analysis. Information obtained from Birds of North American Online (BNA; Poole 2005)

Category	Code	Description
Life History	CS	Clutch size
	NOBR	No. broods
	FBM	Female body mass (gm)
Migration	M.RES	Resident
Nest type	N.OP	Open
	N.CAV	Cavity
	N.ENC	Enclosed
Nest substrate	NS.TR	Tree
	NS.SH	Shrub
	NS.GR	Ground
	NS.R	Rock
	NS.STR	Structure
Diet	D.INV	Insects and invertebrates
	D.SD	Seeds
	D.FR	Fruit
	D.VG	Vegetation (nectar, flowers, shoots, leaves, buds)
	D.OM	Omnivore
Foraging substrate/behavior	FB.NEC	Nectar sipping
	FB.AFL	Aerial flycatching
	FB.FLG	Foliage gleaning
	FB.HWK	Hawking
	FB.GR	Ground gleaning
	FB.GSA	Ground sallying

Category	Code	Description
	FB.FSA	Foliage sallying
	FB.RGL	Rock gleaning
	FB.PCK	Picking (picking fruits/seeds from a single source as opposed to walking about and picking seeds or fruit as encountered)
	FB.PRB	Probing (feeding off crevices, wood pecking)
	FB.BGL	Bark gleaning
Other	DIS.TOL	Disturbance tolerance
	COWB	Cowbird acceptor/rejecter
	HAB.SPE	Habitat specialist

Table 2.4. Final environmental variables used in the 4th corner analysis

Category	Variable	Code	Description
Plant Species Composition	DCA axis 1	DCA1	Chaparral species (-) to inland CSS (+)
Landscape Scale	Landscape PCA 1	LF.1	Chaparral (+) vs. CSS (-)
	Landscape PCA2	LF.2	Increasing native mosaic
	Landscape PCA3	LF.3	Increasing aquatic and woodland habitats
	Landscape PCA 4	LF.4	Increasing agriculture and exotic grassland
	Landscape PCA 5	LF.5	Decreasing urban area
	Distances	Dist.ed	Distance to edge of polygon containing point
		Dist.urb	Distance to nearest urban polygon
Habitat Structure	Structural PCA 1	SF.1	Shrub (+) vs. grass (-)
	Structural PCA 2	SF.2	Litter (+) vs. bare (-)
	Structural PCA 3	SF.3	Increasing coverage of forbs and high patchiness
	Structural PCA 4	SF.4	Increasing coverage of exotic forbs and standing dead material (disturbed)
	Rock		Presence/absence of rocky outcrops
	Tree		Presence/absence of trees

Category	Variable	Code	Description
Climate	Precipitation	Ppt	Mean annual precipitation
	Temperature	Tmin	Mean minimum January temperature
		Tmax	Mean maximum July temperature

Table 2.5. Codes, scientific names, and common names of plant taxa occurring on ≥10% of coastal sage scrub sampling sites. DCA 1 Scores are from the first axis of a detrended correspondence analysis of 235 points in coastal sage scrub vegetation in southern California.

Code	Scientific name	Common name	DCA 1 Score
ERFA	*Eriogonum fasciculatum*	California buckwheat	1.85
ARCA	*Artemisia californica*	California sagebrush	0.99
SAME	*Saliva mellifera*	Black sage	1.54
SAAP	*Salivia apiana*	White sage	1.74
LOSP	*Lotus scoparius*	Deerweed	2.33
MALA	*Malosma laurina*	Laurel sumac	1.57
OPSP	*Opuntia* spp.	Prickly pear and cholla cacti	2.28
ENFA	*Encelia farinosa*	Brittlebush	4.67
RUSP	*Rhus* spp.[a]	Lemonadeberry	0.31
ENCA	*Encelia californica*	California encelia	1.31
GASP	*Galium* spp.	Bedstraw	0.90
ADFA	*Adenostoma fasciculatum*	Chamise	-0.12
HIIN	*Hirschfeldia incana*	Short-pod mustard	4.04
LEFI	*Lessingia filaginifolia*	California aster	3.55
MISP	*Mimulus* spp.	Monkey flower	0.72
GUSP	*Gutierrezia* spp.[b]	Broom matchweed	2.12
RASP	*Rhamnus* spp.[c]	Redberry	1.30

Code	Scientific name	Common name	DCA 1 Score
CNDU	*Cneoridium dumosum*	Bushrue	0.69
YUSP	*Yucaa* spp.[d]	Chaparral and Mojave yuccas	0.48
STSP	*Stephanomeria* spp.	Wirelettuce	3.72
ISOC	*Isocoma* spp.	Goldenbush	1.65
LECO	*Elymus condensatus*	Ryegrass	0.74
MAMA	*Marah macrocarpus*	Wild cucumber	3.58
BRSP	*Brassica* spp.	Mustard	3.65

[a] mostly *R. integrifolia*
[b] mostly *G. californica*
[c] mostly *R. crocea*
[d] *Yucca whiplei* and *Y.schidegera*

Table 2.6. Principal component analysis of habitat structural variables. Entries are factor loadings after Varimax rotation of four components. Bold denotes factor loadings > 0.5. See Table 2.2a for variable names

	Structural components			
Variable	SF.1	SF.2	SF.3	SF.4
PC.Grass	**-0.845**	0.170	-0.020	-0.218
PC.Sh	**0.839**	0.006	-0.271	-0.263
Hits.1-3	**0.738**	0.250	-0.068	-0.160
Hits.3-5	**0.820**	0.194	-0.112	-0.164
Hits.>5	**0.820**	0.038	-0.274	-0.110
No.Sp	**0.828**	-0.020	-0.217	0.058
GC.Lit	**0.810**	0.241	-0.257	-0.059
Lit.Dep	**0.503**	**0.693**	0.007	0.152
GC.Bare	0.260	**-0.746**	0.137	0.214
GC.Wood	0.219	**0.633**	0.313	0.195
Num.Chng	-0.331	0.174	**0.673**	0.212
GC.Rock	-0.212	-0.208	**0.511**	-0.151
PC.Forb	-0.109	0.097	**0.710**	-0.091
PC.Bras	-0.222	-0.354	-0.055	**0.521**
PC.Sn	-0.049	0.178	-0.053	**0.838**

	Structural components			
Variable	SF.1	SF.2	SF.3	SF.4
Component name	Shrub vs. grass	Litter vs. bare	Forbs/patchy	Disturbed
Eigenvalue	5.79	1.88	1.30	1.09
% Total variance	38.61	12.55	8.69	7.28

Table 2.7. Principal component analysis of landscape scale environmental variables. Entries are factor loadings after Varimax rotation of five components. Bold denotes factor loadings > 0.5 See Table 2.2b for variable codes

Variable	Landscape components				
	LF.1	LF.2	LF.3	LF.4	LF.5
CSS.A5	**-.762**	.070	-.369	-.360	.254
Shrb.A5	**.888**	-.232	.044	-.164	.071
Shrb.P5	**.805**	.242	-.011	-.237	.097
Rip.A5	**.619**	.264	-.265	-.181	.323
CSS.PA5	**.765**	.294	.101	.182	.026
Ntgr.A5	.133	**.801**	.079	.021	-.029
CSS.P5	.024	**.772**	-.203	-.086	.275
Wood.A5	.137	**.512**	**.649**	.044	.000
Aqat.A5	.015	-.188	**.827**	-.148	.100
Ag.A5	.033	.074	-.064	**.598**	-.197
Exgr.A5	-.195	-.174	-.043	**.773**	.360
Urb.A5	-.131	-.151	-.107	.010	**-.902**

Variable	Landscape components				
	LF.1	LF.2	LF.3	LF.4	LF.5
Component name	Chaparral vs. CSS	Native mosaic	Aquatic/woodland	Ag/exotic	Urban
Eigenvalue	3.08	1.87	1.39	1.27	1.25
% Total variance	25.65	15.57	11.58	10.56	10.45
Cumulative variance	25.65	41.22	52.79	63.35	73.80

Table 2.8. Statistically significant ($p \leq 0.05$) trait-environment relationships resulting from the 4th corner analysis. Pluses and minuses denote direction of relationship

a. Trait relationships with vegetation composition and abiotic variables

		Vegetation Composition	Abiotic variables		
		Chaparral (-) vs. Inland CSS (+)[a]	Annual Precipitation	January Min Temp	July Max Temp
Category	Variable	DCA1	Ppt.Ttl	Tmin.Jan	Tmax.Jul
Life History	Clutch Size		+		
	No. broods				
	Female body mass				
Migratory status	Resident				
Nest type	Nopen		-		
	Ncav				
	Nencl				
Nest Location	Tree				
	Rock	+			+
	Shrub				

		Vegetation Composition	Abiotic variables		
		Chaparral (-) vs. Inland CSS (+)[a]	Annual Precipitation	January Min Temp	July Max Temp
Category	Variable	DCA1	Ppt.Ttl	Tmin.Jan	Tmax.Jul
	Ground Structure				
Diet	Seed			-	+
	Insects + Invertebrates				
	Vegetation				
	Omnivore				
	Fruit				
Foraging Substrate/behavior	Foliage gleaning	-			
	Ground foraging			-	+
	Rock gleaning	+		-	+
	Probing				
	Bark gleaning		+		

		Vegetation Composition	Abiotic variables		
		Chaparral (-) vs. Inland CSS (+)[a]	Annual Precipitation	January Min Temp	July Max Temp
Category	Variable	DCA1	Ppt.Ttl	Tmin.Jan	Tmax.Jul
	Nectar				
	Aerial flycatching				
	Hawking				
	Ground sallying				
	Foliage sallying				
	Picking seeds and fruit				
Miscellaneous	Disturbance tolerant				
	Cowbird acceptor/rejecter				
	Habitat specialist				

b. Trait relationships with landscape-scale variables

Category	Variable	Landscape-scale variables						
		Chaparral (+) vs. CSS (-)	Native Mosaic (incr)[b]	Aquatic/Woodland (incr)	Ag/Exotic (incr)	Urban (decr)	Distance to nearest ecotone (incr)	Distance to nearest urban (incr)
		LF.1	LF.2	LF.3	LF.4	LF.5	Dist.edge	Dist.urb
Life History	Clutch Size							
	No. broods		-				+	
	Female body mass				+			
Migratory status	Resident					-		
Nest type	Nopen		-	-				
	Ncav	+	+	+				
	Nencl				+			
Nest Location	Tree	+						
	Rock				+			-
	Shrub							

Category	Variable	Landscape-scale variables						
		Chaparral (+) vs. CSS (-)	Native Mosaic (incr)[b]	Aquatic/Woodland (incr)	Ag/Exotic (incr)	Urban (decr)	Distance to nearest ecotone (incr)	Distance to nearest urban (incr)
		LF.1	LF.2	LF.3	LF.4	LF.5	Dist.edge	Dist.urb
	Ground							
	Structure							
Diet	Seed	-						
	Insects + Invertebrates							
	Vegetation							
	Omnivore							
	Fruit							
Foraging Substrate/ behavior	Foliage gleaning				-			
	Ground foraging	-						
	Rock gleaning		-		+			-
	Probing	+	+		-		-	
	Bark gleaning	+	+				-	

Category	Variable	Landscape-scale variables						
		Chaparral (+) vs. CSS (-)	Native Mosaic (incr)[b]	Aquatic/Woodland (incr)	Ag/Exotic (incr)	Urban (decr)	Distance to nearest ecotone (incr)	Distance to nearest urban (incr)
		LF.1	LF.2	LF.3	LF.4	LF.5	Dist.edge	Dist.urb
	Nectar							
	Aerial flycatching							
	Hawking							
	Ground sallying							
	Foliage sallying							
	Picking seeds and fruit							
Miscellaneous	Disturbance tolerant					-	+	
	Cowbird acceptor/rejecter							
	Habitat specialist							

c. Trait relationships with habitat structure (local scale) variables

Category	Variable	Local scale-Habitat Structure variables					
		Shrub (+) vs. Grass (-)	Litter (+) vs. Bare (-)	Forbs/Patchy (incr)	Disturbed (incr)	Rock Outcrop (p/a)[c]	Tree (p/a)
		Struc.Fac.1	Struc.Fac.2	Struc.Fac.3	Struc.Fac4	Rock	Tree
Life History	Clutch Size						
	No. broods						
	Female body mass						
Migratory status	Resident						
Nest type	Nopen						
	Ncav	+					
	Nencl						
Nest Location	Tree						
	Rock		-		+		
	Shrub						
	Ground						
	Structure						
Diet	Seed	-					
	Insects +						

Category	Variable	Local scale-Habitat Structure variables					
		Shrub (+) vs. Grass (-)	Litter (+) vs. Bare (-)	Forbs/Patchy (incr)	Disturbed (incr)	Rock Outcrop (p/a)[c]	Tree (p/a)
		Struc.Fac.1	Struc.Fac.2	Struc.Fac.3	Struc.Fac4	Rock	Tree
	Invertebrates						
	Vegetation						
	Omnivore						
	Fruit						
Foraging Substrate	Foliage gleaning						
	Ground foraging	-	-			+	
	Rock gleaning		-		+	+	
	Probing				-		
	Bark gleaning	+			-	-	
	Nectar						
	Aerial flycatching						
	Hawking						
	Ground sallying						
	Foliage sallying						
	Picking seeds and						

Category	Variable	Local scale-Habitat Structure variables					
		Shrub (+) vs. Grass (-)	Litter (+) vs. Bare (-)	Forbs/Patchy (incr)	Disturbed (incr)	Rock Outcrop (p/a)[c]	Tree (p/a)
		Struc.Fac.1	Struc.Fac.2	Struc.Fac.3	Struc.Fac4	Rock	Tree
	fruit						
Miscellaneous	Disturbance tolerant				+		
	Cowbird acceptor/rejecter						
	Habitat specialist			+			

[a] variable marked + increases along the PC
[b] variable increases along the PC
[c] related to presence of the environmental variable

Chapter 3 : Life history variation in Galliformes across elevational gradients: A test of the fecundity-offspring quality trade-off hypothesis

ABSTRACT

Elevational gradients offer an excellent opportunity to explore how environmental variation influences life history evolution. Patterns from altricial species show that species breeding at high elevations have reduced fecundity due to smaller clutches, fewer broods, longer incubation and nestling periods and increased parental investment through extended parental care. This may result from a trade-off with survival and/or a trade-off with offspring quality achieved through increased parental investment. In this study, I use phylogenetically controlled methods to test the generality of the fecundity/offspring quality trade-off by analyzing patterns of life history variation in a clade of precocial species, Galliformes, across elevational gradients after also controlling for allometry and breeding latitude. In altricial species, parental care is known to constrain clutch size. Hence, precocial species that lack parental care should not vary in clutch size across elevations and reduction in fecundity should result from fewer broods. Offspring quality may be influenced via variation in egg mass, a form of parental investment and a trait analogous to parental care. I found partial support for the hypothesis; clutch size did not vary across elevations and egg mass increased with elevation. Incubation periods were longer at high elevations. Colder temperatures and shorter breeding seasons at high elevations may select for higher offspring quality than number. Variation in temperature, pressure and daylength may drive the evolution of such strategies. This study shows that

selection pressures across elevational gradients drive the evolution of similar strategies despite intrinsic differences across taxa.

INTRODUCTION

Trade-offs are a central feature in evolutionary ecology (Roff 1992). Breeding adults have limited resources and they need to make a series of allocation decisions between reproduction and maintenance and within reproduction, towards number and quality of offspring so as to result in the maximum surviving offspring. As a consequence, trade-offs such as between fecundity and survival, offspring number versus size/quality are common (Stearns 1976, Roff 1992). Variation in local environmental and ecological factors can shape life history strategies and thus influence associated trade-offs. For example, Skutch (1949) proposed that increased nest predation risk could limit clutch sizes in birds by constraining nestling provisioning rates. The smaller clutch sizes of tropical birds as compared to north-temperate birds have thus been attributed to variation in nest predation rates across latitudes (Marin 1996). Thus, understanding how life history strategies are influenced by environmental and ecological factors is crucial to understanding the processes by which natural selection shapes the evolution of life history strategies and the responses of species to environmental change.

Environmental gradients such as elevational gradients are a powerful means to test for patterns of co-variation between environmental factors, life history strategies and how they influence trade-offs between traits. Elevational gradients capture considerable environmental variation albeit over short spatial scales. High elevations are harsh environments characterized by colder temperatures, lower atmospheric pressure, shorter breeding seasons, more prolonged snow cover, and higher environmental stochasticity.

Breeding at high elevations involves significant energetic costs as organisms allocate energy and resources between self-maintenance and reproduction (Martin 2001, Martin and Wiebe 2004). Studies on avian life history variation along elevational gradients have shown that individuals and species breeding at high elevations have smaller clutches, fewer broods, longer developmental periods, increased parental care via higher nestling provisioning rates, and increased post fledging care, increased survival, and higher offspring condition (Badyaev 1997, Badyaev and Ghalambor 2001, Bears et al. 2009, Martin et al. 2009, Lee et al. 2011). Although the generality of these patterns is not assured, and there is variation in the direction of change with respect to specific life history traits, the overall trade-off seems to be one of reduced fecundity versus higher offspring quality and/ or increased juvenile survival through increase in parental care and increase in adult survival (Badyaev and Ghalambor 2011, Bears et al. 2009).

This is in keeping with expectations from life history theory. In temporally variable environments with high juvenile mortality risk organisms should invest less in reproductive effort to maximize adult survival (Murphy 1968, Schaffer 1974) have few, large young, and increase parental care to increase the chances of offspring survival (Stearns 1976, Schultz 1991, Roff 1992). Higher parental investment in offspring may be achieved through multiple avenues- investment in egg mass, biparental care, increase in parental care (nestling provisioning and duration of post-fledging care). Parental care is an energetically expensive process as the energetic demands of feeding a chick are greater than egg production costs (Yom-Tov and Hilborn 1981) and constraints on the allocation of parental care can limit clutch size in altricial species (Styrsky et al. 2005).

Brood manipulation experiments have shown that experimental increases in brood size, results in increase in parental care but there are subsequent costs to both adults and young through loss of body condition, increased mortality and reduced future reproductive success (Martin 1987, Dijkstra et al. 1990). Egg mass also has a significant positive influence on offspring survival and condition and chicks hatching from larger eggs fare better (Schifferli 1973, Williams 1994). However, in altricial species, in later stages of nestling development, parental care can override or confound the influence of egg mass. Fostering experiments have demonstrated that whilst egg mass influences hatchling condition and survival, parental care has a greater effect in the later stages of nestling development (Ricklefs 1984, Amundsen and Stokland 1990, Magrath 1992).

Precocial and altricial species form two ends of a developmental continuum. Precocial species tend to be larger bodied, lay larger eggs and clutches, have longer developmental periods and lack the intensive parental care (nestling and fledgling provisioning) observed in altricial species (Starck and Ricklefs 1998). Precocial species' young are born at an advanced stage of development and are independent soon after they hatch. It has been hypothesized that the lack of intensive parental care as found in altricial species frees up resources that can be invested in eggs and is thus a factor in the larger clutches of precocial species (Winkler and Walters 1983, Jetz et al. 2008). However, parental investment in precocial species may be in the form of investment in egg mass. Egg size has a greater effect on precocial chicks than in altricial species and positively influences chick mass, survival and condition (Magrath 1992, Williams 1994). In ectothermic species that lack parental care (e.g., frogs) smaller clutches of larger eggs have been observed at higher elevations along with delayed age to maturity and larger size (Berven 1982, Chen et al. 2013). Thus, development mode could affect the type of tradeoff and the traits involved therein, but our knowledge is limited as most studies have focused on altricial passerines.

As mentioned above, the life history adopted by a species is a reflection of adjustment between different life history traits as well as response to environmental variation along elevational gradients. Important factors affecting avian life history variation include food availability, predation, daylength, temperature. Food availability is known to affect multiple life history traits (e.g. clutch size, egg size) through direct effects on the laying female as well as indirect effects on other traits such as parental provisioning rates (Lack 1947, 1948, Martin 1987). Variation in ambient temperature can mediate the balance between thermoregulatory needs and investment in offspring (Conway and Martin 2000) and predation risk can affect fecundity and parental investment through differential effects on adult and juvenile mortality risk (Skutch 1949, Martin 1995, Ghalambor and Martin 2001). Latitude as a proxy for the above mentioned environmental factors also has a well-documented effect on avian life history variation. For example, in altricial as well as in some precocial species, clutch size increases with latitude (Lack 1947, 1948, Musvuugwa and Hockey 2011). Different hypotheses have been proposed to explain this pattern. Increasing daylength across latitudes is considered to facilitate greater time to acquire resources favoring a larger clutch size (Lack 1947, Hussell 1972). Ashmole (1963) proposed that clutch size is proportional to the degree of seasonality and is determined by the resource levels in the breeding season relative to population density. Thus, areas of high seasonality such as north-temperate areas favor larger clutches. Skutch (1949) attributed this trend to the higher levels of nest predation and its influence on nestling provisioning rates. Thus, to better understand life history variation along elevational gradients, it is important to interpret the influence of environmental variation on species traits.

Most studies along elevational gradients have focused on intraspecific studies of altricial passerines with only a couple of interspecific comparisons (Badyaev 1997, Badyaev and Ghalambor 2001). Intraspecific studies may reflect local adaptation or phenotypic plasticity. Comparative studies across a wide diversity of species can help elucidate the evolutionary mechanisms governing these trait- environment relationships.

In this study, I aim to investigate the generality of the fecundity/offspring quality trade-off seen across elevational gradients in altricial passerines using comparative analyses on a precocial group- the Galliformes, after controlling for phylogeny, latitude and allometry. Galliforms (grouse, quail, pheasants, megapodes, cracids, and partridges) are precocial and the young are independent and are able to feed themselves immediately upon hatching. Galliforms are distributed across the world from tropical forests to tundra and from sea level to alpine areas. They exhibit a wide range of variation in life history traits and are thus an appropriate choice to study how elevation influences life history variation in precocial species. Galliform phylogeny is also relatively well understood (Kimball et al. 2011, Wang et al. 2013), thus affording opportunity to analyze differences in life history traits given the interrelationships between species. The study has two main objectives

1. To investigate the hypothesis that high elevation environments select for a strategy of reduced fecundity versus higher offspring quality and/or survival. However, the traits involved in this trade-off should vary depending on intrinsic qualities of species such as development mode.

2. Interpret patterns of life history variation in the light of environmental factors along elevational gradients that may influence this life history variation.

If the fecundity/offspring quality trade-off holds for precocial species, the following predictions can be made

1. Across elevational gradients, precocial species breeding at high elevations should have lower fecundity (clutch size x number of broods) as compared to low elevation counterparts. This may be achieved in multiple ways- through a reduction in clutch size and/or number of broods raised. However,

a. If parental care is a constraint on clutch size in altricial species and trades off with clutch size in high elevation species, then precocial species that lack the intensive parental care of altricial species should not vary in clutch size across elevational gradients and

b. Reduction in fecundity for high elevation precocial species should result from a reduction in number of broods attempted.

2. Across elevational gradients, precocial species should increase parental investment in offspring quality by varying egg mass.

METHODS

Species data

Elevational ranges

I recorded upper and lower elevational distributional limits from the literature for 181 species (Appendix 2). Data were obtained from Cramp and Simons (1980), del Hoyo et al. (1994), Madge and McGowan (2002), Poole (2005), BirdLife International (2013), and Neotropical Birds Online, and from regional handbooks and field guides. Where available, known breeding elevation was used. Mean elevation was calculated as the average of maximum and minimum elevation and was used in all subsequent analyses.

Latitudinal ranges

Life history traits such as clutch size tend to vary with latitude (Lack 1948, Musvuugwa and Hockey 2011). I determined the latitudinal extent of breeding ranges using bird species distribution maps from BirdLife International (2013) and NatureServe (2012 http://www.biodiversityinfo.org/spcdownload/u7g0c5/download.htm). I extracted data from the native range of species where it was extant or considered probably extant, and where it was a year-round resident or breeding visitor. In cases where data were not available from the above sources, visual estimation of species global range maps and distribution information from The Handbook of the Birds of the World (del Hoyo et al. 1994) was used to estimate maximum and minimum latitudinal extent. Mean breeding latitude was calculated as the average of maximum and minimum latitude. The absolute value of mean breeding latitude was used in all subsequent analyses.

Life history data

I collected data on life history variables including clutch size, egg mass, egg volume, incubation period, and female body mass from the literature for each of the 181 species (Fig. 3.1, Appendix 2). When data were available at the subspecies level, I averaged values across all subspecies to calculate species means. Only data from species' native range were used. Mean values of variables were used when available; otherwise, means were calculated as the average of the range reported. Data from captivity were also utilized; I assumed that data from captivity fell within the range of variation observed for the trait in the wild. For many species, data on egg mass were not available. In those cases, following Musvuugwa and Hockey (2011), I estimated egg mass from Hoyt's (1979) equation $W= K_w LB^2$, where W= egg mass(g), K_w = specific weight coefficient, L = length of egg (cm) and B = breadth of egg (cm). K_w was calculated from congeners for which egg mass and dimensions were known. Egg mass was estimated for 13 species through this method. Egg volume was calculated following Hoyt (1979) $V= 0.51*LB^2$. In cases where sex-specific body mass was not given, I used the available body mass. Clutch mass was calculated as the product of egg mass and clutch size. Clutch investment was calculated as clutch mass/female body mass.

Phylogeny reconstruction

As species relatedness can confound interspecific comparisons, I took into account phylogenetic relationships between species in the dataset. Phylogenetic relationships for the species in the dataset were established by sampling 4000 phylogenetic trees with a Hackett et al. (2008) backbone from www.birdtree.org (Jetz et al. 2012). These trees were constructed for all of the world's extant birds by inferring dated distributions of backbone trees from existing studies and combining them with additional trees built for species using genetic data and taxonomic information (Jetz et al. 2012). A majority rule consensus tree was built from these 4000 trees using the software Mesquite (Maddison and Maddison 2011) and this tree was used in all subsequent analyses (Fig. 3.2).

Analyses

Percentage data were arc-sine transformed and all the other life history variables were log transformed prior to analyses. As a clutch size of one would become zero after log transformation, I added one as a constant to all log transformed clutch size. As phylogenetic relatedness can confound interspecific comparisons (Harvey and Pagel 1991, Martins and Garland 1991, Garland et al. 1992) differences in life history traits across elevations were investigated through pairwise comparisons as well as Felsenstein's (1985) method of phylogenetically independent contrasts.

Pairwise comparisons

Based on the reconstructed phylogeny, pairs of closely related and congeneric species (Table 3.1) were chosen and comparisons between them were made following the methods of Møller and Birkhead (1992). Pairs of congeneric species were ranked in order of mean elevation and the sign of the difference between life history traits was noted by subtracting the value of the high elevation species from the low elevation species. Concordance with prediction was then tested using a Sign test. Comparing closely related or congeneric species controls for species relatedness and fewer confounding variables may be expected to influence the relationship and thus this serves as a more direct test of the association between elevation and life history traits. As the mean latitude of species occurrences ranged from 29.7°S to 61.1°N, I controlled for latitude by comparing species pairs in which the difference of the absolute values of mean latitudes of the two species did not differ by more than 10 degrees. The choice of 10 degrees of separation is arbitrary, but allows an interpretation of results relatively free from the influence of latitudinal variation. The median latitudinal separation between pairs of species was 4.8 degrees. All analyses were done in SPSS Version 22.0 (IBM Corp 2011). Reported P-values are two-tailed.

Phylogenetically Independent Contrasts

Phylogenetically independent contrasts were calculated following the method of Felsenstein (1985) through the PDAP module (Midford et al. 2009) in Mesquite (Maddison and Maddison 2011). The raw contrasts were standardized by dividing them by the square root of their branch lengths. Adequacy of branch lengths for standardization of independent contrasts was tested by plotting standardized independent contrasts against the square root of the sum of their branch lengths (Garland. et al. 1992). When significant correlations were found, branch lengths were considered inadequate and transformations were employed. Grafen (1989) branch length transformations were applied for egg mass, Nee (1992; cited in Purvis 1995, p. 416) for clutch investment, whereas Constant (all branch lengths equal to 1) branch length transformations were appropriate for latitude and elevation. As the working phylogeny contained multiple polytomies (44 branches of 0 length), following the methods of Purvis and Garland

(1993) and Garland and Diaz-Uriarte (1999), degrees of freedom were bounded whilst calculating independent contrasts as n – 2 – z, where n = number of species and z = number of branches of zero length. As body size tends to be correlated with many life history traits, I controlled for allometric effects by computing linear regressions through the origin using standardized contrasts of life history traits against standardized contrasts of female body mass, and used the resultant residuals in analyses with elevation and latitude. Relationships between life history traits were assessed by correlation analyses through the origin using standardized contrast residuals of traits obtained by regressions against female body mass. To assess the relationship of life history traits with elevation, residuals from the above mentioned analysis were regressed through the origin against standardized contrasts of elevation. To control for the effect of latitude, multiple regression through the origin were performed including the absolute value of the mean breeding latitude and mean breeding elevation as independent variables along with an interaction term of latitude and elevation. I report results from analyses including only elevation as well as elevation and latitude. All regression analyses using standardized independent contrasts were conducted in SPSS Version 22.0 (IBM Corp 2011).

RESULTS

Inter-correlations between life history traits

Heavier females laid significantly heavier eggs and clutches, had longer incubation periods and decreased clutch investment. Larger clutches took longer to incubate, weighed more and represented a larger investment. Heavier eggs contributed to heavier clutches, took longer to incubate and represented a larger investment. (Table 3.2).

Clutch Size

In pairwise comparisons there were no significant differences in clutch size between low and high elevation species (Table 3.3). Simple linear regression using standardized independent contrasts showed that clutch size did not vary with elevation (Table 3.4a; Fig. 3.3A). In multiple regression using standardized independent contrasts including elevation and latitude, clutch size increased only with latitude (Table 3.4b).

Egg mass and volume

In pairwise comparisons, high elevation species laid heavier eggs and of greater volume though the relationship was marginally insignificant for egg mass (Table 3.3). However, using standardized independent contrasts, egg mass showed a strongly positively relationship with elevation whereas the relationship between egg volume and elevation became insignificant (Table 3.4a, Fig. 3.3B, C).

When elevation and latitude were both included in the regression, the significant positive trend of egg mass with elevation persisted but egg mass did not vary across latitude. However, the interaction term between elevation and latitude was also a significant predictor of egg mass (Table 3.4b, Fig.3.4A). Egg volume continued to vary little across both elevation and latitude but the interaction term between elevation and latitude was a significant predictor of egg volume (Table 3.4b, Fig. 3.4B).

Incubation Period

In pairwise comparisons, incubation period did not vary across low and high elevation species (Table 3.3). However, linear regression using standardized independent contrasts showed that incubation period did, in fact, strongly increase with elevation

(Table 3.4a; Fig. 3.3D). When latitude was included in the regression, incubation period increased only with elevation and was not related with latitude (Table 3.4b).

Clutch mass and clutch investment

In pairwise comparisons, clutch mass was significantly greater for high elevation species whereas clutch investment did not vary across elevation (Table 3.3). In simple linear regression using standardized independent contrasts, clutch mass increased with elevation (Table 3.4a; Fig. 3.3E) whereas clutch investment did not vary with elevation (Table 3.4a; Fig. 3.3F) although the relationship with clutch mass was marginally insignificant. When latitude was included in the regression, clutch mass increased with both elevation and latitude although the relationship with latitude was much stronger. Clutch investment was significantly related to latitude but not with elevation (Table 3.4b).

Female body mass

In pairwise comparisons, high elevation species weighed significantly more than low elevation species (Table 3.3). When phylogenetically independent contrasts were used, this relationship disappeared. Linear regression results show that female body mass did not vary with elevation (Table 3.4a; Fig. 3.3G) and this non-significance persisted when both elevation and latitude were considered together (Table 3.4b).

DISCUSSION

Examining patterns of life history variation in precocial birds distributed along elevational gradients helps us gain insights into selection pressures faced by species along such environmental gradients. In this study, we controlled for phylogeny, allometry and latitude in an analysis of life history variation in galliforms across elevational gradients and found partial support for the hypothesis of reduced fecundity and increased offspring investment in high elevation species. This result suggests that precocial species follow patterns seen in altricial passerines and lends support that high elevation environments select for increased investment in offspring at a potential cost of reduced fecundity in diverse taxa irrespective of intrinsic factors such as development mode.

General patterns in variation within life history traits

Many relationships between traits observed in this study are consistent with patterns found in other studies, for example, relationships of traits to female body mass. Female body mass is positively related to egg mass across taxa (Rahn et al. 1975, Berven 1982, ref within Christians 2002) and incubation period (Rahn et al. 1975). However, female body mass was not correlated with clutch size (Bennett and Owens 2002, Figuerola and Green 2006) and larger females had lower clutch investment (Carey 1983). Incubation periods also increased with clutch size (Smith 1989), egg mass (Carey 1983) and consequently also clutch mass. However, we did not find a trade-off between clutch size and egg mass as observed in some other studies (Blackburn 1991, Martin et al. 2006).

Elevational correlates of life history variation

Both elevation and latitude influence clutch size, egg mass, clutch mass, clutch investment and incubation period after controlling for the effects of body mass and phylogeny. Elevation remained a significant predictor of life history traits after controlling for latitude.

As predicted clutch size did not vary with elevation (Fig. 3.3A) but increased with latitude. Latitudinal gradients in clutch size are known for many groups of birds including galliforms (Klomp 1970, Martin 1996, Musvuugwa and Hockey 2011). Also, as predicted, egg mass strongly increased with elevation after controlling for female body mass (Fig. 3.3B, Table 3.1) Incubation period and clutch mass also increased with elevation after controlling for female body mass (Fig.3.3D). Due to inadequate data on number of broods, which can be a more important determinant of annual fecundity than clutch size (Martin 1995), I was not able to detect a reduction in fecundity as predicted. However, given the short breeding seasons at high elevations and longer developmental periods, per clutch, time and resources for additional breeding attempts may be reduced. Most studies along elevational gradients have reported a reduction in number of breeding attempts at high elevations (Baur and Raboud 1988, Badyaev 1997, Badyaev and Ghalambor 2001, Morrison and Hero 2003, Bears et al. 2009). Therefore, we predict that number of broods raised should be lower for galliform species breeding at high elevations as compared to those at low elevations. However, selection may act on components of reproductive effort such as fecundity and parental investment and/or on total reproductive effort (Roff 1992). On first glance, total reproductive effort is apparently greater at higher elevations due to greater clutch mass and longer incubation period. However, if higher elevation species raise fewer broods, total reproductive effort expended during a breeding season may still be similar across elevations. In that case, higher elevation species may be investing in higher quality offspring for similar reproductive effort as compared to lower elevation species that invest in greater offspring number. Indeed, I found that although clutch mass differed across elevations, clutch investment did not. In altricial birds, parental care in terms of feeding nestlings and fledglings is an energetically intensive activity. However, in most galliforms post-hatching parental care is limited to brooding chicks, vigilance behavior and leading chicks to food rich areas. The relatively low parental care needs may allow them to sustain the same clutch size across elevations.

Selection for higher offspring quality may be favored at high elevations if it increases offspring survival probability. Egg mass is a form of parental investment analogous to parental care that influences offspring quality and survival. In general, larger eggs are associated with increased hatching success, and result in larger and heavier chicks that have increased growth and survival (Schifferli 1973, Krist 2011). Although investment in egg mass is a viable strategy for both altricial and precocial species, egg mass has a more pronounced effect on chick fitness and positively influences growth and survival in precocial species (Moss et al. 1981, Williams 1994). For example, in the Australian brush-turkey (*Alectura lathami*), which is one of the most precocial of all birds, egg mass had a significant positive influence on hatchling mass and tarsus length. The latter significantly influenced motor performance and hatchlings from larger eggs were able to dig themselves up from their underground nest faster (Göth and Evans 2004). Interestingly, a few altricial passerine species breeding at high elevations follow a similar strategy and lay larger eggs (Lu et al. 2010, 2011). Larger chicks resulting from larger eggs can also maintain homeothermy in colder temperatures compared to those hatching from smaller eggs (Rhymer 1988). Thus, in precocial species that lack intensive parental care, investing in larger eggs may be a strategy to enhance offspring quality and thereby offspring survival. Investment in heavier eggs is also reflected as an increase in clutch mass with elevation (Fig. 3.3E). There was a significant interaction effect between latitude and elevation on egg mass. Although egg mass increased with elevation across latitudes, the increase was steeper across elevations at low latitudes as compared to high latitudes (Fig.3.4A). This could be because high latitude species also invest in larger clutches; thus, energetic constraints may prevent high latitude species from increasing egg mass considerably given the increased commitment in terms of clutch size. Egg volume was only significantly related to the interaction term between elevation and latitude. At low latitudes, high elevation species lay eggs of greater volume. However, the opposite trend is observed at high latitudes where species at high elevations lay eggs of smaller volume and larger mass (Fig.3.4B). Egg volume can be related to mass as (Egg mass*0.51)/K_w. Hoyt (1979) suggested that the weight coefficient K_w is highly variable between species and is a function of egg shape and density. Thus, it is possible that species occupying high elevations at high latitudes are laying eggs of higher density as compared to their low elevation counterparts. Egg density is influenced by the relative amount of albumin and yolk; eggs of precocial species have greater amounts of yolk to allow for greater energy to hatch well developed independent young (Ricklefs 1977, Carey 1983). Given increased energetic demands of breeding at high elevations at high latitudes, investing in denser and larger eggs may be required to increase offspring quality, development and survival. However, this hypothesis remains to be tested as we have very little information about if and how egg composition varies in species across elevational gradients.

Investment in offspring quality may also be inferred from the prolonged incubation periods observed for high elevation species. Larger clutch sizes generally require longer incubation periods but clutch sizes did not vary across elevations despite longer incubation periods. This trend is similar to observations on altricial passerines along elevational gradients (Badyaev 1997, Badyaev and Ghalambor 2001). Longer incubation periods enable young to hatch at a larger size and at a more mature stage of development. Larger size at hatch also helps increase thermoregulatory efficiency which would be an advantage at high elevations (Rhymer 1988). Hatchlings of precocial species are very independent, mobile and can feed on their own. Selection for longer developmental periods may occur in species whose young are required to be well developed at hatch and may thus be another strategy to increase their chances of survival (Boersma 1982). It is interesting that the longest incubation period in this dataset (49.5 days) was observed in the Australian brush-turkey, a megapode, whose highly precocial young fend for themselves immediately upon hatching with absolutely no parental care. At a proximate level though, longer incubation periods may also reflect energetic constraints on the breeding adult.

Some trends varied between tests using pairwise comparisons and standardized independent contrasts. The increasing trend of female body mass and egg volume with elevation as seen in pairwise comparisons disappeared in regressions using standardized independent contrasts. This could reflect methodological differences in the two techniques. Regressions using standardized independent contrasts utilized many more species and thus had a higher sample size than did pairwise comparisons. The change in trends could reflect greater statistical power in analysis utilizing independent contrasts. Also methods using independent contrasts account for phylogeny more comprehensively resulting in strengthening of some patterns and disappearance of others. The pairwise comparisons matched pairs based on a less than ten-degree latitudinal difference. Though intended to be a conservative way to account for latitude, the arbitrary nature of the rule means different pairs of species can be compared. On the other hand, the independent contrasts treat the data more continuously and may thus reveal a more robust pattern.

Environmental correlates of life history variation

Evolutionary adjustments in species life history strategies accrue through the proximate effect of environmental and ecological influences on life history traits. Some of the well documented proximate factors that influence avian life history variation include food availability, seasonality of temperature and resources, nest predation risk, and variation in daylength (Lack 1947, 1948, Skutch 1949, Ashmole 1963, Hussell 1985, Martin 1996). Clutch size did not vary with elevation but increased with latitude. This latitudinal pattern has been found in many other studies (Lack 1947, 1948, Martin 1996, Böhning-Gaese et al. 2000, Jetz et al. 2008, Musvuugwa and Hockey 2011). Clutch mass increased with both latitude and elevation. However, different traits contributed to this increase along different gradients. Egg mass contributed to increasing clutch mass along elevational gradients and clutch size contributed along latitudinal gradients. Clutch size increases along latitudinal gradients have been attributed to the effect of increasing daylength on time available for foraging (Lack 1947, Hussell 1972). However, daylength does not vary along elevational gradients and species breeding at high elevations have similar daylight hours to forage, and in some cases may in fact have less foraging time due to adverse temperatures and higher solar radiation (Melcher et al. 1990). Thus, lack of variation in daylength may select for investment in offspring size more than offspring number across elevational gradients. Although experimental evidence exists to confirm the influence of daylength on clutch size variation along latitudinal gradients (Rose and Lyon 2013), its applicability along elevational gradients remains to be tested.

With increasing elevation, atmospheric pressure becomes lower leading to greater water vapor loss from eggs and more hypoxic conditions. Water loss from eggs can be mitigated by increasing the water content of eggs, leading to larger eggs, and/or decreasing nest attentiveness and lengthening the incubation period (Rahn et al. 1975). Hypoxic conditions at high elevations have been shown to decrease metabolic rate and growth rate of chicken embryos that may therefore, lengthen the incubation period (Wangensteen et al. 1974). Egg mass and incubation period both increased with elevation. Thus, variation in atmospheric pressure may exert proximate constraints to modify life history traits. In addition, colder temperatures at higher elevations can place greater thermoregulatory demands on birds and increase energetic costs during reproduction as energy is needed not only to invest in offspring but also for self-maintenance (White and Kinney 1974, Williams 1996). Larger eggs and larger clutch masses lose heat less rapidly in colder temperatures (Reid et al. 2000) and thus maybe advantageous at high elevations. For species with female only incubation such as most galliforms, colder temperatures may necessitate staying away from the nest more to gather resources to meet energetic demands (Carey 1980, Conway and Martin 2000), thus lengthening incubation periods (Martin 2001). Larger eggs and a larger clutch mass that cools less rapidly may thus be required when species have to forage away from the nest.

Nest predation is a significant factor in shaping life history strategies (Slagsvold 1982, Lima 1987, Martin 1988). Studies on altricial passerines show that high nest predation rates are associated with smaller clutches, longer incubation periods, shorter re-nesting intervals and reduced nestling provisioning rates (Skutch 1949, Slagsvold 1982, Martin 2002, Fontaine and Martin 2006) In an interspecific study on precocial species, (Sandercock et al. 2005) reasoned that alpine ptarmigan laid smaller clutches than those at lower elevations in keeping with higher predation rates. However, the study was in north-temperate sites and latitude was a confounding factor. Boyle (2008) showed that nest predation declines with elevation and is highest in intermediate elevations in the neotropics. Similarly, in cardueline finches (Badyaev 1997) nest predation declined with elevation. If nest predation was low, then clutch sizes should be larger and incubation periods should be longer at high elevations. However, clutch size did not vary with elevation whilst incubation period increased. Thus, nest predation does not explain patterns in life history traits satisfactorily.

Food availability is known to influence all aspects of the breeding cycle from egg laying to nestling period and adult survival (Martin 1987). Lack (1968) hypothesized that clutch size in precocial birds is limited by food availability to the laying female. Eggs of precocial birds are larger in size, and have a higher yolk content and caloric density compared to altricial eggs (Carey 1983). Precocial species that lack parental care also are likely to deplete their energy reserves much more than altricial species during egg laying and incubation (Martin 1987). Thus food limitation should have a greater effect on clutch size, egg mass, and incubation period in precocial species and an increase in food availability should result in larger clutch size and/or egg mass and shorter incubation period as parents spend less time foraging resulting in increased nest attentiveness (Martin 1987). In this study, clutch size did not increase with elevation. Thus, food availability probably did not vary across elevations or influence clutch size. However, egg mass increased with elevation signifying higher food availability but incubation period also increased, which signifies food limitation. Additionally study on effects of food provisioning in ring-necked pheasants (*Phasianus colchicus*) and Tibetan eared-pheasants (*Crossoptilon harmani*) showed that food supplementation either did not influence clutch size (Hoodless et al. 1999) or had only a weak positive effect on egg and clutch size (Lu and Zheng 2003). Thus food availability is unable to fully explain patterns in life history variation across elevations.

Overall, variation in environmental factors such as temperature, atmospheric pressure and daylength are more likely to explain interspecific patterns of life history variation along elevational gradients and deserve further attention.

Conclusions

In conclusion, comparative analyses of life history variation in precocial species after controlling for multiple confounding factors such as latitude, phylogeny and allometry has demonstrated selection pressures operating along elevational gradients and provided additional support to the fecundity/offspring quality trade-off in life history strategies postulated across elevational gradients. Patterns observed here are similar to those reported in altricial passerines. Thus high elevation environments in general, select for increased investment in offspring quality at a potential cost of reduced fecundity. Intrinsic factors such as development mode determine the traits involved in the trade-off and not the trade-off itself. Precocial species increase investment in offspring quality through increases in egg mass as compared to increase in parental care for altricial species. A reduction in fecundity is expected through reduction in number of breeding attempts although this remains to be shown. Proximate influences on life history traits that deserve greater attention include effects of temperature, daylength and atmospheric pressure.

REFERENCES

Ali, S., and S. D. Ripley. 1969. Handbook of the birds of India and Pakistan. Oxford University Press, New Delhi.

Amundsen, T., and J. N. Stokland. 1990. Egg size and parental quality influence nestling growth in the shag. Auk: 410–413.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103:458–473.

Badyaev, A. V. 1997. Avian life history variation along altitudinal gradients: An example with cardueline finches. Oecologia 111:365–374.

Badyaev, A. V., and C. K. Ghalambor. 2001. Evolution of life histories along elevational gradients: Trade-off between parental care and fecundity. Ecology 82:2948–2960.

Baker, E. C. S. (Ed.). 1928. The fauna of British India including Ceylon and Burma. 2nd edition. Taylor and Francis, London.

Baker, E. S. 1935. Nidification of the birds of the Indian Empire. London: Taylor and Francis.

Baur, B., and C. Raboud. 1988. Life history of the land snail *Ariana arbustorum* along an altitudinal gradient. Journal of Animal Ecology: 71–87.

Bears, H., K. Martin, and G. C. White. 2009. Breeding in high-elevation habitat results in shift to slower life-history strategy within a single species. Journal of Animal Ecology 78:365–375.

Bennett, P. M., and I. P. Owens. 2002. Evolutionary ecology of birds. Oxford University Press Oxford.

Bent, A. C. 1963. Life histories of North American gallinaceous birds. Dover Publication, New York.

Berven, K. A. 1982. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*. I. An experimental analysis of life history traits. Evolution: 962–983.

BirdLife International. 2013. Data from IUCN/BirdLife Species Information Service, accessed July 2013.

BirdLife International and NatureServe. 2012. Bird species distribution maps of the world. Version 2.0. BirdLife International Cambridge, UK and NatureServe Arlington, USA.

Blackburn, T. M. 1991. An interspecific relationship between egg size and clutch size in birds. Auk 108:973–977.

Boersma, P. D. 1982. Why some birds take so long to hatch. American Naturalist 120:733–750.

Böhning-Gaese, K., B. Halbe, N. Lemoine, and R. Oberrath. 2000. Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. Evolutionary Ecology Research 2:823–839.

Boyle, W. A. 2008. Can variation in risk of nest predation explain altitudinal migration in tropical birds? Oecologia 155:397–403.

Carey, C. 1980. Adaptation of the avian egg to high altitude. American Zoologist 20:449–459.

Carey, C. 1983. Structure and function of avian eggs. Pages 69–103 *In* R. F. Johnston (ed.), Current ornithology, Vol I. Plenum Press, New York.

Chen, W., Z. H. Tang, X. G. Fan, Y. Wang, and D. A. Pike. 2013. Maternal investment increases with altitude in a frog on the Tibetan Plateau. Journal of evolutionary biology 26:2710–2715.

Christians, J. K. 2002. Avian egg size: Variation within species and inflexibility between individuals. Biological Reviews 77:1–26.

Coates, B. J. 1985. The birds of Papua New Guinea: Including the Bismarck Archipelago and Bougainville. Dove Publications, Alderley, Queensland.

Conway, C., J., and T. Martin E. 2000. Effects of ambient temperature on avian incubation behavior. Behavioral Ecology 11:178–188.

Cramp, S., and K. E. L. Simons (Eds.). 1980. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic, Vol II: Hawks to Bustards. Oxford University Press, Oxford.

Delacour, J., D. Amadon, A. E. Gilbert, D. R. Henry, and G. M. Sutton. 1973. Curassows and related birds. American Museum of Natural History, New York.

Dement'ev, G. P., N. A. Gladkov, Y. A. Isakov, N. N. Kartashev, S. V. Kirikov, A. V. Mikheev, and E. S. Ptushenko. 1967. Birds of the Soviet Union. Israel Program for Scientific Translations, Washington, D. C.

Dijkstra, C., A. Bult, S. Bijlsma, S. Daan, T. Meijer, and M. Zijlstra. 1990. Brood size manipulations in the kestrel (*Falco tinnunculus*): Effects on offspring and parent survival. Journal of Animal Ecology: 269–285.

Dunning, J., B. Jr. (Ed.). 2008. CRC handbook of avian body masses. 2nd edition. CRC Press, Boca Raton, FL.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist: 1–15.

Figuerola, J., and A. J. Green. 2006. A comparative study of egg mass and clutch size in the Anseriformes. Journal of Ornithology 147:57–68.

Fontaine, J. J., and T. E. Martin. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecology Letters 9:428–434.

Garland, T., and R. Diaz-Uriarte. 1999. Polytomies and phylogenetically independent contrasts: Examination of the bounded degrees of freedom approach. Systematic Biology 48:547–558.

Garland, Jr., 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.

Ghalambor, C. K., and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292:494–497.

González-García, F. 1995. Reproductive biology and vocalizations of the horned guan *Oreophasis derbianus* in Mexico. Condor: 415–426.

Göth, A., and C. S. Evans. 2004. Egg size predicts motor performance and postnatal weight gain of Australian brush-turkey (*Alectura lathami*) hatchlings. Canadian Journal of Zoology 82:972–979.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 326:119–157.

Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W. A. Cox, K.-L. Han, J. Harshman, C. J. Huddleston, B. D. Marks, K. J. Miglia, W. S. Moore, F. H. Sheldon, D. W. Steadman, C. C. Witt, and T.

Yuri. 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320:1763–1768.

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

Hilty, S. L. and B. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey.

Hoodless, A. N., R. a. H. Draycott, M. N. Ludiman, and P. A. Robertson. 1999. Effects of supplementary feeding on territoriality, breeding success and survival of pheasants. Journal of Applied Ecology 36:147–156.

Howell, S. N. G., and S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford University Press Inc., New York.

Del Hoyo, J., A. Elliott, and J. Sargatal. 1994. Handbook of the birds of the world. Lynx Edicions, Barcelona.

Hoyt, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96:73–77.

Hume, A. O., and C. H. T. Marshall. 1880. The game birds of India, Burmah and Ceylon. Vol. 1. Published by the authors, Calcutta.

Hussell, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecological Monographs: 317–364.

Hussell, D. J. T. 1985. Clutch size, daylength, and seasonality of resources: Comments on Ashmole's hypothesis. Auk: 632–634.

IBM Corp. 2011. IBM SPSS statistics for Windows. IBM Corp., Armonk, NY.

Jetz, W., C. H. Sekercioglu, and K. Böhning-Gaese. 2008. The worldwide variation in avian clutch size across species and space. PLoS biology 6:e303.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. Nature 491:444–448.

Johnsgard, P. A. 1988. The quails, partridges, and francolins of the world. Oxford University Press, New York.

Johnsgard, P. A. 1999. The pheasants of the world: Biology and natural history. Smithsonian Institution Press Washington, DC.

Johnson, N., and C. Cicero. 1986. Richness and distribution of montane avifaunas in the White-Inyo region, California. Pages 137–159 *in* C. A. H. Jr. and D. J. Young, editors. Natural history of the White-Inyo range, eastern California and western Nevada, and high altitude physiology. University of California White Mountain Research Station Symposium, August 23 – 25, 1985, Bishop, CA.

Jones, D. N., R. W. Dekker, and C. S. Roselaar. 1995. The megapodes. Oxford University Press, New York.

Kimball, R. T., C. M. S. Mary, and E. L. Braun. 2011. A macroevolutionary perspective on multiple sexual traits in the phasianidae (Galliformes). International Journal of Evolutionary Biology 2011:1–16.

Klaus, S., Y. H. Sun, Y. Fang, and W. Scherzinger. 2009. Autumn territoriality of Chinese grouse *Bonasa sewerzowi* at Lianhuashan Natural Reserve, Gansu, China. International Journal of Galliform Conservation 1:44–48.

Klomp, H. 1970. The determination of clutch-size in birds. A review. Ardea 58:1–124.

Krist, M. 2011. Egg size and offspring quality: A meta-analysis in birds. Biological Reviews 86:692–716.

Lack, D. 1947. The significance of clutch-size. Ibis 89:302–352.

Lack, D. 1948. The significance of clutch-size. Part III.—Some interspecific comparisons. Ibis 90:25–45.

Lack, D. L. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Lee, J. K., O.-S. Chung and W.-S. Lee. 2011. Altitudinal variation in parental provisioning of nestling varied tits (*Poecile varius*). The Wilson Journal of Ornithology 123:283–288.

Lima, S. L. 1987. Clutch size in birds: A predation perspective. Ecology: 1062–1070.

Lu, X., D. Ke, Y. Guo, S. Tang, L. Zhang, and C. Wang. 2011. Breeding ecology of the black redstart *Phoenicurus ochruros* at a Tibetan Site, with special reference to cooperative breeding. Ardea 99:235–240.

Lu, X., T. Yu, W. Liang, and C. Yang. 2010. Comparative breeding ecology of two white-bellied redstart populations at different altitudes. Journal of Field Ornithology 81:167–175.

Lu, X., and G.-M. Zheng. 2003. Reproductive ecology of Tibetan eared pheasant *Crossoptilon harmani* in scrub environment, with special reference to the effect of food. Ibis 145:657–666.

Mackworth-Praed, C. W., and C. H. B. Grant. 1973. African handbook of birds. Vol 1. 2nd edition. Longmans, Green.

Maddison, W. P., and D. R. Maddison. 2011. Mesquite: A modular system for evolutionary analysis.

Madge, S., and P. McGowan. 2002. Pheasants, partridges and grouse. Princeton University Press, Princeton.

Magrath, R. D. 1992. The effect of egg mass on the growth and survival of blackbirds: A field experiment. Journal of Zoology 227:639–654.

Marchant, S., and P. J. Higgins (Eds.). 1993. Handbook of Australian, New Zealand and Antarctic birds. Oxford University Press, Melbourne, Australia.

Martin, K. 2001. Wildlife in alpine and sub-alpine habitats. Pages 239–260 *in* D. H. Johnson and T. A. O'Neil, editors. Wildlife habitats and relationships in Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Martin, K., and K. L. Wiebe. 2004. Coping mechanisms of alpine and arctic breeding birds: extreme weather and limitations to reproductive resilience. Integrative and Comparative Biology 44:177–185.

Martin, M., A. F. Camfield, and K. Martin. 2009. Demography of an alpine population of savannah sparrows. Journal of Field Ornithology 80:253–264.

Martin, T. E. 1987. Food as a limit on breeding birds: A life-history perspective. Annual Review of Ecology and Systematics 18:453–487.

Martin, T., E. 1988. Nest placement: Implications for selected life-history traits, with special reference to clutch size. American Naturalist 132:900–910.

Martin, T., E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65:101–127.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? Journal of Avian Biology 27:263–272.

Martin, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. Proceedings of the Royal Society B: Biological Sciences 269:309–316.

Martin, T. E., R. D. Bassar, S. K. Bassar, J. J. Fontaine, P. Lloyd, H. A. Mathewson, A. M. Niklison, and A. Chalfoun. 2006. Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. Evolution 60:390–398.

Martins, E. P., and T. Garland Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: A simulation study. Evolution: 534–557.

Melcher, J. C., K. B. Armitage, and W. P. Porter. 1990. Thermal influences on the activity and energetics of yellow-bellied marmots (*Marmota flaviventris*). Physiological Zoology: 803–820.

Meyer de Schauensee, R., and W. H. Phelps Jr. 1978. A guide to the birds of Venezuela. Princeton University Press, Princeton, New Jersey, USA.

Midford, P. E., T. Garland, Jr., and W. P. Maddison. 2009. PDAP: PDTREE package of Mesquite. Version 1.15 http:// mesquiteproject.org/pdap_mesquite/.

Møller, A. P., and T. R. Birkhead. 1992. A pairwise comparative method as illustrated by copulation frequency in birds. American Naturalist: 644–656.

Morrison, C., and J.-M. Hero. 2003. Geographic variation in life-history characteristics of amphibians: A review. Journal of Animal Ecology 72:270–279.

Moss, R., A. Watson, P. Rothery, and W. W. Glennie. 1981. Clutch size, egg size, hatch weight and laying date in relation to early mortality in red grouse *Lagopus lagopus scoticus* chicks. Ibis 123:450–462.

Murphy, G. I. 1968. Pattern in life history and the environment. American Naturalist: 391–403.

Musvuugwa, T., and P. A. R. Hockey. 2011. Latitudinal patterns of reproductive effort in gamebirds and waterfowl: Bucking the trend? Ibis 153:165–169.

Neotropical Birds Online Schulenberg, T. S. (Ed.). Ithaca: Cornell Lab of Ornithology. Retrieved from Neotropical Birds Online http://neotropical.birds.cornell.edu/portal/home, Ithaca.

Poole, A. 2005. The birds of North America online: http://bna.birds.cornell.edu/BNA/. Cornell Laboratory of Ornithology, Ithaca, NY.

Purvis, A. 1995. A composite estimate of primate phylogeny. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 348:405–421.

Purvis, A., and T. Garland. 1993. Polytomies in comparative analyses of continuous characters. Systematic Biology 42:569–575.

Rahn, H., C. V. Paganelli, and A. Ar. 1975. Relation of avian egg weight to body weight. Auk 92:750–765.

Reid, J. M., P. Monaghan, and G. D. Ruxton. 2000. The consequences of clutch size for incubation conditions and hatching success in starlings. Functional Ecology 14:560–565.

Rhymer, J. M. 1988. The effect of egg size variability on thermoregulation of mallard (*Anas platyrhynchos*) offspring and its implications for survival. Oecologia 75:20–24.

Ricklefs, R. E. 1977. Composition of eggs of several bird species. Auk: 350–356.

Ricklefs, R. E. 1984. Components of variance in measurements of nestling European starlings (*Sturnus vulgaris*) in southeastern Pennsylvania. Auk: 319–333.

Roff, D. A. 1992. Evolution of life histories: Theory and analysis. Routledge, Chapman and Hall, New York.

Rose, A. P., and B. E. Lyon. 2013. Day length, reproductive effort and the avian latitudinal clutch size gradient. Ecology 94:1327–1337.

Sandercock, B. K., K. Martin, and S. J. Hannon. 2005. Life history strategies in extreme environments: Comparative demography of arctic and alpine ptarmigan. Ecology 86:2176–2186.

Schaffer, W. M. 1974. Optimal reproductive effort in fluctuating environments. American Naturalist 108:783–790.

Schifferli, L. 1973. The effect of egg weight on the subsequent growth of nestling great tits *Parus major*. Ibis 115:549–558.

Schönwetter, M. 1961. Handbuch der oologie. Lieferung 4-5. Berlin.

Schultz, D. L. 1991. Parental investment in temporally varying environments. Evolutionary Ecology 5:415–427.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish. Ibis 91:430–455.

Slagsvold, T. 1982. Clutch size variation in passerine birds: The nest predation hypothesis. Oecologia 54:159–169.

Smith, H. G. 1989. Larger clutches take longer to incubate. Ornis Scandinavica: 156–158.

Starck, J. M., and R. E. Ricklefs. 1998. Avian growth and development: Evolution within the altricial-precocial spectrum. Oxford University Press, New York.

Stearns, S. C. 1976. Life-history tactics: A review of the ideas. Quarterly review of biology: 3–47.

Styrsky, J. N., J. D. Brawn, and S. K. Robinson. 2005. Juvenile mortality increases with clutch size in a neotropical bird. Ecology 86:3238–3244.

Urban, E. K., C. H. Fry, and S. Keith. 1986. Birds of Africa. Academic Press, London.

Wang, N., R. T. Kimball, E. L. Braun, B. Liang, and Z. Zhang. 2013. Assessing phylogenetic relationships among Galliformes: A multigene phylogeny with expanded taxon sampling in Phasianidae. PLoS ONE 8:e64312.

Wangensteen, O., H. Rahn, R. Burton and A. Smith. 1974. Respiratory gas exchange of high altitude adapted chick embryos. Respiration Physiology 21: 61-70

Wells, D. R. 1999. The birds of the Thai-Malay peninsula. Academic Press, San Diego.

White, F. N., and J. L. Kinney. 1974. Avian incubation. Science 186:107-115.

Williams, J. B. 1996. Energetics of avian incubation. Pages 375–415 *in* C. Carey, editor. Avian energetics and nutritional ecology. Chapman and Hall, New York.

Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. Biological Reviews 69:35–59.

Winkler, D. W., and J. R. Walters. 1983. The determination of clutch size in precocial birds. Current ornithology 1:33–68.

Yom-Tov, Y., and R. Hilborn. 1981. Energetic constraints on clutch size and time of breeding in temperate zone birds. Oecologia 48:234–243.

Table 3.1. Closely related species used in pairwise comparisons

	Low elevation species	High elevation species
1	*Crax globulosa*	*Crax alector*
2	*Crax daubetoni*	*Crax rubra*
3	*Mitu mitu*	*Pauxi pauxi*
4	*Mitu tomentosum*	*Mitu salvini*
5	*Ortalis superciliaris*	*Ortalis motmot*
6	*Ortalis garrula*	*Ortalis ruficauda*
7	*Ortalis leucogastra*	*Ortalis vetula*
8	*Ortalis cinereiceps*	*Ortalis erythroptera*
9	*Penelope jacquacu*	*Penelope perspicax*
10	*Penelope marail*	*Penelope albipennis*
11	*Penelope pileata*	*Penelope purpurascens*
12	*Penelope obscura*	*Penelope dabbenei*
13	*Pipile pipile*	*Pipile cumanensis*
14	*Callipepla douglasii*	*Callipepla squamata*
15	*Callipepla gambelii*	*Callipepla californica*
16	*Dendrortyx leucophrys*	*Dendrortyx macroura*
17	*Odontophorus leucolaemus*	*Odontophorus guttatus*
18	*Odontophorus gujanensis*	*Odontophorus columbianus*
19	*Alectoris graeca*	*Alectoris magna*

	Low elevation species	High elevation species
20	*Alectoris rufa*	*Alectoris chukar*
21	*Arborophila rufipectus*	*Arborophila torqueola*
22	*Arborophila atrogularis*	*Arborophila rufogularis*
23	*Arborophila gingica*	*Arborophila crudigularis*
24	*Bambusicola throacicus*	*Bambusicola fytchii*
25	*Centrocercus urophasianus*	*Centrocercus minimus*
26	*Chrysolophus pictus*	*Chrysolophus amherstiae*
27	*Coturnix delegorguei*	*Coturnix chinensis*
28	*Crossoptilon mantchuricum*	*Crossoptilon auritum*
29	*Dendragapus canadensis*	*Dendragapus falcipennis*
30	*Francolinus castaneicollis*	*Francolinus erckelii*
31	*Francolinus leucoscepus*	*Francolinus squamatus*
32	*Francolinus levaillantoides*	*Francolinus levaillanti*
33	*Francolinus gularis*	*Francolinus francolinus*
34	*Gallus varius*	*Gallus gallus*
35	*Gallus lafayetii*	*Gallus sonneratii*
36	*Lagopus lagopus*	*Lagopus muta*
37	*Lophophorus impejanus*	*Lophophorus sclateri*
38	*Lophura edwardsi*	*Lophura swinhoii*
39	*Lophura nycthemera*	*Lophura leucomelanos*
40	*Lophura erythropthalma*	*Lophura inornata*

	Low elevation species	High elevation species
41	*Pavo cristatus*	*Pavo muticus*
42	*Perdicula manipurensis*	*Perdicula erythrorhyncha*
43	*Phasianus versicolor*	*Phasianus colchicus*
44	*Polyplectron chalcurum*	*Polyplectron inopiniatum*
45	*Polyplectron napoleonis*	*Polyplectron germaini*
46	*Syrmaticus ellioti*	*Syrmaticus humiae*
47	*Syrmaticus soemmerringii*	*Syrmaticus reevesii*
48	*Tetraogallus caucasius*	*Tetraogallus tibetanus*
49	*Tetraogallus altaicus*	*Tetraogallus caspius*
50	*Tragopan caboti*	*Tragopan temmickii*
51	*Chamaepetes unicolor*	*Penelopina nigra*
52	*Dactylortyx thoracicus*	*Cyrtonyx montezumiae*
53	*Caloperdix oculeus*	*Melanoperdix niger*

Table 3.2. Correlation coefficients for inter-correlations between life history traits

	Clutch Size	Egg Mass	Egg Volume	Clutch Mass	Clutch Investment	Incubation Period
Female Body Mass	-0.03	0.512***	0.038	0.458**	-0.355***	0.386**
Clutch Size		0.097	-0.109	0.816**	0.639**	0.238**
Egg Mass			0.058	0.492**	0.402**	0.202*
Egg Volume				-0.008	-0.004	0.098
Clutch Mass					0.744**	0.341**
Clutch Investment						0.169

* $\alpha < 0.05$, ** $\alpha < 0.01$

Table 3.3. Results from pairwise comparisons of life history traits across low and high elevation species. Values are calculated as high elevation species – low elevation species. N = number of pairs used in analysis, n = number of species in which the value of the trait was greater for the high elevation species

Trait	Z	P value	N	n
Female Body Mass	-2.00	.046**	49	32
Clutch Size	-1.25	.212	53	25
Egg Mass	-1.79	.074	45	29
Egg Volume	-2.09	.037**	47	30
Clutch Mass	-2.09	.037**	45	30
Clutch Investment	-0.94	.349	41	24
Incubation Period	-1.08	.281	35	19

* $\alpha < 0.1$, **$\alpha < 0.05$

Table 3.4. Results of regressions using phylogenetically independent contrasts of elevation, and elevation and latitude on life history 4traits

a. With elevation

Trait	Elevation			N
	β_{st}	t	*p*	
Female Body Mass	0.107	1.394	.165	170
Clutch Size	-0.078	-1.008	.315	169
Egg Mass	0.334	4.457	.001***	159
Egg Volume	-0.082	-1.039	.3	162
Clutch Mass	0.153	1.94	.054*	158
Clutch Investment	0.024	0.304	.762	158
Incubation Period	0.245	2.868	.005***	130

* $\alpha < 0.1$, ** $\alpha < 0.05$, *** $\alpha < 0.01$

b. With elevation and latitude

Trait	Elevation			Latitude			Interaction			N
	β_{st}	t	*p*	β_{st}	t	*p*	β_{st}	t	*p*	
Female Body Mass	0.104	1.359	.176	0.086	1.130	.260	-0.072	-0.936	.351	170
Clutch Size	-0.080	-1.088	.278	0.300	4.072	.001**	-0.044	-0.587	.558	169
Egg Mass	0.333	4.431	.001**	0.028	0.373	.710	-0.216	-2.912	.004**	159
Egg Volume	-0.084	-1.063	.289	0.075*	0.951	.343	-0.236	-3.063	.003**	162
Clutch Mass	0.145	1.883	.062*	0.232	3.013	.003**	-0.083	-1.072	.286	158
Clutch Investment	0.013	0.168	.867	0.227	2.910	.004**	-0.060	-0.760	.449	158
Incubation Period	0.238	2.724	.007**	0.038**	0.436	.664	-0.121	-1.365	.175	130

*α < 0.1, **α < 0.05

Figure 3.1. Frequency histograms of distribution of life history variables

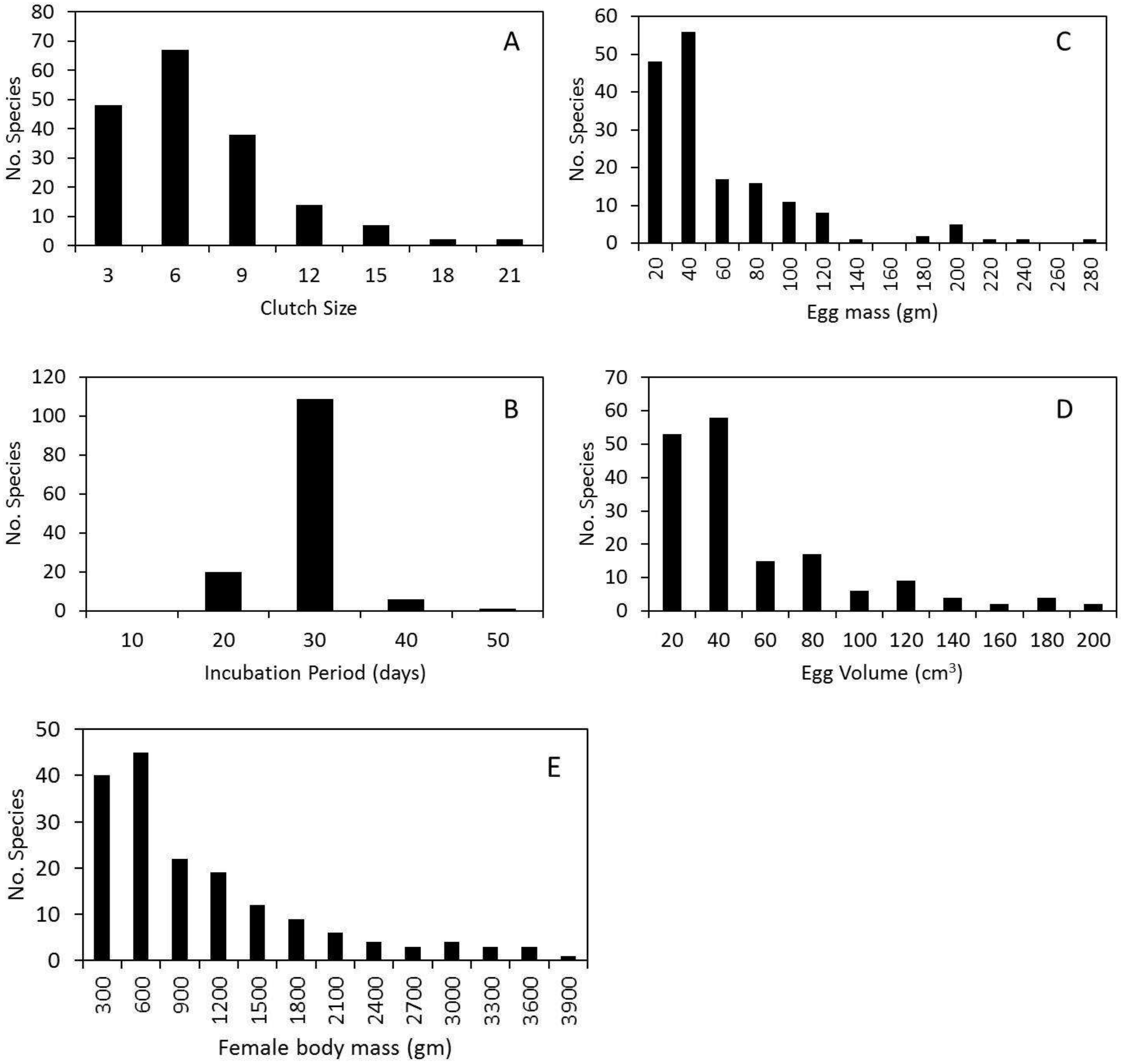


Figure 3.2. Phylogenetic tree of the species in the dataset

Figure 3.3. Plots of standardized contrasts of elevation and life history variables

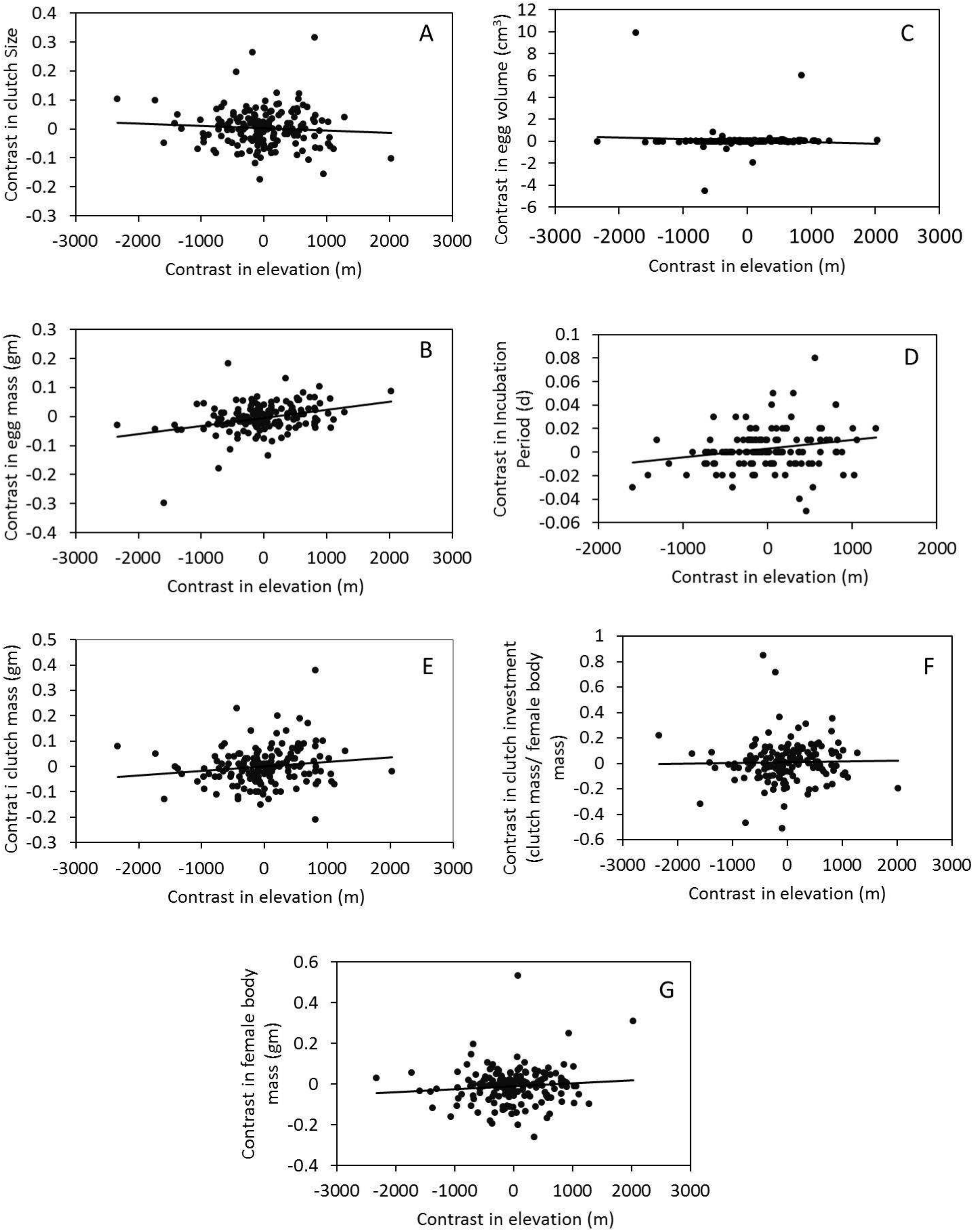
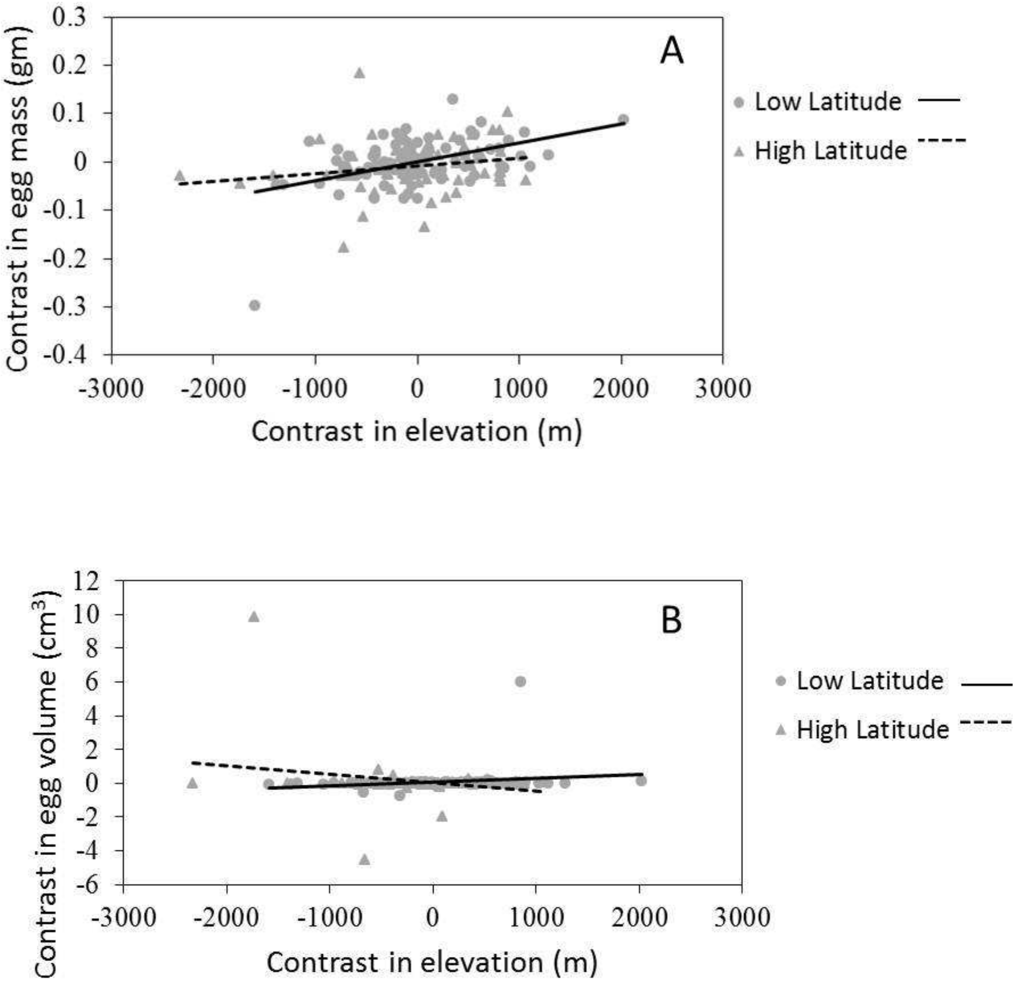


Figure 3.4. Interaction effect of latitude and elevation on egg mass and volume



GENERAL CONCLUSIONS

The approach of relating species traits to environmental variables of the habitat to understand ecological relationships has been around for long. However, analysis of trait-environment linkages has gained popularity recently, due to the increased need to understand and predict responses of species and communities to environmental change. Underlying this approach are two ideas. One, that natural selection acts on traits possessed by individuals to favor those that enhance fitness resulting in the evolution of species-specific life history strategies. Secondly, that the occurrence of a species in a habitat is the result of a match between the combination of traits possessed by a species and the environmental attributes of its habitat, allowing the species to cope with the constraints posed by its environment. While the former is a process operating over evolutionary time scales, the latter is an ecological process that can be modified by rapid human-induced environmental change.

The projects covered in this dissertation demonstrates that studying patterns across different spatial and temporal scales can help us better understand the causes and consequences of the diversity of ecological and life history traits in bird species. Such knowledge can be further useful in understanding the potential impacts of human induced change on species and communities.

To understand how environmental variation shapes life history evolution, I investigated patterns of life history variation across elevational gradients in a precocial group of birds, the Galliformes. Patterns seen in altricial passerines across elevational gradients indicate that high elevation species and populations have reduced fecundity due to smaller clutch sizes and fewer breeding attempts. Additionally, they have longer incubation and nestling periods and have prolonged parental care. These patterns suggest that environmental variation across elevation gradients select for a strategy of reduced fecundity and greater investment in offspring quality via prolonged parental care at high elevations as a means to increase offspring survival. If parental care constrains clutch size as is known in altricial species, clutch sizes of precocial species that lack such intensive care should not be affected and thus not vary across elevational gradients. Reductions in fecundity at high elevations should be mainly through a reduction in the number of broods raised. Investment in offspring quality should occur mainly through variation in egg mass across elevations. Using methods to control for phylogeny, latitude and allometry, I found that clutch size did not vary across elevations in galliform species and egg mass increased towards high elevations as predicted. I also found patterns similar to those seen in altricial passerines in terms of increase in incubation period at high elevations after controlling for body mass. Clutch mass increased with latitude and elevation. Increase in clutch size with latitude contributed to clutch mass variation across latitudes and increase in egg mass with elevation contributed to clutch mass variation across elevations. I hypothesize that increase in daylength towards higher latitudes may influence latitudinal variation in clutch mass by selecting for larger clutch sizes and lack of variation in daylength across elevational gradients may influence clutch mass variation across elevational gradients by selecting for greater investment in egg mass (offspring quality) rather than number. Out of the various proximate factors proposed to explain avian life history variation such as food availability, nest predation risk etc.; I found that variation in abiotic variables such as temperature, atmospheric pressure and daylength have greater potential to explain these patterns. Through large scale comparative analysis, this study has demonstrated partial support for the hypothesis of a tradeoff between fecundity and investment in offspring quality across elevational gradients and has demonstrated how environmental variation along such gradients can select for different life history strategies. Further, variation in abiotic variables across elevational gradients deserves further attention as they are potential proximate drivers shaping the evolution of such strategies.

The occurrence of species in a habitat is determined by ecological processes that result from the fit between species traits and constraints posed by the environment. Thus, the presence of distinct associations between traits and environmental variables made apparent by differences in community composition along environmental gradients is a first step to understand how environments filter species based on their traits. Studies along elevational gradients have so far been limited to comparisons across phylogenetically paired taxa or within species comparisons. However, if environmental variation across elevational gradients act as a filter and select for certain traits, then such selection pressures must apply to species irrespective of phylogenetic relatedness. By analyzing distribution patterns of a breeding bird community across an elevational gradient, I was able to demonstrate distinct trait relationships with environmental variables associated with elevation. Communities at high elevations were comprised of species in which males fed females during incubation and had longer nestling periods. As hypothesized we found patterns that resemble those seen in comparisons of phylogenetically paired taxa. The primary axis describing environmental varying along elevation included abiotic variables such as temperature and precipitation as well as variables related to vegetation structure and composition. Although, it is not possible to tease out the independent effects of each environmental variable on the traits, the effects of temperature on life history variation is well known and deserves further study. For example, in altricial passerines, colder temperatures necessitate male incubation feeding as a means to offset energetic costs of breeding in females. Such constraints may also influence changes in the duration of nestling period duration. This chapter demonstrates that trait variations along an elevational gradient can result in compositional differences in communities distributed across an environmental gradient and that the selection pressures offered by such environmental variation apply across taxa irrespective of diverse phylogenetic histories.

Knowledge of trait-environment relationships is especially useful to understand the mechanisms behind species persistence and to understand the implications for community structure and composition in the face of rapid human induced environmental change. I analyzed the relationships between environmental attributes and ecological and life history traits of a breeding bird community across local and landscape scales distributed in the threatened coastal sage scrub vegetation type subjected to intense anthropogenic disturbance. I showed that distinct trait associations were found with disturbance variables as well as native vegetation variables across local and landscape scales. Disturbance variables marked by land use changes such as exotic grasslands, agriculture, urbanization were associated with larger body masses, residents, and disturbance tolerance. Previous studies have shown similar associations with urbanization. Agricultural areas could favor species with larger body masses by ensuring food availability throughout the year. Foraging traits such as probing and bark gleaning were positively associated with native vegetation variables and negatively with disturbance. These traits thus may be potentially sensitive to disturbance and could serve as indicator traits. Additionally foraging and nesting behaviors such as seed eating, ground foraging, rock gleaning, and rock nesting were positively associated with disturbance and native vegetation variables. Species with these traits may thus be favored even with continued environmental change in this landscape. I found that breeding productivity of birds in this landscape was low as indexed by number of broods, and clutch size was positively related to rainfall. Thus, long term changes in temperature and precipitation has the potential to negatively affect productivity in this community. The effect of spatial scale was prominent. Whilst life history traits like clutch size respond to abiotic variables that vary over larger spatial scales, ecological traits related to foraging and nesting behavior can be influenced by changes occurring at smaller spatial scales. Traits that were positively related to disturbance responded similarly across both local and landscape scales indicating that structural and compositional changes resulting from disturbance influenced species traits in a similar fashion. This study thus demonstrates that in habitats that are subject to rapid modification by anthropogenic change, it is important to establish how species traits relate to varied environmental attributes ranging from structural, compositional and abiotic across multiple spatial scales to understand potential ways by which community structure and composition may change in response to environmental change.

APPENDICES

Chapter 2: Linking species ecological and life history traits to environmental attributes: Evidence of environmental filters at small spatial scales

Appendix 1: Site names, codes, owners/managers and locations, NCCP coastal sage scrub survey 1995-1997. See also Fig.2.1

			Location UTM[a]			
Site	Code	Owner/Manager	Easting (x 10^4)	Northing (x 10^5)	County	No. of points per site
Black Canyon	BLCA	U.S. Forest Service	51.6	36.6	San Diego	5
Box Springs	BOSP	Riverside County Parks	47.2	37.6	Riverside	9
Chula Vista	CHVI	Chula Vista Parks and Open Space	49.8	36.1	San Diego	8
Kabian Park	KABI	Riverside County Parks	47.7	37.3	Riverside	10
Lake Perris	LAPE	California Parks and Recreation	48.4	37.5	Riverside	20
Lake Skinner	LASK	Metropolitan Water District	49.7	37.2	Riverside	10
Limestone Canyon	LICA	Irvine Co./Nature Conservancy	43.7	37.3	Orange	22
Motte Rimrock	MRRE	University of California	47.6	37.4	Riverside	10

Site	Code	Owner/Manager	Location UTM[a]		County	No. of points per site
			Easting (x 10^4)	Northing (x 10^5)		
Reserve						
Orange Hills	ORHI	Orange County Regional Parks	42.7	37.4	Orange	6
Pamo Valley	PAVA	U.S. Forest Service	51.5	36.7	San Diego	7
Point Loma	POLO	Naval Research and Development	47.7	36.2	San Diego	3
Rancho Mission Viejo	RMVI	Rancho Mission Viejo	44.7	37.1	Orange	10
Sand Canyon Reservoir	SACA	Orange County	42.7	37.2	Orange	4
Santa Margarita	SAMA	San Diego State University	48.4	37	Riverside	5
Starr Ranch	STRA	National Audubon Society	44.9	37.2	Orange	20
Sweetwater River	SWRI	U.S.D.I. National Wildlife Refuge	50.5	36.2	San Diego	22
Sycamore Canyon	SYCA	Riverside County Parks	47	37.6	Riverside	6
Sycamore Hills	SYHI	Orange County	43	37.2	Orange	10

Site	Code	Owner/Manager	Location UTM[a]		County	No. of points per site
			Easting (x 10^4)	Northing (x 10^5)		
Torrey Pines State Park	TPSP	California Parks and Recreation	47.6	36.4	San Diego	9
University of California, Riverside	UCR	University of California	47	37.6	Riverside	5
Wild Animal Park	WAPA	San Diego Zoological Society	50.2	36.6	San Diego	12

Chapter 3: Life history variation in Galliformes across elevational gradients: A test of the fecundity-offspring quality trade-off hypothesis

Appendix 2: Absolute value of mean breeding latitude (Abs.lat), mean breeding elevation (Av.elev), mean clutch size (Av.Clu), mean egg mass (Av.EWt), mean egg volume (Av.EVol), clutch mass (CMass), mean incubation period (Av.IP), female body mass (FWt) of Galliformes species used in the analysis

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Aepypodius arfakianus	5.33	1550	20.00	166.50	170.45	3330.00	-	1365.00	1,2
Afropavo congensis	1.38	600	2.50	69.00	76.64	172.50	26.50	1144.50	1,3
Alectoris barbara	29.56	1650	11.30	19.50	18.61	220.35	24.50	376.00	1,43,4
Alectoris chukar	39.78	2250	13.00	22.00	20.25	286.00	23.50	565.00	1,3,5,6
Alectoris graeca	42.07	1200	11.00	20.00	19.69	220.00	25.00	565.00	1,4
Alectoris magna	36.14	2650	12.30	20.40	18.86	250.92	23.00	528.50	1,7
Alectoris melanocephala	19.35	1625	6.50	29.46	27.12	191.49	24.50	522.00	1,8

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Alectoris rufa	42.73	1000	11.95	19.00	18.62	227.05	23.50	452.50	1,4
Alectura lathami	22.59	750	21.00	194.33	162.80	4080.93	49.50	2245.00	1,2,9
Ammoperdix griseogularis	34.21	1000	7.50	12.00	12.07	90.00	21.00	193.50	1,10
Ammoperdix heyi	22.92	800	10.00	14.00	12.69	140.00	22.50	190.00	1
Anurophasis monorthonyx	4.11	3600	3.00	25.40	24.99	76.20	-	401.00	1,7,11
Arborophila atrogularis	24.01	750	4.50	16.30	15.47	73.35	-	256.00	1,7,11
Arborophila brunneopectus	18.62	1175	4.00	16.60	15.38	66.40	-	268.00	1,3,6,7
Arborophila chloropus	15.33	700	3.00	19.80	18.34	59.40	-	275.00	1,7,11
Arborophila crudigularis	23.59	1500	7.00	19.50	18.02	136.50	24.00	212.00	1,7,11
Arborophila gingica	26.44	1100	6.00	-	-	-	23.00	253.00	1,3
Arborophila javanica	7.38	1650	4.00	22.40	20.73	89.60	-	271.50	1,7
Arborophila mandellii	27.99	1425	4.00	25.80	26.58	103.20	-	268.00	1,6,7
Arborophila orientalis	8.02	1350	3.00	21.40	21.01	64.20	-	268.00	1,7

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Arborophila rufipectus	28.62	1625	5.00	-	-	-	-	365.00	1
Arborophila rufogularis	21.28	1450	4.50	20.20	18.13	90.90	20.50	323.50	1,3,7
Arborophila torqueola	26.88	2300	4.00	22.80	20.45	91.20	24.00	306.50	1,6,7
Argusianus argus	2.36	750	2.00	74.30	68.93	148.60	24.50	1645.00	1,6,12
Bambusicola fytchii	22.78	1750	5.00	17.40	17.78	87.00	18.50	298.00	1, 6,7
Bambusicola thoracicus	27.52	1000	5.00	11.90	10.98	59.50	18.00	271.00	1,7,11
Bonasa bonasia	54.05	1000	9.00	19.00	17.16	171.00	25.00	364.50	1,13
Bonasa sewerzowi	31.32	2500	6.19	22.88	20.66	141.63	27.00	338.50	1,14
Callipepla californica	37.32	1400	12.55	8.93	9.36	112.07	22.50	162.00	1,5
Callipepla douglasii	25.13	775	10.00	10.80	9.88	108.00	22.50	175.00	1,3,7
Callipepla gambelii	35.01	825	13.00	10.00	9.25	130.00	23.00	156.00	1,5,15
Callipepla squamata	29.80	1467.5	12.67	11.00	10.36	139.37	22.00	202.00	1,3,5
Caloperdix oculeus	4.88	600	9.00	-	-	-	19.00	230.00	1,3,11

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Catreus wallichi	31.74	2050	9.50	71.60	42.06	680.20	26.00	1130.00	1,12
Centrocercus minimus	38.44	2625	8.00	-	-	-	26.00	1899.00	1
Centrocercus urophasianus	43.89	1676	7.50	46.10	41.83	345.75	26.00	1550.00	1,5,16
Chamaepetes unicolor	9.68	1775	2.50	-	-	-	-	1135.00	1
Chrysolophus amherstiae	27.31	3200	6.50	31.00	28.74	201.50	24.00	714.00	1,3,4
Chrysolophus pictus	29.38	1200	7.00	27.00	25.94	189.00	22.00	625.00	1,3
Colinus cristatus	7.73	1600	12.00	9.50	18.36	114.00	22.50	136.00	1,3,7
Colinus leucopogon	11.00	900	10.00	10.70	9.91	107.00	22.00	115.00	1,3,7,17
Colinus virginianus	30.10	1250	13.45	8.50	8.81	114.33	23.00	170.00	1,5,11
Coturnix chinensis	5.14	1000	5.50	5.00	4.51	27.50	17.00	38.50	1,6,7,11
Coturnix coturnix	15.02	1500	8.25	8.00	7.87	66.00	18.50	112.50	1,4,6,18,19
Coturnix delegorguei	6.29	925	6.00	8.50	7.59	51.00	16.00	79.00	1,7
Coturnix japonica	41.98	1925	8.00	7.60	7.34	60.80	18.50	90.00	1,7,20

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Coturnix ypsilophora	22.56	1850	5.00	9.20	8.52	46.00	21.50	112.50	1,7,21
Crax alector	3.47	850	2.00	-	4.51	-	30.00	2912.50	1,22
Crax blumenbachiii	17.40	250	2.50	220.00	152.43	550.00	28.00	3500.00	1,23
Crax daubetoni	9.40	800	2.00	-	-	-	28.00	2325.00	1
Crax globulosa	6.93	150	2.00	173.73	168.33	347.45	-	2500.00	1
Crax rubra	10.84	950	2.00	200.00	193.79	400.00	33.00	3685.00	1,23
Crossoptilon auritum	35.37	3550	8.00	52.10	48.14	416.80	26.00	1665.00	1,3,12
Crossoptilon crossoptilon	29.68	3650	6.50	58.40	53.98	379.60	24.00	1725.00	1,12
Crossoptilon mantchuricum	37.87	1850	8.80	44.50	41.11	391.60	26.50	1737.50	1,3,12
Cyrtonyx montezumae	25.24	1750	11.10	10.60	10.20	117.66	25.50	184.50	1,5,17
Dactylortyx thoracicus	19.06	1625	5.00	8.40	9.00	42.00	-	160.50	1,7,17
Dendragapus canadensis	56.45	1800	5.50	21.95	21.25	120.73	22.50	500.00	1
Dendragapus falcipennis	51.55	650	6.50	24.68	23.90	160.43	23.50	695.00	1,13

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Dendragapus obscurus	48.99	1800	7.00	32.68	32.02	228.76	26.50	865.00	1,3,5
Dendrortyx barbatus	20.10	2000	6.00	24.70	22.84	148.20	29.00	405.00	1,7
Dendrortyx leucophrys	12.73	1600	4.50	26.40	20.20	118.80	-	340.00	1,7
Dendrortyx macroura	18.29	2400	4.00	30.50	28.16	122.00	-	410.00	1,7
Francolinus africanus	29.78	1375	6.00	17.20	18.39	103.20	22.00	382.00	1,7
Francolinus castaneicollis	7.26	2600	5.50	37.50	34.61	206.25	-	600.00	1,7,8
Francolinus erckelii	13.09	2750	7.00	33.80	31.25	236.60	-	1136.00	1,3,7
Francolinus francolinus	27.28	1250	8.25	24.00	23.17	198.00	19.50	425.00	1,4,13
Francolinus gularis	26.99	175	3.50	19.60	18.08	68.60	-	510.00	1,6,7
Francolinus hildebrandti	7.41	2250	6.00	23.70	21.93	142.20	-	455.00	1,7,8
Francolinus icterorhynchus	4.27	950	7.00	19.90	18.36	139.30	-	441.00	1,7,8
Francolinus jacksoni	0.17	2950	-	32.90	30.73	-	-	-	1,7
Francolinus leucoscepus	5.41	1200	5.00	31.00	28.05	155.00	19.00	507.50	1

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Francolinus levaillantii	16.32	2400	7.50	21.20	20.57	159.00	22.00	434.50	1,7
Francolinus levaillantoides	23.22	1250	4.50	18.75	18.85	84.38	20.50	414.50	1,7
Francolinus nahani	1.17	950	4.00	13.40	12.41	53.60	-	247.00	1,7
Francolinus natalensis	22.37	900	5.00	27.00	24.99	135.00	20.00	426.00	1,3,7
Francolinus sephaena	8.40	1100	5.50	17.30	19.17	95.15	20.50	286.50	1,7,18
Francolinus shelleyi	15.08	1850	4.00	17.30	15.99	69.20	22.00	426.00	1,3,7,8
Francolinus squamatus	0.15	1900	6.00	21.70	20.09	130.20	-	446.00	1,7
Francolinus streptophorus	0.42	1200	4.50	-	-	-	-	-	1
Galloperdix bicalcarata	7.40	1000	2.00	19.80	18.26	39.60	-	256.00	1,6,7
Galloperdix spadicea	17.95	1300	3.50	19.40	18.69	67.90	-	369.00	1,6,7
Gallus gallus	10.33	1200	5.50	29.60	26.29	162.80	19.50	767.50	1,6,12
Gallus lafayettii	7.59	1000	2.00	30.40	28.11	60.80	20.50	567.50	1,12
Gallus sonneratii	17.45	1200	4.50	33.40	31.46	150.30	20.50	745.00	1,6,12

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Gallus varius	8.07	1000	3.50	29.20	27.01	102.20	21.00	624.50	1,12
Haematortyx sanguiniceps	3.18	1250	8.50	-	-	-	18.50	-	1
Ithaginis cruentus	31.56	3500	4.50	28.80	23.18	129.60	27.50	532.50	1,12,20
Lagopus lagopus	61.16	1340	9.50	23.03	21.91	218.79	22.00	587.50	1,4
Lagopus leucura	51.39	2734.5	5.50	20.71	19.66	113.88	24.00	840.00	1
Lagopus muta	57.83	2500	6.50	22.30	21.17	144.95	22.50	565.00	1,4
Lerwa lerwa	32.11	4250	3.50	37.80	34.90	132.30	-	581.50	1,6,7
Lophophorus impjeanus	31.94	3200	4.00	70.70	65.29	282.80	27.00	1975.00	1,6,12
Lophophorus lhuysii	31.98	3850	4.00	97.10	92.24	388.40	28.00	3178.00	1,12
Lophophorus sclateri	27.33	3350	4.00	70.50	66.28	282.00	-	2196.50	1,3,6,12
Lophura bulweri	1.35	825	-	45.30	41.99	-	24.50	960.00	1,12
Lophura diardi	15.96	575	6.00	38.20	35.35	229.20	24.50	852.50	1,12
Lophura edwardsi	16.67	150	5.50	32.20	29.74	177.10	21.50	1050.00	1,12

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Lophura erythrophthalma	0.55	150	4.50	33.20	30.72	149.40	24.00	837.00	1,12,24
Lophura ignita	4.30	500	6.00	47.60	44.06	285.60	24.00	1600.00	1,12
Lophura inornata	2.26	1425	2.00	36.70	33.95	73.40	22.00	-	1,12
Lophura leucomelanos	22.50	1862.5	7.50	37.40	31.97	280.50	21.00	794.50	1,6,12
Lophura nycthemera	19.03	1250	6.90	42.80	39.56	295.32	25.50	1225.00	1,3,6,12
Lophura swinhoii	23.63	1300	6.00	40.60	37.56	243.60	25.00	1100.00	1,12
Margaroperdix madagascariensis	18.56	1350	17.50	17.90	16.57	313.25	18.50	235.00	1,7
Megapodius reinwardt	11.75	950	12.50	122.90	123.24	1536.25	-	875.00	1,2
Melanoperdix niger	0.55	600	4.00	23.00	21.95	92.00	18.50	281.00	1,7
Meleagris gallopavo	33.77	1400	11.50	66.66	68.44	766.59	27.50	3200.00	1,5,25
Meleagris ocellata	17.94	150	12.00	47.19	60.54	566.28	28.00	3000.00	1,17
Mitu mitu	10.00	200	2.50	196.00	127.31	490.00	30.00	2745.00	1,26

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Mitu salvini	0.85	450	2.00	279.65	196.32	559.30	32.00	3100.00	1
Mitu tomentosum	2.31	300	2.00	190.00	133.39	380.00	-	1862.50	1,26
Mitu tuberosum	9.62	670	2.50	230.14	161.57	575.35	31.00	2320.00	1,27
Nothocrax urumutum	3.22	425	2.00	108.00	100.57	216.00	28.50	1250.00	1,22,26
Numida meleagris	7.56	1500	9.00	39.00	39.56	351.00	27.00	1479.00	1
Odontophorus columbianus	10.51	1600	6.00	19.12	18.33	114.71	30.00	336.00	1
Odontophorus gujanensis	3.55	900	4.00	15.30	14.67	61.20	26.00	298.00	1,3,7
Odontophorus guttatus	13.91	1550	4.00	18.60	17.21	74.40	17.00	288.00	1,7,17
Odontophorus leucolaemus	9.74	1275	5.00	20.16	18.69	100.81	16.50	220.00	1
Odontophorus melanotis	11.92	800	4.00	16.10	14.93	64.40	-	329.00	1,7
Oreophasis derbianus	15.79	2450	2.00	95.40	145.74	190.80	35.00	1940.00	1,27,28
Oreortyx pictus	38.63	1750	9.50	11.80	12.23	112.10	23.00	230.00	1,3
Ortalis cinereiceps	10.17	850	3.00	-	48.66	-	22.00	515.00	1,22

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Ortalis erythroptera	1.35	925	3.00	69.00	63.05	207.00	27.00	632.50	1,26
Ortalis garrula	9.13	400	3.00	62.95	60.35	188.85	26.00	630.00	1,22
Ortalis leucogastra	13.92	750	2.50	51.00	53.75	127.50	24.00	499.50	1,26
Ortalis motmot	0.18	850	3.00	63.00	39.23	189.00	-	502.50	1,26,29
Ortalis ruficauda	9.42	800	3.50	68.00	64.29	238.00	28.00	615.00	1,26,29
Ortalis superciliaris	4.16	500	2.50	56.57	35.23	141.43	-	-	1
Ortalis vetula	18.37	925	3.00	58.00	54.20	174.00	25.00	558.50	1,26
Ortalis wagleri	24.65	650	3.00	81.00	72.17	243.00	-	-	1,17,26
Pauxi pauxi	8.81	1350	2.00	190.00	127.31	380.00	35.00	2650.00	1,26
Pauxi unicornis	13.38	925	1.00	-	-	-	-	3600.00	1
Pavo cristatus	19.95	1000	4.50	100.50	105.59	452.25	29.00	3375.00	1,12,26
Pavo muticus	12.54	1500	4.50	114.90	106.12	517.05	27.00	1110.00	1,6,12
Penelope albipennis	6.04	842.5	2.50	110.52	103.13	276.30	30.50	1750.00	1,17

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Penelope dabbenei	21.18	2000	3.00	94.96	88.61	284.88	-	1230.00	1
Penelope jacquacu	4.83	1000	2.50	84.00	101.36	210.00	-	1270.00	1,26
Penelope marail	2.69	400	2.50	87.00	81.19	217.50	29.00	1110.00	1,26
Penelope montagnii	3.49	2450	2.00	-	-	-	-	829.00	1
Penelope obscura	25.69	1370	2.50	88.00	104.23	220.00	28.00	1080.00	1,23,26
Penelope perspicax	3.58	1753	2.00	111.39	103.95	222.78	29.00	-	1
Penelope pileata	5.83	400	4.00	114.00	110.35	456.00	-	1350.00	1,23
Penelope purpurascens	10.17	1500	2.00	95.00	101.36	190.00	-	2025.00	1,15,26
Penelopina nigra	15.28	2000	2.00	-	90.53	-	26.50	890.00	1
Perdicula erythrorhyncha	16.60	1300	5.50	5.30	8.44	29.15	17.00	68.75	1,6,7
Perdicula manipurensis	24.87	500	4.00	9.60	9.03	38.40	-	67.50	1,7,11,20
Perdix hodgsoniae	32.05	4600	9.00	15.40	14.19	138.60	-	372.00	1,3,6,7
Perdix perdix	50.54	1300	16.00	14.50	13.38	232.00	24.00	440.00	1,13

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Phasianus colchicus	36.72	1300	11.50	33.00	29.74	379.50	22.00	1044.00	1,13
Phasianus versicolor	36.00	532.5	9.00	26.00	24.32	234.00	24.00	831.00	1,12,26
Philortyx fasciatus	18.22	900	5.50	9.30	8.65	51.15	22.60	126.00	1,7
Pipile cumanensis	8.40	550	2.00	92.00	99.86	184.00	26.00	1275.00	1,22,26
Pipile jacutinga	25.52	925	3.00	104.00	79.52	312.00	28.00	1250.00	1,23
Pipile pipile	10.76	650	2.00	107.00	97.55	214.00	-	2900.00	1,26
Polyplectron chalcurum	0.01	1300	2.00	35.00	32.39	70.00	22.00	253.50	1,12
Polyplectron germaini	12.51	700	1.50	30.40	28.11	45.60	21.00	397.00	1,12
Polyplectron inopinatum	4.27	1410	2.00	40.20	51.26	80.40	20.00	-	1
Polyplectron malacense	3.84	150	1.00	40.50	39.58	40.50	23.50	497.50	1
Polyplectron napoleonis	9.88	400	2.00	32.20	29.74	64.40	19.00	322.00	1,11,12
Polyplectron schleiermacheri	1.35	535	1.00	-	-	-	21.00	-	1

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Ptilopachus petrosus	9.33	1050	5.00	11.00	10.81	55.00	-	-	1,7
Pucrasia macrolopha	32.78	3000	6.00	40.00	36.61	240.00	26.50	1032.50	1,3,12,20
Rhizothera longirostris	3.64	750	3.50	14.60	13.54	51.10	18.50	697.00	1,7
Syrmaticus ellioti	27.96	1050	6.50	30.20	27.12	196.30	25.50	908.00	1,12
Syrmaticus humiae	23.30	1850	7.50	30.05	28.74	225.38	27.50	750.00	1,12
Syrmaticus mikado	23.59	2450	7.50	46.20	25.25	346.50	28.00	1015.00	1,12
Syrmaticus reevesii	30.96	1400	7.50	34.80	32.12	261.00	24.50	949.00	1,12
Syrmaticus soemmerringii	35.77	900	7.00	32.00	29.63	224.00	24.50	907.00	1,3,12
Tetrao mlokosiewiczi	41.51	2400	5.50	31.00	33.37	170.50	22.50	766.00	1,4
Tetrao tetrix	55.06	1500	8.00	33.83	33.05	270.64	26.00	925.00	1,4
Tetraogallus altaicus	47.66	2000	6.50	85.70	79.20	557.05	28.00	2540.00	1,7
Tetraogallus caspius	36.04	2900	7.00	75.00	71.22	525.00	28.50	2072.00	1
Tetraogallus caucasicus	42.41	2900	6.50	78.00	72.30	507.00	28.00	1730.00	1,4

Species	Abs.lat (degrees)	Av.elev (metres)	Av.Clu	Av.EWt (gm)	Av.EVol (cm^3)	CMass (gm)	Av.IP	FWt (gm)	References
Tetraogallus himalayensis	38.21	4250	8.00	84.20	76.76	673.60	30.00	1650.00	1,5
Tetraogallus tibetanus	33.56	4750	4.50	68.50	61.41	308.25	-	1385.00	1,6,7
Tragopan blythii	24.56	2550	3.50	62.00	57.69	217.00	29.00	1250.00	1,12
Tragopan caboti	26.44	1200	4.00	44.20	40.80	176.80	28.00	900.00	1,6,11,12
Tragopan melanocephalus	32.96	2675	4.00	61.30	50.76	245.20	-	1325.00	1,6,12
Tragopan satyr	29.26	3225	2.50	63.30	60.71	158.25	28.00	1100.00	1,12,20
Tragopan temminckii	27.44	3050	4.00	52.90	45.95	211.60	27.00	1003.50	1,12,20

1, del Hoyo et al. (1994); 2, Jones et al. (1995); 3, Madge and McGowan (2002); 4, Cramp and Simons (1980); 5, Poole(2005); 6, Baker (1935); 7, Johnsgard (1988); 8, Mackworth-Praed and Grant (1973) ; 9, Marchant and Higgins (1993); 10, Hume and Marshall (1880); 11, BirdLife International (2013); 12, Johnsgard (1999); 13, Dement'ev et al. (1967); 14, Klaus et al. (2009); 15, Howell and Webb (1995); 16, Johnson and Cicero (1986); 17, Neotropical Birds Online; 18, Urban et al. (1986); 19, Ali and Ripley (1969); 20, Baker (1928); 21, Coates (1985); 22, Hilty and Brown (1986); 23, Delacour et al. (1973); 24, Wells (1999); 25, Bent (1963); 26, Schönwetter (1961); 27, Dunning (2008); 28, González-García (1995); 29, Meyer de Schauensee and Phelps (1978)