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# Limits to Species' Distributions: Spatial Structure and Dynamics of Breeding Bird Populations Along an Ecological Gradient

A Dissertation submitted in partial satisfaction
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ABSTRACT OF THE DISSERTATION

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by

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All species are limited to a particular geographic area, whether of great or small extent, by historical contingency and interactions between extrinsic biotic or abiotic environmental factors, and intrinsic dispersive and adaptive traits. Distribution margins often occur on ecological gradients, along which the species' range may expand or contract over time. If the distribution of a species is reflective of its adaptive niche, then marginal areas will act as population "sinks" with reduced habitat quality. However, if environmental conditions change at distribution margins so that they are no longer limiting, fitness should improve and result in a range expansion. The general objective of this dissertation research was to elucidate the nature of distribution limits by studying their causes and consequences in marginal populations. Distribution limits of breeding birds were investigated along an arid shrubland gradient in southern California undergoing rapid climate warming. Through the use of multi-scale surveys and historical data, the comparative structure and dynamics of marginal distributions among avian

species were related to environmental factors. Elevational distributions were remarkably consistent across three years (2005–2007) and three elevational transects (200–1800 m), with strongly individualistic environmental associations among species. However, over a 26-year period, five species (out of 28 tested) showed statistically significant distribution shifts, all upward in elevation. The average elevational shift for all 28 species was an increase of 116 m, and low-elevation desert species were most likely to show upward shifts. Among species, individual productivity tended to increase with elevation, regardless of whether the species' lower or upper distribution limit occurred along the study gradient. For a focal species, the Black-throated Sparrow (*Amphispiza bilineata*), breeding success tended to be greater at higher-elevation chaparral sites at the distribution margin compared to lower-elevation desert scrub sites where the bird was more common, but this species did not show an upward elevational shift over a 26-year period. Desert species may be most likely to be at or near their temperature and aridity tolerance limits within their current range, and range shifts can be delayed or prevented by decoupled environmental factors.

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## General Introduction

The causes and consequences of the spatial distribution of a species are fundamental aspects of ecology and evolution. Range boundaries are intriguing when there are no obvious dispersal barriers, and biologists have long pondered the turnover of species along gradients such as mountainsides. The distribution of a species is generally presumed to reflect underlying habitat quality, or the set of environmental factors, both biotic and abiotic, to which a species is best adapted. Distribution limits often occur on ecological gradients, along which distributions are expected to expand or contract over time in relation to environmental change, such as with climate change. However, the presence or abundance of individuals is not always a reliable indicator of habitat quality (Van Horne 1983), and we are often unable to predict current or future distributional responses based on past habitat associations (Rotenberry 1986, Peterson 2001, O'Connor 2002, Rotenberry and Wiens 2009). Furthermore, limiting factors within a species' range can be different from those that influence a distribution boundary, but few studies have focused on limiting factors in marginal populations (Mayr 1963, Antonovics 1976, Hoffman and Blows 1994, Parmesan et al. 2005). The general objective of this dissertation research is to elucidate the nature of distribution limits by studying the comparative spatial structure and dynamics of populations at their distribution margin, and the relative influence of environmental factors. In this introduction I will give a brief overview of the study of distribution limits in terms of ecology, evolution, and behavior, followed by an outline of the dissertation research.

There have been many approaches to explaining the structure and dynamics of distributions, and most are related to the niche concept. Joseph Grinnell described the "ultimate associational niche" of the California Thrasher (*Toxostoma redivivum*) by emphasizing the bird's adaptation to chaparral habitat (Grinnell 1917). In comparing vertebrate distributions, Grinnell found a tendency for higher densities at distribution centers with gradual declines at margins, and attributed this pattern to two general causes: (1) favorable environmental conditions at distribution centers promoting a relatively high rate of reproduction, and (2) radial dispersal away from the population center due to intraspecific competition (Grinnell 1904, 1914). James H. Brown hypothesized that species are limited by multiple environmental variables that have some degree of stochasticity and are spatially correlated, such that density distributions tend to decline toward outer limits and approximate the adaptive niche (Brown 1984, Brown et al. 1995). In both models, habitat quality tends to decline toward the margins of a distribution where environmental conditions (biotic or abiotic) become unfavorable.

Many extrinsic biotic and abiotic factors have been identified that limit distributions (e.g., Andrewartha and Birch 1984, Parmesan et al. 2005) and the relative importance of different factors has long been debated. Darwin suggested that most distributions are limited by biotic factors, influenced only indirectly by climate, except where abiotic conditions become extreme (Darwin 1859, p. 121). Interspecific competition has commonly been hypothesized to drive microhabitat partitioning (e.g., MacArthur 1958), and in turn also drive habitat selection and distributional patterns (e.g., Hutchinson 1959, Rosenzweig 1981). Although examples of sharp borders between congeners can be found

along environmental gradients (e.g., Yeaton 1981), the most common pattern is species-independent where populations form a continuum or compositional gradient with no distinct borders between species (e.g., Whittaker 1967, Terborgh 1977, Rotenberry and Wiens 1980). The distribution of two competing species is likely determined by both competition and individual physiological tolerances (e.g., Connell 1961, Chappell 1978), and interactions between biotic and abiotic factors can produce fairly abrupt borders, even along climatic gradients where little physiologic effect can be measured (Watkinson 1985).

Even if extrinsic predictive factors can be identified, they do not answer the evolutionary question of why a species is unable to adapt to marginal conditions, or why many distribution limits are relatively stable over time even in highly dispersive organisms. One possibility is that there are trade-offs between adaptations that are more advantageous in central versus marginal habitat (MacArthur 1972, Futuyma 2001). If there is a gradient of habitat quality, then source-sink dynamics (Pulliam 1988) can produce strong asymmetric gene flow from central to marginal habitat. Range expansion may be prevented in margins by the swamping effect of gene flow from the population center (Haldane 1956, Mayr 1963). Local expansion or contraction likely depends both on the strength of the environmental gradient relative to dispersal and the potential for adaptation (Kirkpatrick and Barton 1997), and interspecific competition can have a strong stabilizing effect (Price and Kirkpatrick 2009). However, range shifts are generally studied over broad spatial and temporal scales, and finer-scale studies at distribution margins are needed.

Distributional limits and stability can also be explained in terms of habitat selection, especially for highly vagile organisms such as many bird species. The process of habitat selection is partly determined by an innate preference for appropriate habitat types (habitat preference) and dispersal tendency. If individuals recognize the appropriate habitat type, a biological advantage is conferred (Lack 1933). Innate habitat recognition mechanisms trigger a territorial or choice response and can be modified by imprinting or learning (Svarsdon 1949), which has now been demonstrated in a wide variety of animals (e.g., Wecker 1963, Partridge 1978, Taylor 1987, Jaenike and Holt 1991). Habitat cues can be direct or indirect, as in selection for vegetation structure by birds, which indirectly predicts resource availability (e.g., Cody 1981, Rotenberry 1985, Marshall and Cooper 2004). Habitat selection can have a stabilizing effect if individuals choose to settle in lower quality habitat when higher quality habitat is "full" (Kluyver and Tinbergen 1953, Fretwell and Lucas 1970), which may be likely at distribution limits. Alternatively, habitat preference can become uncoupled from habitat performance, such as in maladaptive habitat selection (Rausher 1979, Van Horne 1983, Knick and Rotenberry 2000, Leyva et al. 2000) or conspecific attraction (e.g., Stamps 1994, Greene and Stamps 2001). The need to interact with potential mates can override the tendency to distribute ideally according to habitat, and can instead produce clumped patterns independent of habitat differences. Social cohesion certainly occurs in colonial or flocking species, and is likely an important factor for territorial species as well, especially at distribution limits.

Although it is well-demonstrated that species generally tend to be adapted to the habitat in which they occur, to what degree are distribution limits expected to correspond

to niche limits? Are there other explanations for distribution limits? A neutral model of limited dispersal in a stochastic environment alone is expected to produce clumped distribution patterns, especially when a species has a high intrinsic rate of increase coupled with moderate dispersal rates (Roughgarden 1979). Niche-neutral distribution models (e.g., MacArthur and Wilson 1967, Hanski and Gilpin 1997, Hubbell 2001) assume demographic and ecological equivalence of species, and predict that distribution and diversity patterns will evolve by neutral extinction-colonization (or speciation) dynamics. Even though there are no niche differences and habitat is unimportant, these models can perform surprisingly well at predicting large-scale biodiversity patterns (e.g., Hubbell 2001). The habitat still has some maximum carrying capacity, but the current boundary of the population or species may be arbitrary with respect to the species' fundamental environmental tolerances or biotic interactions. Instead, current range boundaries are primarily due to limited dispersal, regional dynamics, historical contingency, or stochasticity (e.g., Holt 2005), and so are niche-neutral. Local occurrence can be mostly due to regional conditions and dispersal, rather than to any local niche relationships. In addition to limited dispersal, social cohesion and site fidelity are expected to cause further niche-neutral aggregation.

Two general models emerge for distribution limits along an ecological gradient. First, in a niche-limited model, there should be a tendency for distribution limits to correspond to niche limits along an ecological gradient due to natural selection and habitat selection. Marginal populations are expected to fall on a gradient of habitat quality. A source-sink gradient should exist where there is a tendency for individuals to passively or actively

settle in unsuitable or reduced quality habitat in marginal areas due to dispersal and negative density-dependent habitat selection. Thus, habitat-dependent fitness should be reduced in marginal areas. A second, niche-neutral model predicts non-equilibrium extinction-colonization dynamics along a gradient primarily influenced by regional conditions and dynamics. Current distribution boundaries are arbitrary with respect to the species' fundamental tolerances, and this can be further enhanced by threshold minimum population sizes (Allee 1931), restricted dispersal, and conspecific attraction. In this scenario, distributions are spatially autocorrelated, and there should be no difference in habitat-dependent fitness between central and marginal areas. In other words, distribution limits are arbitrary with respect to adaptations.

These two models are not mutually exclusive, but they provide a framework for the study of distribution limits and the relative influence of environmental factors. The causes and consequences of distribution limits are expected to be influenced by behavioral plasticity, by different life history strategies, and especially by the spatial and temporal scale of study. To elucidate the nature of distribution limits, I studied avian-habitat relationships and their dynamics along an ecologically "steep" gradient, that is, a gradient encompassing a wide range of environmental conditions over a relatively short geographical space. I established three study areas on the eastern slope of the Peninsular Mountains in the Colorado Desert, California, each encompassing an elevation range from 200–1800 m from lower elevation Sonoran desert scrub to upper elevation chaparral (Fig. A.1). Through the use of multi-scale surveys and historical data, I examined the comparative spatial structure and dynamics of breeding bird populations at their

distribution margins (Chapters One and Two), and within this broader population-level context, I tested for reduced breeding performance in marginal areas (Chapters Three and Four). If distribution limits are niche-limited, there should be strong environmental associations at margins with both reduced abundance and reduced breeding performance. If environmental conditions change, then distributions should shift in the expected direction. Territorial birds are good models for species-habitat relationship studies, because they clearly exhibit habitat selection behavior with little dispersal-restriction, and are relatively easy to census. I studied multiple bird species (AOU 1998), but with a particular focus on two relatively abundant passerines with contrasting distributions: Black-throated Sparrows (*Amphispiza bilineata*), common in desert scrub (Johnson et al. 2002), and Black-chinned Sparrows (*Spizella atrogularis*), common in chaparral (Tenney 1997, Hargrove in press). Along an ecologically steep gradient, differences in breeding performance are expected to be pronounced if the species' distribution is niche-limited, and birds should be capable of rapid distribution shifts in response to environmental change.

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# Chapter 1: Spatial Structure and Dynamics of Breeding Bird Populations at a Distribution Margin


## ABSTRACT

Local-scale processes at distribution margins can affect larger-scale distribution dynamics, but are rarely studied. The objective of this research was to elucidate the nature of distribution limits by studying the comparative structure, dynamics, and environmental associations of breeding bird populations at their distribution margin. We studied distribution patterns along a low-elevation (200–1800 m) desert gradient in southern California that is undergoing rapid climate change (locally, annual mean maximum temperature at the low end of this gradient has increased by 3.8°C since 1962). We used logistic regression with hierarchical partitioning to determine the independent effects of environmental variables on distributions, and to isolate the relative effects on distribution limits vs. within-range patterns at the margin. Distribution patterns were highly variable among species, but were remarkably static over three study areas and three years. Climate was relatively important in setting the lower distribution limits of higher-elevation species (chaparral birds), and there was a shift to greater importance of biotic habitat for determining within-range abundances. However, upper-elevation-limited species (desert scrub birds) were more likely to shift upward in elevation over a 26-year period. This research highlights the usefulness of studying environmental

relationships at distribution margins and the importance of considering biotic interactions in forecasting distribution shifts.

## INTRODUCTION

Historically, patterns in the distribution and abundance of species have been explained by the ecological niche concept (Grinnell 1917). If species are limited by multiple environmental variables that have some degree of stochasticity and are spatially correlated, then the density distribution of a species will approximate the adaptive niche with a tendency for greater density toward distribution centers and lower density at margins (Brown 1984, Brown et al. 1995). Thus, the niche of a species is defined by the set of biotic and abiotic environmental variables to which the species is best adapted, which is often inferred by its distribution and in turn is used to predict future distribution shifts under changing environmental conditions (e.g., Beaumont et al. 2005). Despite substantial recent advances in areas such as bioclimatic modeling, our ability to predict distribution changes is still limited (Heikkinen et al. 2006). Local-scale processes at the distribution margin of a species can affect larger-scale range dynamics (Thomas et al. 2001), but are rarely studied. The general objective of this research is to elucidate the nature of distribution limits by studying the comparative fine-scale structure, dynamics, and environmental correlates of avian populations at their distribution margin.

Avian breeding distributions are largely determined by habitat selection and territoriality, which are expected to link adaptive traits of individuals to suitable habitat.

A choice of high quality habitat is particularly important for passerines during the breeding season because they often remain in their territories throughout the nesting cycle, and the local conditions, resources, predators, and competitors can have a strong effect on nest success. Many distribution boundaries occur on elevational gradients, along which many varying factors can affect avian reproductive success (Badyaev and Ghalambor 2001), and hence distribution patterns. Climate is thought to play a large role in setting outer distribution limits, but it is difficult to separate the relative contributions of abiotic and biotic factors due to covariation and indirect effects (Gaston 2003). It has also been suggested that biotic interactions and habitat specializations limit distributions at lower latitudes while abiotic conditions limit distributions at higher latitudes (Dobzhansky 1950, MacArthur 1972), and this has been applied to elevational gradients as well (Brown et al. 1996). Similar trade-offs are thought to exist along desert elevational gradients, with abiotic conditions limiting species where aridity becomes extreme (Tieleman et al. 2003, Tieleman et al. 2004).

In southern California, upward elevational shifts in bird distributions have been documented along a desert elevational gradient in association with a rapid warming trend over a recent 26-year period (Hargrove and Rotenberry in press). To further investigate distribution limits in this dynamic low-elevation system, we quantified fine-scale spatial structure, temporal dynamics, and environmental correlates of avian populations at their distribution margins over a three-year period, and compared species with their lower or upper elevation limit along the study gradient. To determine the relative importance of environmental variables in limiting bird distributions, we used multiple logistic

regression at two scales: (1) “full” scale along the entire elevation gradient (200–1800 m), and (2) “within-range” scale with sites outside the species’ elevational distribution limit excluded. Since environmental factors tend to be correlated along an elevational gradient, we used hierarchical partitioning to identify the relative independent contribution of environmental variables in explaining avian distribution patterns, and to test for shifts in importance between the two scales. If climate plays a relatively large role in setting distribution limits, then climate is predicted to explain distribution patterns relatively well at the full scale while biotic habitat features are predicted to explain distribution patterns relatively well at the within-range scale. We also hypothesize that higher-elevation species are limited by the abiotic desert conditions at low elevations, while lower-elevation desert species are limited by biotic specializations at higher elevations where it becomes more mesic. Thus, climate is predicted to explain distribution limits relatively well for species with their lower elevation limit along the study gradient.

## METHODS

Three study areas were established along the elevation gradient between the Peninsular Range and Colorado Desert in southern California (Fig. A.1). Bird presences and abundance were established by point-transect sampling at 159 sites, each at least 500 m apart and spanning an elevational range of 200–1800 m at each study area. Point counts were conducted over a three-year period (2005–2007) during the breeding season

(March–June) during morning hours and under fair weather conditions. Point count duration was 15 minutes with farthest distance observations (2%) for each species removed. Point counts were repeated 2–3 times within years and averaged within and across years. Non-territorial species frequently seen as migrants (e.g., warblers) or with highly dispersive foraging or flocking (e.g., swifts and doves), and species present at fewer than 15% of sites were not included.

At each of the 159 points, nine environmental variables in four categories were quantified: habitat structure, habitat floristics, climate, and geography. The following 10 habitat "structural" characteristics were visually estimated within a 50-m radius centered on the point: % cover of trees, % cover of shrubs, % cover of succulents, % cover of herbs (grasses and annuals), % cover of rocks, % cover open ground, % cover of litter (leaves and other organic debris), number of large snags (>10 dm diameter), number of small snags (<10 dm diameter but large enough for a cavity nest), and average height of the shrub layer. These variables were reduced by principal components analysis (McCune and Mefford 2006), with the first two axes explaining over 50% of the variance (Table A.1). The first principal component axis ("habitat structure 1") corresponded to a gradient from open, rocky habitat with succulents at one end to denser shrubs and trees with more snags and litter at the other end. The second principal component axis ("habitat structure 2") corresponded to a gradient from shrub to tree cover. To quantify habitat floristics, % cover of all common plant species was estimated within each 50-m radius circle. Detrended correspondence analysis (McCune and Mefford 2006) was applied to these data to quantify plant community composition (Table A.2, Rebman and Simpson 2006).

The first axis corresponded to a gradient from desert scrub at one end, to chaparral and oak-pine forest at the other end and was correlated with elevation ("habitat floristics 1"). The second axis corresponded to a gradient from dry washes to semi-riparian ("habitat floristics 2").

For each of the 159 points, the following climate variables were obtained from PRISM (PRISM Group, Oregon State University, http://www.prismclimate.org, accessed 12 October 2009) and averaged for the months of March–June over the 2005–2007 period: maximum temperature, minimum temperature, and cumulative precipitation (July–June rain year starting with the previous July). Principal components analysis was used for maximum and minimum temperature to create a single axis describing temperature, which explained 95% of the variation in these two variables (Table A.3).

Geographic variables were elevation, longitude, and latitude at each point. All environmental variables were centered and standardized (mean of zero, standard deviation of one). Pearson correlation was used to assess the intercorrelation of environmental variables with elevation.

To analyze species' elevational distributions, we constructed cumulative abundance curves by summing the average abundance of a species from its lowest to highest altitudinal occurrence within 11 elevation bins. Because observations were normalized by the total number of individuals observed, cumulative abundance at the highest elevation site will always be 100%. For species with at least 2% relative abundance at each study area each year (compared to other species), differences between cumulative elevational distributions were tested by Kolmogorov-Smirnov two-sample testing (Sokal and Rohlf

1995). Species were categorized as upper-elevation limited if they were more abundant at lower elevations and absent or rare from higher elevations, and as lower-elevation limited if they were more abundant at higher elevations and absent or rare from lower elevations.

For each species, multiple logistic regression was used to analyze the effect of the nine environmental variables on its presence-absence. The average relative abundance for each species was ranked by point, and points representing less than 2% of the species' cumulative abundance were categorized as 'absent'. To control for intercorrelations among predictor variables, hierarchical partitioning was performed using all possible models (every combination of variables) to determine the independent contribution of predictor variables toward full model likelihood by separating independent and joint effects (Chevan and Sutherland 1991). This method performs well at determining relative independent effects when variables are intercorrelated (Murray and Conner 2009). The analysis was performed using the 'hier.part' package in 'R' (Walsh and Mac Nally 2008) with log-likelihood used to estimate goodness of fit for each model. The sum of the independent effects equals the difference between the log likelihood of the full model (all nine variables) and the null model (intercept only). The analysis was performed at two scales: (1) the full scale including all $n = 159$ points, and (2) the within-range scale where points beyond the species' 98% cumulative elevational abundance were removed. To test the statistical significance of independent effects, randomization tests were performed on each variable with 1000 randomizations. An independent effect was considered statistically significant if it fell above the upper $95^{th}$ percentile of its randomized distribution. To test for a shift in relative importance of climate to habitat variables

between lower-elevation limited and upper-elevation-limited species, a two-sample *t*-test was performed. To test for a shift in relative importance of climate to habitat variables between the full-scale and reduced-scale analyses, paired-sample *t*-tests were performed on the two categories of species.

## RESULTS

Except for latitude and habitat floristics 2, environmental variables were strongly correlated with elevation, especially climate and habitat floristics 1 (Table 1.1).

Twenty-eight species were present at the minimum threshold of 15% of the study points and qualified for analysis (Table 1.2). To test for elevational shifts of birds between study areas and years, cumulative abundance distributions were analyzed for each species (Fig. 1.1). Out of the twenty-eight species, six fell below 2% relative abundance at each study area each year (compared to other species) so were not tested for elevational shifts (Greater Roadrunner, Nuttall's Woodpecker, Ladder-backed Woodpecker, Northern Flicker, Blue-gray Gnatcatcher, and Rock Wren). Although elevational distributions varied among species, each was highly stable over the three years surveyed (2005–2007), with none of twenty-two species tested showing significant ($P < 0.05$) shifts between years. The majority of species also showed highly consistent elevational distributions among the three study areas, with only three of the twenty-two species tested showing significantly ($P < 0.05$) different elevational distributions between study areas (Anna's Hummingbird, Black-tailed Gnatcatcher, and Phainopepla). Based on

their elevational distributions, 13 species were categorized as upper-elevation limited (more common at lower elevations and rare or absent from highest elevations), and 15 as lower-elevation limited (more common at higher elevations and rare or absent from lowest elevations) (Table 1.2).

For each of the twenty-eight species, the independent effects of nine predictor variables toward likelihood of bird presence was determined by hierarchical partitioning at both the full scale ($n$ = 159) and within-range scale where sites beyond the species' 98% elevation distribution were removed (Table 1.2, Fig. 1.2). All variables showed strong importance, with statistical significance of the full model (logistic regression with all nine variables) for 24 species at the full scale and for 22 species at the within-range scale (Table 1.2, $P < 0.05$, likelihood-ratio test comparing the full model to the null model). Patterns of relative variable importance were highly individualistic among species, but across all species at the full scale, habitat floristics 1 (plant community composition scores based on the first detrended correspondence axis) was ranked most highly, while at the within-range scale, habitat floristics 2 was ranked most highly. The influence of biotic habitat (structure and floristics) relative to climate (temperature and precipitation) was also expressed as a ratio (Table 1.2). Scott's Oriole had the highest ratio of biotic habitat relative to climate at the full scale, while Verdin had the highest ratio at the within-range scale and the strongest shift between scales (Table 1.2).

Environmental variables were grouped into four sets and compared at the full scale and within-range scales between upper-elevation-limited species and lower-elevation limited species (Fig. 1.3). Across all upper-elevation-limited species, there was little

difference between the full-scale and within-range-scale analyses, while for lower-elevation-limited species there was an increase in the influence of habitat structural variables and reduction in the influence of climatic variables at the within-range scale compared to the full scale. Expressed as the influence of biotic habitat (structure and floristics) relative to climate (temperature and precipitation), this shift between scales was statistically significant among lower-elevation-limited species ($n = 15$, $P < 0.001$, paired-sample *t*-test, one-tailed), but not among upper-elevation-limited species ($n = 13$, $P = 0.3$). At the full scale, the importance of biotic habitat relative to climate was greater for upper-elevation-limited species compared to lower-elevation-limited species ($P = 0.04$, two-sample *t*-test, one-tailed), while at the within-range scales there was no difference between the two groups of species ($P = 0.5$). Environmental variables (climate and biotic habitat) were more important compared to spatial variables for lower-elevation-limited species at both the full scale ($P = 0.01$, paired-sample *t*-test, one-sided) and within-range scale ($P = 0.02$), but were relatively weak for upper-elevation-limited species with little difference compared to spatial variables at the full scale ($P = 0.06$) and no difference at the within-range scale ($P = 0.4$).

## DISCUSSION

Marginal distribution patterns and environmental correlates were highly individualistic among species, but there was a strong consistency in elevational distributions among the three study areas and three years, with essentially no between-

year shifts. Although there were strong differences among species, lower-elevation-limited species tended to have stronger associations with environmental variables compared to upper-elevation-limited species, and showed a shift toward greater importance of biotic habitat relative to climate at the within-range scale. Our prediction that climate would be relatively more important for distribution limits of lower-elevation-limited species in this system was supported, and our prediction that there would be a shift toward greater importance of biotic habitat at the within-range scale was supported, but only by lower-elevation-limited species.

Climate can influence distribution limits both directly and indirectly (Emlen 1976). Although birds are expected to select habitat and territories based largely on biotic habitat features, climate can indirectly shape habitat preferences through past influences on reproductive success, and current climatic conditions can influence territorial choices both directly through weather and indirectly though effects on resources. Many studies have found broad-scale correlations between range boundaries and climatic factors (e.g., Bohning-Gaese and Lemoine 2004), but few studies have attempted to isolate the relative effects of environmental factors at a distribution margin, or to compare species at a fine-scale, as this study has. Along a desert elevational gradient, climate becomes more extreme or harsh at lower elevations and is thought to limit upper-elevation species, while lower-elevation species that are adapted to the desert climate are thought to be limited at higher elevations by biotic interactions such as habitat specializations, competition, and predation. In this system, upper-elevation species associated with chaparral habitat tended to be limited at lower elevations by climate, while lower-elevation species associated

with desert scrub habitat showed more variability in their limitation with weaker group-level associations.

Distribution margins had strong environmental associations in this system, but with highly individualistic differences among species in relative variable importance and how they shifted between scales. Individualistic responses have been found in many broad-scale studies, which can also vary regionally (e.g., Taper et al. 1995), but few studies have tested for fine-scale differences at a margin. Across species, the log likelihood of the full model tended to be weaker at the within-range scale, which is expected from the reduction in sample sizes. However, it became larger at the within-range scale for four species: Greater Roadrunner, Scott's Oriole, Ladder-backed Woodpecker, and California/Gambel's Quail. This is likely due to the occurrence of these four species at mid-elevations, such that their relationship with elevation was relatively non-linear. The Phainopepla was the only species for which the full model was not statistically significant at either scale, but this is not surprising given that this species is closely associated with mistletoe (*Phoradendron* spp.), which was not directly measured.

Each environmental variable showed importance for many species, but across species, spatial variables played a relatively minor role. Spatial variables are more likely to be important along weaker environmental gradients or among other taxa with greater dispersal limitations. Latitude was the least important variable; but interestingly, it was relatively important for the two hummingbird species, Costa's and Anna's Hummingbirds. Perhaps variables that were not measured contributed to this effect, such as flower densities or distance to urbanization. Elevation was relatively important for

many species, which could also be due to other unmeasured variables that have some degree of correlation with elevation, such as competition, predation, or other climatic or resource-related factors.

Habitat structure and floristics are known to be important in explaining avian distributions, with their relative importance shown to vary with study scale (Wiens and Rotenberry 1981). In this study, the relative importance of structure and floristics varied among species, but notable was a strong increase in the relative importance of floristics 2 at the within-range scale for many species, including an eight-fold increase for Blue-gray Gnatcatcher, Mountain Quail, and California Thrasher. This floristics variable was related to a moisture gradient independent of elevation. Across species, the relative importance of biotic habitat variables vs. climate had a greater increase for chaparral species at the within-range scale, but again, there were strong differences among species and greater variation among desert species. The greatest increase in the importance of biotic habitat relative to climate when shifting to the within-range scale occurred for a desert species, the Verdin, which suggests that this species is limited by climate at higher elevations.

In this system, environmental variables were strongly correlated with elevation. This reduces our ability to determine relative variable importance with accuracy, but the method of hierarchical partitioning is a useful but underutilized tool for separating independent and joint effects (Murray and Conner 2009), and strengthened our ability to make inferences when testing for shifts in relative variable importance between scales and between groups of species. Although there were strong environmental associations

for many species, experimental tests would be needed to confirm the relative importance of environmental variables in terms of habitat preferences and suitability for individual species.

Locally, annual mean maximum temperature at the low end of this gradient has increased by 3.8°C since 1962, and there have been upward shifts in elevational distributions of breeding birds over the past 26-year period, mostly by lower elevation desert scrub species (Hargrove and Rotenberry in press). Although chaparral species were found in this study to be more strongly limited by climate, biotic habitat was more important for within-range patterns and upward shifts were less likely for these species in the longer-term trends. For desert scrub species, current distribution patterns were less correlated with climate, yet these species were more likely to show upward longer-term shifts. In this system, desert scrub species have been shown to have increased reproductive success at higher elevations at distribution margins compared to lower elevations where the birds are more common, which seems to support the tendency toward upward shifts, but not all species shifted upward and some species may have a persistent preference for desert scrub habitat despite lower reproductive success (Chapter Four). Thus, distributional correlations with climate may be less sensitive than local-scale reproductive success in predicting distribution shifts, and it is possible that biotic associations can override or delay climate-induced range shifts. Results from the North American Breeding Bird Survey indicate decreasing population trends overall for the Sonoran and Mojave deserts from 1966 to 2007 (Sauer et al. 2008), but more study is needed on the causes of these population declines.

Bioclimatic models are commonly used to predict large-scale shifts under climate change, but biotic interactions are rarely considered even when clearly important (Araujo and Luoto 2007, Suttle et al. 2007, Preston et al. 2008). Given strong differences among species, predictive models will need to be individually-tailored for each species with the inclusion of important biotic variables, but even then predictive ability may still be poor (Rotenberry and Wiens 2009). Local-scale study of the structure, dynamics, and environmental associations of populations at distribution margins can provide important information for understanding niche-relationships and distribution limits, and can also provide important clues toward understanding larger-scale distribution dynamics.

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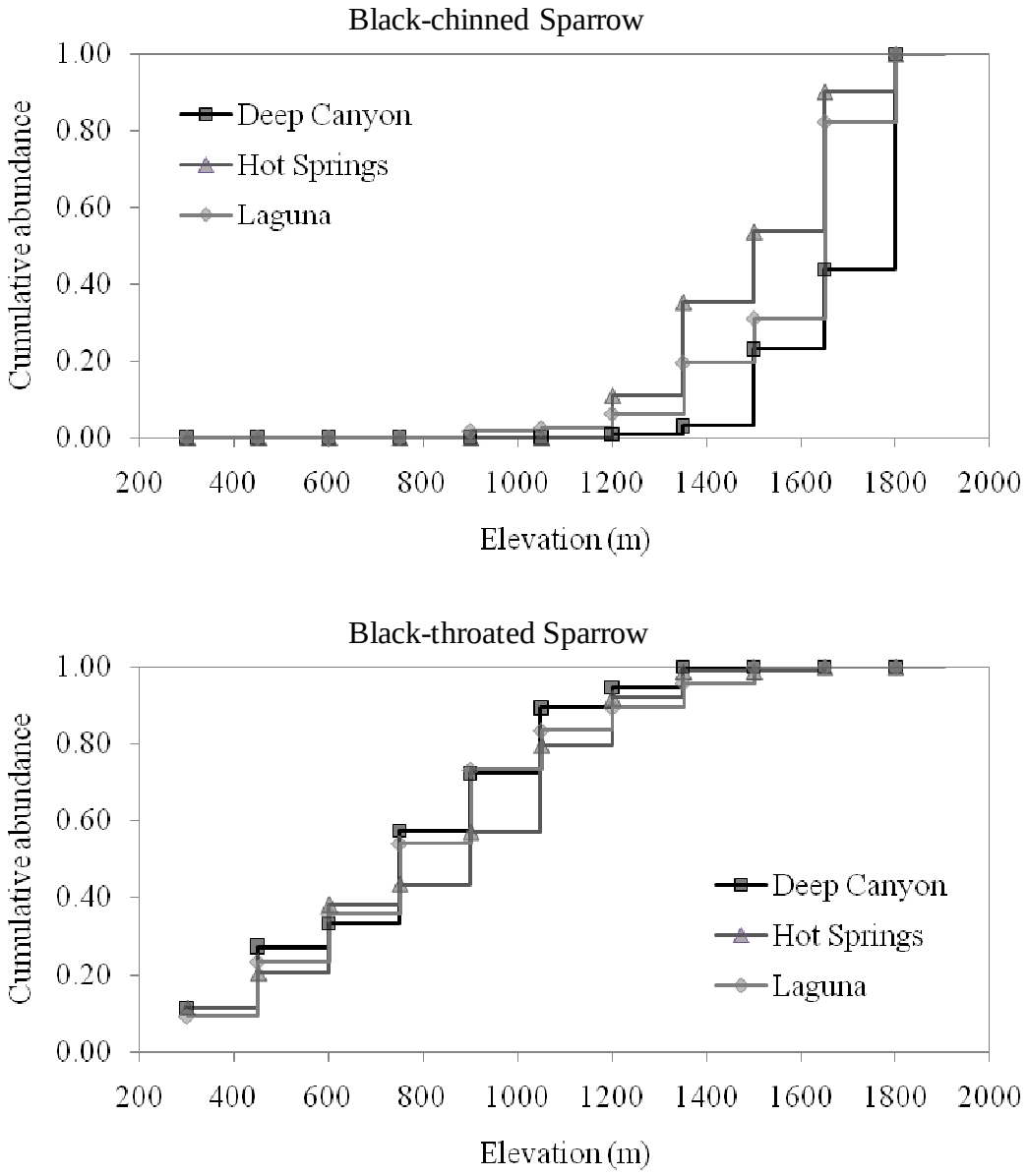


**Figure 1.1** Elevational distributions of Black-chinned (top) and Black-throated (bottom) sparrows at three study areas (Deep Canyon, Hot Springs, and Laguna) averaged over a three-year period (2005–2007) at 159 point count sites. Cumulative abundance is the proportional average abundance of birds summed over 11 elevation bins.

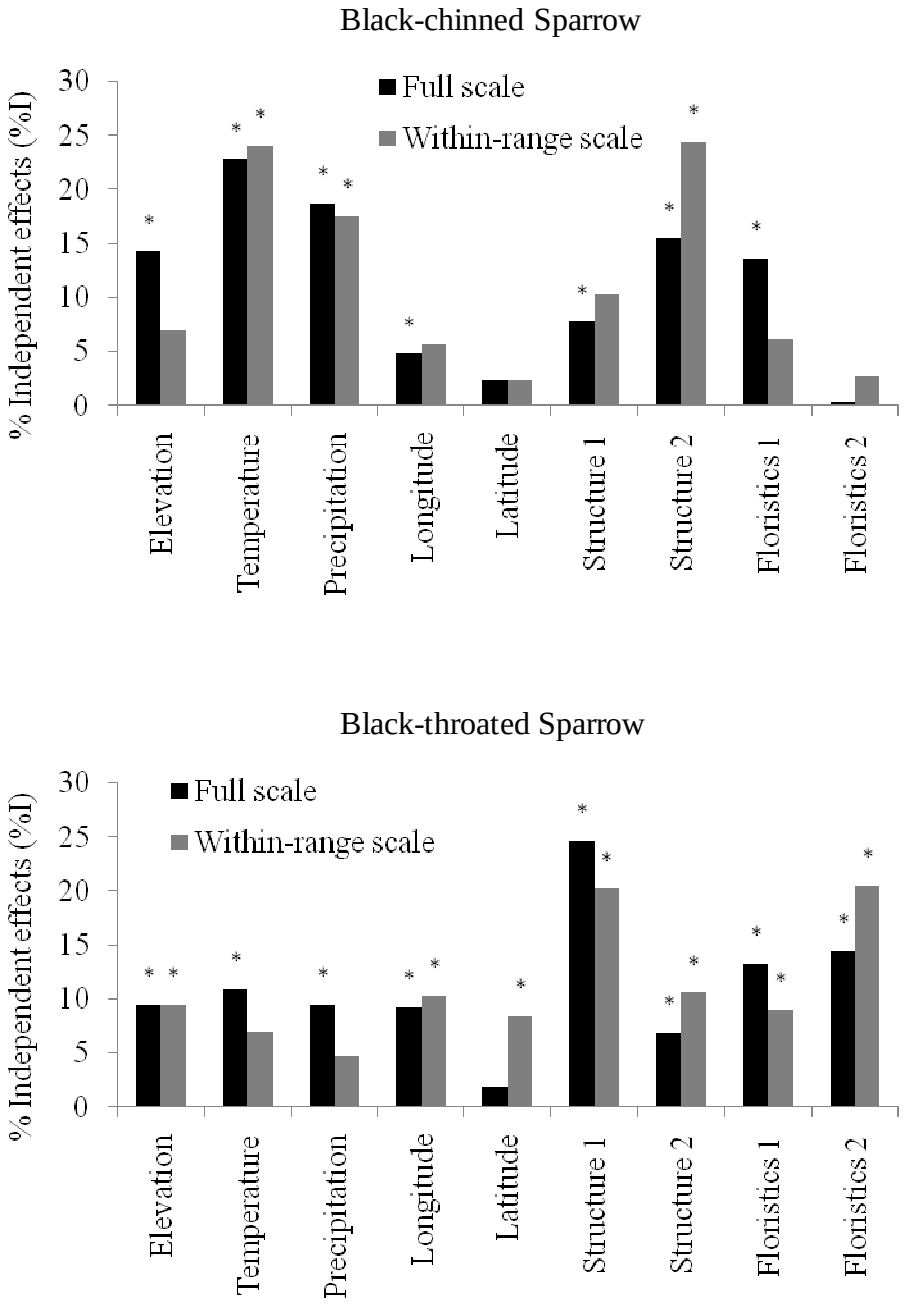


**Figure 1.2** The relative independent effects of predictor variables for Black-chinned (top) and Black-throated (bottom) sparrow presence at full and within-range scales, as estimated from hierarchical partitioning. Asterisks indicate statistical significance of the independent effect of each variable based on randomization tests (upper 95$^{th}$ percentile with 1000 repetitions).

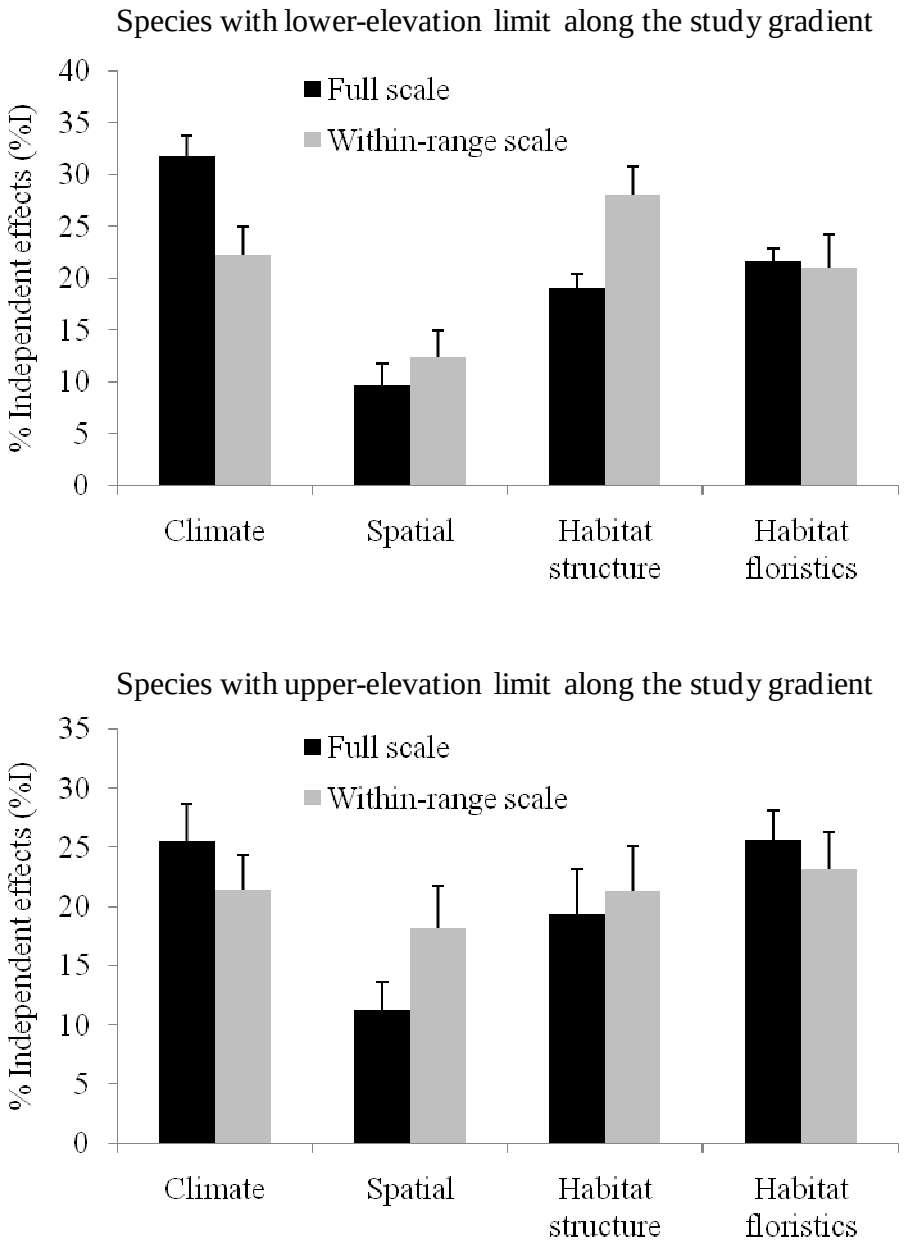


**Figure 1.3** The relative independent effects of predictor variable sets for bird presence averaged for all lower-elevation-limited species (top, $n = 15$) and upper-elevation-limited species (bottom, $n = 13$) at full and within-range scales as estimated from hierarchical partitioning (± SE). Climate includes temperature and precipitation, spatial includes longitude and latitude, habitat structure includes two variables derived by principal components analysis, and habitat floristics includes two variables derived by detrended correspondence analysis. Elevation is included as a control variable (not shown).

**Table 1.1** Correlation of environmental variables with elevation at 159 sample points.

| Variable | $r^2$ | $P$ |
|---|---|---|
| Temperature | – 0.93 | < 0.001 |
| Precipitation | 0.94 | < 0.001 |
| Longitude | – 0.54 | < 0.001 |
| Latitude | – 0.03 | 0.71 |
| Habitat structure 1 | 0.66 | < 0.001 |
| Habitat structure 2 | 0.35 | < 0.001 |
| Habitat floristics 1 | 0.96 | < 0.001 |
| Habitat floristics 2 | 0.08 | 0.30 |

**Table 1.2** Comparisons of relative importance of variables (percentage of total independent effects) using two logistic regression analyses: full scale (n = 159 sites, left side of slash) and within-range scale (sites beyond 98% elevational limit trimmed, right side of slash). Species are listed in descending order by mean elevation, and are categorized into two groups: lower-elevation limited and upper-elevation limited.

| Species | Mean elevation (m)[a] | Sites present | Independent effects (full scale/within-range scale)[b] LL Sum[c] | Elevation (%) | Longitude (%) | Latitude (%) | Temp. (%) | Precip. (%) | Structure1 (%) | Structure2 (%) | Floristics1 (%) | Floristics2 (%) | Biotic: Climate[d] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lower-elevation limited | | | | | | | | | | | | | |
| Northern Flicker *(Colaptes auratus)* | 1548 | 30 | **31.2/8.9** | **13.9**/4.2 | **9.9**/12.9 | 1.8/5.0 | **17.7**/10.9 | **10.6**/4.9 | **13.5**/11.7 | 2.7/17.9 | **29.5/30.9** | 0.4/1.7 | 0.8/2.0 |
| Black-headed Grosbeak *(Pheucticus melanocephalus)* | 1512 | 39 | **45.3/19.1** | **13.0/11.3** | **6.6**/7.6 | 2.7/3.8 | **27.9/31.9** | **13.7**/9.0 | **9.4**/5.6 | 2.8/2.6 | **21.4/17.0** | 2.5/**11.2** | 0.4/0.4 |
| Black-chinned Sparrow *(Spizella atrogularis)* | 1507 | 53 | **42.7/16.9** | **14.3**/6.9 | **4.8**/5.6 | 2.3/2.3 | **22.8/24.0** | **18.7/17.5** | **7.7**/10.3 | **15.4/24.4** | **13.6**/6.1 | 0.3/2.7 | 0.4/0.5 |
| Blue-gray Gnatcatcher *(Polioptila caerulea)* | 1499 | 30 | **16.7**/8.3 | **14.6**/4.0 | 4.6/5.2 | 9.2/**21.7** | **17.5**/7.9 | **18.5**/11.3 | **10.8**/10.0 | 4.2/8.6 | **17.4**/6.0 | 3.1/**25.4** | 0.5/1.3 |
| Oak Titmouse *(Baeolophus inornatus)* | 1487 | 57 | **34.5**/6.2 | **17.8**/5.0 | **6.4**/14.4 | 2.0/14.3 | **18.4**/8.9 | **13.4**/4.0 | **21.1/34.7** | 1.6/5.7 | **18.9**/8.4 | 0.4/4.5 | 0.7/2.1 |
| Spotted Towhee *(Pipilo maculatus)* | 1426 | 84 | **82.4/22.2** | **16.9/9.1** | **3.3**/4.8 | 1.7/4.8 | **16.1/16.6** | **16.4/14.3** | **8.9**/3.0 | **7.2**/7.5 | **18.1/11.7** | **11.4/28.4** | 0.7/0.8 |
| Wrentit *(Chamaea fasciata)* | 1415 | 86 | **79.9/43.1** | **12.8/10.8** | **4.6**/1.8 | **2.0**/3.2 | **16.4/18.7** | **15.7/16.2** | **8.7/5.7** | **11.9/9.5** | **15.8/16.2** | **12.0/17.8** | 0.8/0.7 |
| Nuttall's Woodpecker *(Picoides nuttallii)* | 1402 | 25 | **25.7/18.9** | **8.5**/7.0 | **25.8/30.2** | 4.3/5.6 | **7.8**/4.7 | 6.2/3.8 | **10.7**/8.4 | 4.5/4.4 | **19.0/16.7** | **13.2/19.2** | 1.7/2.9 |
| Mountain Quail *(Oreortyx pictus)* | 1387 | 80 | **38.8/15.7** | **14.9**/7.1 | **11.8/21.0** | 2.6/4.9 | **22.5/16.3** | **15.7**/6.3 | **8.1**/3.1 | 3.8/3.5 | **16.7**/6.9 | 3.8/**30.8** | 0.4/1.0 |
| Bushtit *(Psaltriparus minimus)* | 1377 | 60 | **42.0/13.6** | **14.1**/12.1 | **4.6**/4.2 | 2.5/3.0 | **15.4**/7.7 | **12.7**/4.6 | **19.4/32.2** | 2.7/3.8 | **28.0/28.5** | 0.5/4.0 | 0.9/2.8 |
| Anna's Hummingbird *(Calypte anna)* | 1356 | 56 | **22.5/19.1** | **10.4/11.8** | **10.4**/9.2 | **25.4/25.9** | **7.7/10.8** | **14.9/12.6** | 6.6/**8.7** | 7.0/8.6 | **7.6/9.3** | **9.9**/3.2 | 0.7/0.6 |
| California Thrasher *(Toxostoma redivivum)* | 1348 | 85 | **49.6**/4.9 | **19.7**/7.3 | **3.8**/2.3 | 1.7/3.8 | **19.4**/12.3 | **17.7**/6.9 | **9.3**/2.8 | **6.2**/18.4 | **20.4**/12.9 | 1.9/33.4 | 0.5/1.8 |
| Western Scrub-Jay *(Aphelocoma californica)* | 1339 | 95 | **48.5/11.2** | **18.1/37.6** | **3.7**/1.8 | 1.9/3.5 | **19.7**/9.3 | **17.4**/5.9 | **8.9**/8.3 | **8.4/18.2** | **21.6**/4.1 | 0.3/11.2 | 0.5/1.4 |
| Bewick's Wren *(Thryomanes bewickii)* | 1280 | 113 | **47.6/33.9** | **13.3/11.3** | **4.8**/3.5 | 1.4/1.7 | **16.5/8.9** | **13.6/12.6** | **28.1/37.5** | **4.4**/4.1 | **15.1/12.9** | 2.8/**7.5** | 0.8/1.4 |
| California Towhee *(Pipilo crissalis)* | 1144 | 99 | **18.8/8.8** | 8.5/8.4 | **13.3**/7.2 | 4.4/7.6 | **14.0**/5.1 | **11.6**/10.3 | **17.8**/17.3 | **18.9/37.2** | 8.6/6.6 | 2.8/0.3 | 0.9/2.0 |

**Table 1.2** Continued.

| Species | Mean elevation (m)[a] | Sites present | Independent effects (full scale/within-range scale)[b] LL Sum[c] | Elevation (%) | Longitude (%) | Latitude (%) | Temp (%) | Precip (%) | Structure1 (%) | Structure2 (%) | Floristics1 (%) | Floristics2 (%) | Biotic: Climate[d] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Upper-elevation limited | | | | | | | | | | | | | |
| Greater Roadrunner *(Geococcyx californianus)* | 1079 | 45 | 7.6/**21.1** | 11.2/**20.6** | **25.5**/3.2 | 21.4/4.3 | 5.6/**11.6** | 6.5/**14.2** | 3.3/**21.6** | 9.2/5.1 | 5.2/**11.6** | 12.0/7.8 | 1.2/0.9 |
| Scott's Oriole *(Icterus parisorum)* | 951 | 79 | **15.8/18.7** | 6.9/**22.8** | 2.3/5.7 | 1.6/**11.2** | 5.9/**12.0** | 6.7/**12.5** | **34.9**/1.6 | **16.2/14.3** | 6.9/**9.6** | **18.6/10.3** | 3.1/0.7 |
| Ladder-backed Woodpecker *(Picoides scalaris)* | 942 | 27 | 4.9/**10.2** | **37.4/39.5** | 2.9/2.3 | 5.3/2.3 | 3.3/7.9 | 16.2/11.8 | 14.7/2.3 | 4.2/**19.3** | 15.6/13.7 | 0.4/0.8 | 0.9/0.9 |
| California/Gambel's Quail *(C. californica/gambelii)*[e] | 936 | 77 | 8.2/**13.3** | 13.1/**15.8** | 3.8/6.8 | 3.9/**16.9** | 8.4/5.9 | 7.0/**11.9** | 11.2/4.7 | 6.7/**15.9** | **29.0/15.2** | 16.8/7.0 | 2.1/1.2 |
| Rock Wren *(Salpinctes obsoletus)* | 810 | 65 | **34.0/20.9** | **6.2**/3.1 | **12.2/23.5** | **7.9/21.9** | **7.1/8.1** | **5.7**/2.5 | **32.7/19.5** | **6.4/9.8** | **15.1**/4.0 | **6.6**/7.7 | 2.4/1.9 |
| Black-throated Sparrow *(Amphispiza bilineata)* | 754 | 106 | **56.2/27.2** | **9.4/9.4** | **9.2/10.3** | 1.9/**8.4** | **10.9**/7.0 | **9.4**/4.7 | **24.6/20.2** | **6.8/10.6** | **13.3/9.0** | **14.4/20.4** | 1.5/2.6 |
| Costa's Hummingbird *(Calypte costae)* | 734 | 91 | **20.7/19.3** | **15.1/16.4** | **14.5/16.1** | **22.7/25.6** | **14.5/14.4** | **11.3/10.3** | 4.6/2.5 | 1.6/2.6 | **15.4/11.9** | 0.3/0.3 | 0.4/0.3 |
| Phainopepla *(Phainopepla nitens)* | 722 | 54 | 6.0/5.1 | 16.0/7.9 | 3.9/1.1 | 1.2/2.9 | 10.9/6.0 | 16.8/20.4 | 6.8/8.3 | 3.7/16.8 | **33.7**/29.9 | 7.1/6.9 | 0.9/1.2 |
| Cactus Wren *(C. brunneicapillus)*[f] | 626 | 71 | **53.0/16.4** | **11.1**/5.7 | **6.9**/4.7 | **4.9**/9.1 | **10.6**/4.5 | **17.3/15.8** | **18.2/16.7** | **4.1**/3.0 | **10.8**/3.7 | **16.0/36.7** | 0.9/1.5 |
| Northern Mockingbird *(Mimus polyglottos)* | 530 | 44 | **21.0**/8.4 | **15.9**/12.2 | 4.1/8.7 | 5.9/10.4 | **18.8/23.8** | **24.1/23.5** | **5.3**/1.2 | **8.6**/5.0 | **14.4**/10.9 | 3.1/4.4 | 0.4/0.2 |
| Loggerhead Shrike *(Lanius ludovicianus)* | 489 | 48 | **48.5/10.9** | **18.8/18.2** | **4.5/4.1** | 2.0/**2.4** | **19.1/14.3** | **20.2/13.8** | **6.9/2.0** | 1.7/**0.5** | **18.6/11.3** | **8.1/33.3** | 0.4/0.8 |
| Verdin *(Auriparus flaviceps)* | 397 | 49 | **66.2/20.3** | **20.2**/4.0 | **6.9**/8.9 | **3.9**/6.9 | **18.6**/4.5 | **19.4**/2.9 | **7.4/39.0** | 2.3/**15.6** | **19.6**/5.3 | 1.8/**12.9** | 0.4/4.9 |
| Black-tailed Gnatcatcher *(Polioptila melanura)* | 317 | 26 | **33.2**/5.8 | **22.8/24.0** | 4.7/10.2 | 3.4/10.3 | **18.8**/8.5 | **19.2**/6.5 | 4.2/12.5 | 0.9/7.2 | **24.0**/10.3 | 1.9/10.5 | 0.4/1.4 |

[a] Mean elevation within study system weighted by abundance.

[b] The nine environmental variables are expressed as percentages of the sum of independent effects. Bold indicates statistical significance ($P < 0.05$) based on randomization tests.

[c] LL sum is the sum of independent effects, which is the difference between the log likelihood of the full model and the null model. Bold indicates statistical signficance of the full model based likelihood ratio tests ($P < 0.05$).

[d] Biotic:climate is the mean relative effect of biotic habitat variables (structure and floristics) divided by the mean relative effect of climate variables (temperature and precipitation).

[e] *Callipepla californica/gambelii*: two interbreeding species combined for this analysis.

[f] *Campylorhynchus brunneicapillus*

## Chapter 2: Elevational Shifts in Breeding Bird Distributions Over a 26-year Period in a Southern California Desert Region

ABSTRACT

The biogeographical distribution of a species is generally limited by the set of environmental conditions (ecological "niche," including climate and habitat) to which the species is best adapted. Distribution limits often occur at well-defined points along ecological gradients, such as temperature isotherms or transition zones between habitat types. If limiting environmental conditions change, then populations at distribution margins should show evidence of expansion or retraction in association with that change. Testing for distributional shifts was performed along an arid elevation gradient in the Santa Rosa Mountains of southern California that is undergoing rapid climate change (locally, annual mean maximum temperature at the low end of this gradient has increased by 3.8°C since 1962). Increasing temperatures and aridity in this system are expected to cause upward shifts in elevational distributions. Over the past 26 years, five species (out of 28 tested) showed statistically significant distribution shifts, all upward in elevation. The average elevational shift for all 28 species was an increase of 116 m. Low-elevation desert species were most likely to show upward shifts. These results reveal that very rapid shifts in avian distributions may be associated with climate change, which will have profound implications for this arid ecosystem. Management strategies will need to incorporate this rapid dynamism into future conservation efforts.

## INTRODUCTION

Biogeography, or the spatial distribution of species, is a fundamental aspect of ecology and evolution, and understanding distribution change is essential to conservation and management. Across the range of a species, locations with higher abundances tend to be associated with more favorable conditions (the adaptive ecological "niche" of a species), while abundances tend to taper off toward range limits where conditions become unfavorable (Brown et al. 1995, Brown et al. 1996). In vagile organisms such as birds, the behaviors of habitat selection and territoriality largely determine distribution, and are expected to link adaptive traits of individuals to suitable habitat. When there are no barriers to dispersal, range limits are often set by biotic interactions, or by physiological or reproductive constraints directly or indirectly associated with climate. Consequently, species often show strong distributional patterns when surveyed along latitudinal and, especially, elevational gradients because of climatic differences. In birds, climate may be a direct limiting factor on distributions when associated with a species' physiological temperature tolerance limits, and it may also affect species' distributions indirectly through its influence on patterns in vegetation and resource availability. Geographic-scale studies of birds often identify climate as an important range boundary predictor (e.g., Root 1988, Bohning-Gaese and Lemoine 2004), while vegetation structure and composition are often identified as important predictors of bird distribution and abundance locally (Cody 1985, Wiens 1989, Block and Brennan 1993).

To the extent that species distributions reflect climatic limitations, distributions are expected to shift in response to climate change. For example, if average temperatures increase, then distributions are expected to expand where a species is cold-limited, and retract where it is heat-limited. Many predicted and observed changes in species' distributions have been linked to climate change. Poleward latitudinal range expansions are well-documented and demonstrate a 'fingerprint' of global warming (Walther et al. 2002, Root et al. 2003, Parmesan and Yohe 2003, Parmesan 2006). However, range retractions and elevational shifts are less well known (Shoo et al. 2006, Thomas et al. 2006). Strong climatic gradients can be found with changes in elevation over a relatively short distance, and thus provide a potentially sensitive system for detecting distribution shifts in association with climate change. Recent upward elevational shifts in species assemblages consistent with climate change effects have been reported for vascular plants (Walther et al. 2005, le Roux and McGeouch 2008, Lenoir et al. 2008, Kelly and Goulden 2008), butterflies (Konvicka et al. 2003, Franco et al. 2006, Wilson et al. 2007), reptiles and amphibians (Raxworthy et al. 2008), and small mammals (Moritz et al. 2008); but only inconsistent shifts have been reported for birds (Archaux 2004). Fine-scale studies of elevational shifts in birds are greatly needed but are lacking (Sekercioglu et al. 2008). Ideally, tests of elevational shifts should also be linked to mechanistic studies that determine how climate change impacts the demography of local populations, and how that varies among regions and species.

Elevation-based studies usually address climate impacts on high-elevation montane species rather than low-elevation desert species, and predictions of the effects of climate

change tend to emphasize extinction risk due to warmer temperatures at high-elevation sites (e.g., Thomas et al. 2006). Although it is generally thought that deserts will be relatively little affected by global warming (e.g., Sala et al. 2000, Thomas et al. 2004), little is known about biological responses to climate change in arid ecosystems. Desert species are strongly responsive to variation in precipitation, and may be particularly sensitive to changes in both temperature and precipitation due to interaction. Yet, how climate parameters change, and how ecosystems respond to those changes, may vary widely among regions. In the Chihuahuan Desert, the replacement of grassland by desert scrub has been attributed to an increase in winter precipitation (Brown et al. 1997). The desert regions of southern California are generally predicted to become warmer and drier, and variation in extreme events such as floods and droughts is expected to increase (e.g., Hayhoe et al. 2004, Seager et al. 2007). In deserts, although interannual variance in productivity associated with variation in rainfall tends to be high, increasing variance in annual rainfall can reduce population viability (survival and reproduction) by intensifying droughts (Saltz et al. 2006). Extinctions of desert bighorn sheep (*Ovis canadensis*) populations in California have been more likely at lower, more arid locations (Epps et al. 2004). In southern California, temperature strongly decreases with elevation while precipitation increases, but higher-elevation areas are relatively limited in extent and species-rich. Thus, if desert species need to shift upward in elevation, they may be restricted by limited space and competition.

Along a desert-to-mountain transition, distribution shifts of both desert and montane species can be tested simultaneously. To test for distribution shifts in association with

climate change, current distributions of breeding birds were quantified along a desert-to-mountain elevational gradient in southern California that is undergoing rapid climate change, and compared to data collected 26 years ago. A warmer, more arid climate is predicted to cause an upward elevational shift in distributions of both desert and montane species. For desert species, the upper elevational limit is expected to advance upward, while for montane species, the lower elevational limit is expected to retract upward. Here, the results are presented as a case study followed by a discussion of the possible implications of climate change for desert ecosystems, and suggestions for research needs and management strategies.

## METHODS

The study was conducted at the "Deep Canyon Transect" located at the Philip L. Boyd Deep Canyon Desert Research Center, part of the University of California Natural Reserve System, on the north- and east-facing slopes of the Santa Rosa Mountains in central Riverside County, California (Fig. A.1). The Deep Canyon Transect spans an elevation range from near sea-level to 2600 m over a distance of 35 km along the transition between the Peninsular Ranges and Colorado Desert. The Peninsular Ranges, which include the Santa Rosa Mountains, run north-south and form a rain shadow for the Colorado Desert to the east. The Colorado Desert is an extension of the Sonoran Desert, and includes areas that rank among the hottest, driest places on earth (Meigs 1953, UNEP 1997). The vegetation varies from Sonoran desert scrub at lower elevations, to chaparral

and pinyon-juniper woodland at mid-elevations, up to mixed coniferous woodland at upper elevations (Fig. 2.1).

A series of plot transects, each typically one km long, were established along the elevation gradient in 1979 and were systematically surveyed as walked transects with numbers of all vertebrates recorded (Mayhew 1981, Weathers 1983). In spring of 2005–2007, using the same methods, surveys were repeated at 15 of the existing plot transects within an elevation range of 200–2400 m and compared to data collected at these same locations during the first three years of surveys, 1979–1981, using only morning surveys with good weather conditions. The analyses were restricted to 28 breeding bird species. Species were excluded that were rare, non-breeding migrants, wide-ranging foragers (e.g., swifts), not always identified to species (e.g., hummingbirds), or completely absent during one of the two survey periods. Although the elevation ranges and distribution limits varied widely by species, species were categorized as "desert" if they tended to be more restricted to lower-elevation sites in this study area (with an upper limit distribution margin falling within this transect) or "montane" if they tended to be more restricted to higher-elevation sites (with a lower limit distribution margin falling within this transect).

Temperature and precipitation data from local weather stations were analyzed for trends. Data were obtained from two weather stations for comparison: Boyd Deep Canyon Desert Research Center, elevation 292 m (M. Fisher *pers. comm.*), and Idyllwild, elevation 1640 m (WRCC 2007). Long-term trends were tested for maximum temperature (yearly averages of mean monthly maximum temperatures), minimum

temperature (yearly averages of mean monthly minimum temperatures), and precipitation (July to June rain-year). To compare cumulative precipitation between the two survey periods, precipitation was summed over a five-year period (each period containing the three survey years plus two preceding years).

To test for distribution shifts, methods were used that were robust to any differences in absolute abundance between the two time periods that might have arisen, for example, due to observer differences. For each species, abundance was calculated as the average number of birds detected over a one-km transect for each of the 15 sites, for each three-year period. A weighted mean elevation was calculated for each species for each three-year period as the sum of elevations the species was present at, each multiplied by the abundance of that species at that site, and divided by the sum of abundances for that species. Proportion of cumulative abundance was calculated for each species at each site as follows: (1) Abundance for a site is the average number of birds observed during that three-year period at that site, (2) Cumulative abundance sums the abundance at a site with abundances at all sites lower in elevation during that period, (3) Proportion cumulative abundance is cumulative abundance for that site divided by the total cumulative abundance of the species observed during that period at all 15 sites. A Kolmogorov-Smirnov test was used to test for differences in the cumulative elevational distribution of individual species between the two periods and a paired-sample *t*-test was used to test for upward elevational shifts in weighted mean elevations at the community level. Three community groups were considered: all species, desert species alone, and montane species alone.

## RESULTS

In the desert (Boyd Deep Canyon Desert Research Center, elevation 292 m), mean maximum temperature increased by 3.8°C from 1962 to 2006 while there was no change in mean minimum temperature (Fig. 2.2). The increase in mean maximum temperature was even greater during the main breeding season when surveys were conducted: 5.0°C since 1961 ($r^2$ = 0.48, March to June). In contrast, at a montane site near the upper end of the transect (Idyllwild, elevation 1640 m), there was no trend in the mean maximum temperature, but the mean minimum temperature increased 1.7°C from 1960 to 2006 ($r^2$ = 0.39). In the desert, there was no long-term trend in precipitation over the 45 years from 1962 to 2007, but the most recent survey period, 2003–2007, had 44% less cumulative precipitation than the survey period 26 years ago, 1977–1981 (each period containing the three survey years plus two preceding years, using July to June rain-years).

To test for elevational shifts in distributions, the elevational distributions of bird species were compared between the two three-year time periods at Deep Canyon, 26 years apart. Five individual species (out of 28 tested) showed statistically significant shifts in their cumulative elevational distributions (K-S test, $P \leq 0.05$, $n = 15$) (Fig. 2.3, Table 2.1). Of these, all had an upward shift in their weighted mean elevation, with an average increase of 496 m. Moreover, there was an upward elevational shift in the avian community as a whole (paired-sample *t*-test, $P < 0.01$, $n = 28$ species). The average weighted mean elevation for all 28 species increased by 116 m. Species categorized as "desert" were more likely than those categorized as "montane" to show upward

elevational shifts (paired-sample *t*-test, $P < 0.05$, $n = 14$), with an average increase of 171 m, while montane species were less likely, but the average direction of shift was still upward in elevation, with an average increase of 60 m (paired-sample *t*-test, $P = 0.12$, $n = 14$).

## DISCUSSION

These results suggest that significant elevational shifts in breeding bird distributions are possible over a relatively short time. The upward shifts are consistent with expectations given the warmer, drier conditions now vs. 26 years ago. Compared to montane species, desert species were more likely to show upward shifts. These distribution shifts occurred in a diverse group of breeding bird species, each likely to have a different set of direct and indirect ecological links to climate. Response to temperature and precipitation can be direct (e.g., mortality and nest timing), or mediated through biotic factors linked to climate (e.g., habitat and food availability). In desert birds, physiological adaptations to heat and aridity likely involve decreases in metabolic rates and water loss (Tieleman and Williams 2000). Increasing maximum temperatures at desert sites can exceed tolerance limits, while increasing minimum temperatures at montane sites can improve suitability. Drought is known to cause reproductive failure in many bird species, even in relatively arid environments (e.g., Bolger et al. 2005). Many bird species are associated strongly with certain habitats, and there is a suggestion that vegetation is similarly shifting upward in this area (Kelly and Goulden 2008). This is

likely associated with recent die-off of desert shrubs at low elevations (Miriti et al. 2007). Thus although changing climate can have direct effects on species distributions, biotic interactions (such as species-habitat relationships) can amplify the effects of climate change if one component of the relationship is more sensitive than another. Therefore biotic interactions should also be an important consideration in predictive distribution modeling (Preston et al. 2008).

In this study system, desert species were especially likely to show upward elevational shifts. Although it is generally thought that desert species will be relatively little impacted by global warming because desertification will create more desert habitat (e.g., Sala et al. 2000, Thomas et al. 2004), desert species are likely to be closer to their limits of temperature and precipitation tolerance than species of humid habitats. Although some desert species may be able to adapt to further increases in temperature and aridity within their current range, it is unlikely that adaptive evolutionary processes can keep pace with the high rate of temperature increase in this system. Results from the North American Breeding Bird Survey indicate decreasing population trends overall for the Sonoran and Mojave deserts from 1966 to 2007 (Sauer et al. 2008), but more study is needed on the causes of these population declines. With increasing desertification throughout the region, relatively mobile species such as birds may be able to shift into new areas as they become habitable. However, in southern California, higher elevations are limited in extent, and in the more mesic coastal areas, natural habitats that might otherwise undergo conversion to desert vegetation types are highly fragmented by urbanization. In addition, there is unlikely to be any “backfill” or immigration by new species if lower elevations

become increasingly inhospitable to current desert species—the Colorado Desert is already one of the hottest and driest areas on earth.

Predictions or forecasts from most climate-change models are averaged over large geographical spaces and long periods of time. However, organisms and their habitats are impacted by local temperature, precipitation, and short-term extreme events. The distributional shifts observed in this study system over a 26-year period could be partly due to short-term climate fluctuations, but this rapid dynamism suggests that longer-term effects can be even more pronounced. Elevational distributions of birds were found to be relatively static over a three-year period (Chapter One), which further suggests that these 26-year shifts are due to longer-term changes. The strong differences in temperature with opposing trends observed in this study system over a short distance are likely to have very different biological effects. Thus, climate-change predictions at a much finer scale are needed to manage biodiversity for these challenges. Furthermore, although trends in temperature and precipitation extremes are less well known, they are even more likely to be biologically relevant than annual averages.

Understanding distributional change is essential to conservation management. As species shift across management boundaries, management perspectives must encompass broader spatial and temporal scales. Species' distributions naturally shift over time, but little is known about the rates and mechanisms involved. Additional monitoring of distribution shifts is needed along elevational gradients and at other transition zones where distribution limits occur. Ideally, monitoring should be linked to mechanistic studies as well. Both ecological and evolutionary studies of distribution limits are greatly

needed (Hoffman and Blows 1994, Parmesan et al. 2005). Management strategies will need to incorporate dynamic processes into future conservation efforts and encompass broader spatial and temporal scales across management boundaries.

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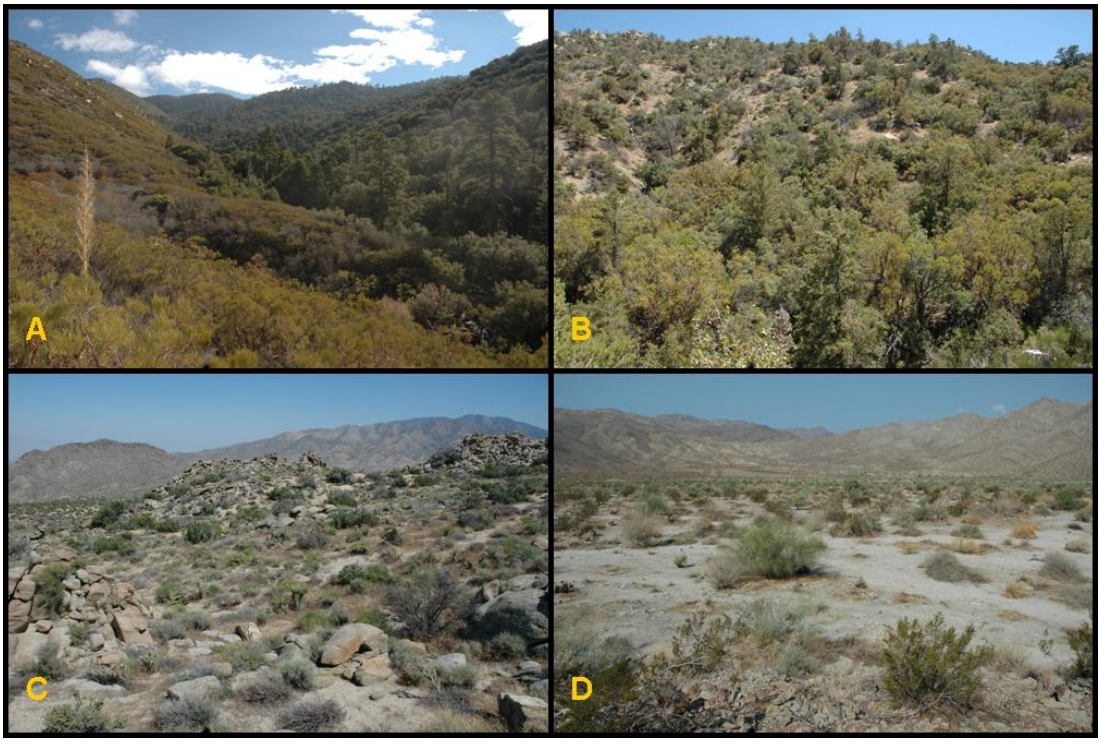


**Figure 2.1** The range of vegetation types surveyed along the Deep Canyon Transect: A. chaparral and oak-conifer woodland (elevation 1800 m), B. chaparral and pinyon-juniper woodland (elevation 1200 m), C. mid-elevation desert scrub (elevation 900 m), Sonoran desert scrub and palo verde wash (elevation 200 m).

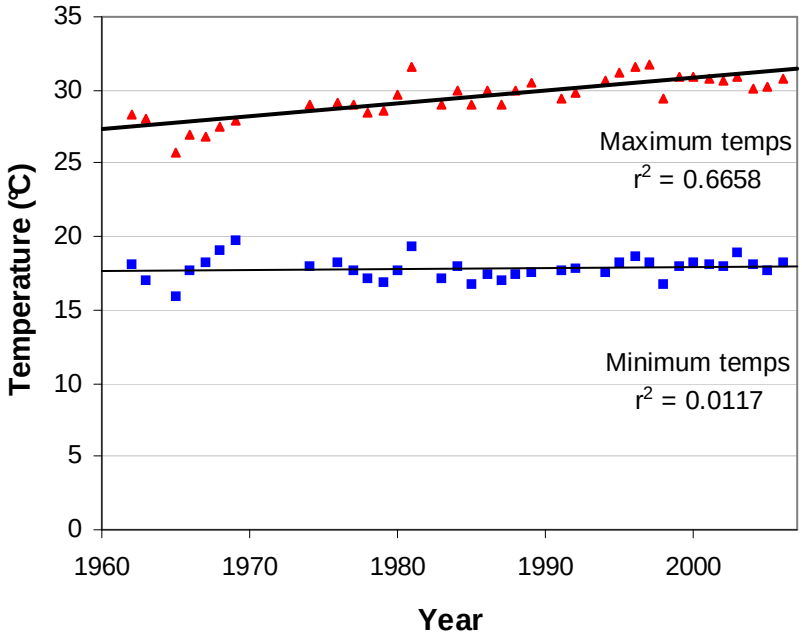


**Figure 2.2** Annual mean maximum and minimum temperature trends in the desert, 1962–2006 (Boyd Deep Canyon Desert Research Center, elevation 292 m). Values are daily maximum and minimum temperatures, averaged for each year. $r^2$ denotes proportion of variance in temperature statistically explained by linear regression on year.

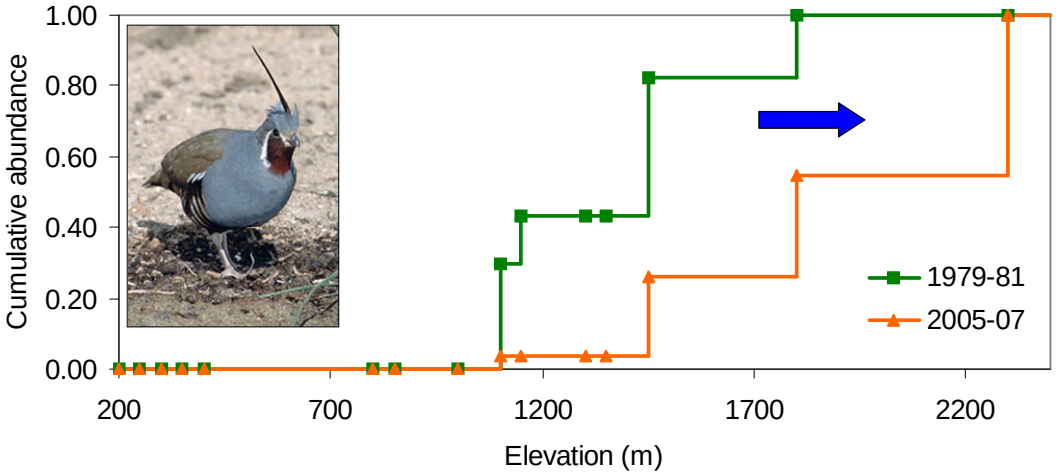


**Figure 2.3** Upward shift in the elevational breeding distribution of Mountain Quail (*Oreortyx pictus*) over a 26-year time period, Boyd Deep Canyon Desert Research Center, Riverside County, California. Elevational distributions are shown for the two time periods (1979–1981 green/squares vs. 2005–2007 orange/triangles). For each time period, the graph shows the proportion of cumulative abundance of Mountain Quail observed at each of the 15 sites as elevation increases, from 200 to 2400 m. Because observations are normalized to the total number of individuals observed, cumulative abundance at the highest elevation site will always be 100%. In 2005–2007, lower proportions of Mountain Quail were found at lower elevation sites compared to 1979–1981 (shown by the rightward shift in the distribution), indicating that there was an upward shift in the elevational distribution of abundance for this species.
(Photo credit: Peter LaTourrette/birdphotography.com)

**Table 2.1** Species in order of weighted mean elevation (m) in 1979–1981 at 15 sites, Boyd Deep Canyon Desert Research Center, Riverside County. "D" (desert) indicates that the species was more common at low elevation sites in this study system, while "M" (montane) indicates that the species was more common at higher elevation sites. Elevational shift is the difference in weighted mean elevation between the two time periods (1979–1981 vs. 2005–2007). Positive values indicate upward elevational shifts. The Kolmogorov-Smirnov test was used to compare the cumulative elevational distributions between the two time periods.

| Species | Desert/ Montane | Weighted mean elevation (m) 1979-1981 | Elevational shift 2005-2007 | Kolmogorov-Smirnov test |
|---|---|---|---|---|
| Black-tailed Gnatcatcher (*Polioptila melanura*) | D | 245 | 6 | Ns |
| Verdin (*Auriparus flaviceps*) | D | 248 | 81 | Ns |
| Phainopepla (*Phainopepla nitens*) | D | 269 | 562 | $P \leq 0.05$ |
| Northern Mockingbird (*Mimus polyglottos*) | D | 270 | 293 | Ns |
| Say's Phoebe (*Sayornis saya*) | D | 270 | 260 | $P \leq 0.05$ |
| American Kestrel (*Falco sparverius*) | D | 365 | 755 | $P \leq 0.05$ |
| California-Gambel's Quail (*C. californica-gambelii*)[a] | D | 487 | 93 | Ns |
| Cactus Wren (*C. brunneicapillus*)[b] | D | 530 | 226 | Ns |
| Loggerhead Shrike (*Lanius ludovicianus*) | D | 616 | 29 | Ns |
| Rock Wren (*Salpinctes obsoletus*) | D | 638 | 65 | Ns |
| Ladder-backed Woodpecker (*Picoides scalaris*) | D | 820 | 307 | $P \leq 0.05$ |
| Black-throated Sparrow (*Amphispiza bilineata*) | D | 914 | –251 | Ns |
| Scott's Oriole (*Icterus parisorum*) | D | 929 | –44 | Ns |
| Bushtit (*Psaltriparus minimus*) | M | 1165 | 309 | Ns |
| Greater Roadrunner (*Geococcyx californianus*) | D | 1216 | 9 | Ns |
| California Towhee (*Pipilo crissalis*) | M | 1262 | –10 | Ns |

**Table 2.1** Continued.

| Species | Desert/ Montane | Weighted mean elevation (m) 1979-1981 | Elevational shift 2005-2007 | Kolmogorov-Smirnov test |
|---|---|---|---|---|
| Western Scrub-Jay (*Aphelocoma californica*) | M | 1290 | 48 | Ns |
| Pinyon Jay[c] (*Gymnorhinus cyanocephalus*) | M | 1298 | –2 | Ns |
| Bewick's Wren (*Thryomanes bewickii*) | M | 1351 | 64 | Ns |
| Mountain Quail (*Oreortyx pictus*) | M | 1370 | 594 | $P \leq 0.05$ |
| California Thrasher (*Toxostoma redivivum*) | M | 1424 | –88 | Ns |
| Oak Titmouse (*Baeolophus inornatus*) | M | 1509 | –38 | Ns |
| Spotted Towhee (*Pipilo maculatus*) | M | 1597 | –53 | Ns |
| Wrentit (*Chamaea fasciata*) | M | 1598 | 47 | Ns |
| Black-chinned Sparrow (*Spizella atrogularis*) | M | 1739 | –14 | Ns |
| Northern Flicker (*Colaptes auratus*) | M | 2215 | –59 | Ns |
| House Wren (*Troglodytes aedon*) | M | 2314 | 66 | Ns |
| Mountain Chickadee (*Poecile gambeli*) | M | 2336 | –25 | Ns |

[a] Data combined for two hybridizing species (*Callipepla californica* and *Callipepla gambelii*).
[b] *Campylorhynchus brunneicapillus.*
[c] Pinyon Jays were highly localized at intermediate elevation sites.

## Chapter 3: Avian Breeding Success Along a Desert Elevational Gradient


ABSTRACT

Distribution margins of species often occur on ecological gradients, along which range limits may contract or expand over time. If distributions reflect an adaptive "niche", then habitat quality should decline at the margin. Along an arid scrub elevational gradient (200–1800 m) in southern California that is undergoing a gradual warming trend, we related abundance patterns of bird species to reproductive success from 2006–2008. Across species, individual productivity tended to increase with elevation regardless of whether the species' lower or upper elevation limit occurred along the study gradient. Differences in productivity were best explained by nest initiations rather than by nest survival because fewer nesting attempts were made during the drier years of the study. Comparing two focal species, the Black-chinned Sparrow (*Spizella atrogularis*, common in higher-elevation chaparral), and the Black-throated Sparrow (*Amphispiza bilineata*, common in lower-elevation desert scrub), variation among years was stronger for the Black-throated Sparrow, mostly due to a lack of nesting attempts at lower elevations during the drier years of the study. These results support the prediction that species will tend to shift upward in elevation in association with increasing temperature and aridity, due both to retracting lower margins and advancing upper margins.

## INTRODUCTION

The distribution boundary of a species can be described as a spatial gradient in probability of occurrence that may shift over time (Fortin et al. 2005). Various approaches have been used to relate boundaries to their possible functional significance in terms of the mechanisms of range limitation. One approach is to distinguish between an empirical boundary, marking the absolute limit of occurrence, and a functional boundary, marking the limit of habitat suitability (Emlen et al. 1986, Pulliam 2000). Habitat suitability (or a species' ecological "niche") is defined as the set of environmental conditions, both biotic and abiotic, for which the population growth rate is greater than or equal to zero. If the distribution of a species is niche-limited, habitat quality is expected to decline toward the margins of the distribution where both abundance and fitness should be reduced. However, habitat quality is usually only indirectly scored by occurrence or abundance, rather than by fitness (Van Horne 1983). Tests of functional differences in terms of habitat quality are needed in marginal areas. Although many studies have attempted to link population density and habitat type to reproductive success, especially in birds (Bock and Jones 2004), few studies have focused on distribution boundaries (Hoffman and Blows 1994, Parmesan et al. 2005) where limiting mechanisms may strongly differ from elsewhere in the range. The objective of this research is to determine the relative strength of niche-limitation on distribution boundaries by testing for differences in breeding success of birds along a marginal distribution gradient.

Many distribution boundaries occur along elevational gradients where various interactions and trade-offs can affect fitness. In birds, many trade-offs have been identified between annual fecundity and adult survival, which are often related to food limitation or predation (Martin 1995). At higher elevations, there may be a tendency toward reduced fecundity and increased parental care both among species (Badyaev and Ghalambor 2001) and within species (Bears et al. 2009). However, along a desert elevational gradient where aridity becomes extreme at lower elevations, there may be a tendency toward reduced fecundity, reduced parental effort, and greater survival at lower elevations (Tieleman et al. 2004). The relative influence of environmental factors and predation on these trade-offs remains unclear, and among species, it may be strongly dependent on the direction of the distribution margin with respect to the elevation gradient. Few studies have focused on trade-offs at distribution margins, which is where limiting factors should be most closely linked to range limitation, and where there should be evidence of linkage between range shifts and climate change.

For many bird species, territorial choices can be especially critical during the breeding season, both because the pair and their offspring are dependent on local resources throughout the nesting cycle, and because nest predation is particularly common for open-cup nesters (Martin 1992). Breeding success is dependent on many factors, but overall productivity should be most closely related to numbers of fledglings produced within a season. Environmental factors related to resource availability can have a strong influence on nest initiation (e.g., Bolger et al. 2005) while predation (or catastrophic

weather) should have a strong influence on nest survival. If breeding distributions are niche-limited, then limiting factors should be accentuated near distribution boundaries. To test this hypothesis we measured nest initiations, nest survival rates, and fledgling production in multiple species along a desert–montane shrubland elevational gradient (200–1800 m). We compared species that were more common at higher elevations (with a lower limit to distribution along the study gradient) to species more common at lower elevations (with an upper limit to distribution along the study gradient). Our prediction is that breeding success should be reduced toward distribution margins, which will show a reversed pattern along the elevation gradient between the two groups of species.

## METHODS

The study system is an arid scrub gradient between the Peninsular Mountains and Colorado Desert in southern California (Fig. A.1), encompassing the transition between chaparral at higher elevations and Sonoran desert scrub at lower elevations. We used PRISM data (PRISM Group, Oregon State University, http://www.prismclimate.org, accessed 22 March 2009) to generate an approximation of climatic conditions during the three survey years, and compared them to 40-year means (1968–2008). For 26 sites along the elevation gradient we calculated yearly cumulative precipitation during the July to June rain-year, and the mean monthly minimum and maximum temperatures.

To determine elevational distributions, bird abundances were established by point-transect sampling at 176 points, each at least 500 m apart and spanning an elevational range of 200–1800 m. Point counts were conducted over a four-year period (2005–2008) during the breeding season (March–June), and during morning hours with fair weather conditions. Point count duration was 15 minutes. Point counts were repeated 2–3 times within years and averaged within and across years. Non-territorial species frequently seen as migrants (e.g., warblers) or with highly dispersive foraging or flocking (e.g., swifts and doves) were not included.

To monitor breeding activity, we established 26 study plots along the elevation gradient at the "Laguna" study area clustered into three habitat categories: chaparral, transition, and desert scrub. Each study plot was approximately 24 ha in area (1200 m x 200 m). We conducted weekly censuses and nest monitoring at 22 plots throughout the breeding season from 2006–2008, and at four additional plots from 2007–2008 using standardized methods (Ralph et al. 1993). We monitored all nests found and recorded all fledglings observed. For two focal species, Black-chinned Sparrows (*Spizella atrogularis*) and Black-throated Sparrows (*Amphispiza bilineata*), we placed additional effort into finding all nests by mapping locations of territories weekly and monitoring each territory for evidence of breeding activity from vantage points that were unlikely to cause disturbance. Nest checks were as brief and unobtrusive as possible, at intervals of 3–8 days, and we avoided approaching nests during construction or egg-laying.

As an index of relative productivity, we calculated a fledgling index (proportion of fledglings relative to adults) based on total numbers of adults and fledglings present on each study plot estimated from point counts and weekly plot censuses. Plots where adults were absent or present only as an outlier were excluded from the analysis. We related the fledgling index to elevation and compared slopes among chaparral and desert scrub species using sign tests and log-linear analysis (Zar 1999).

To estimate daily nest survival probability, we only used nests for which final outcome was known, and we considered nests with nestlings within ~2 days of fledging to be successful. We generated a maximum-likelihood estimate of daily nest survival probability assuming constant daily survival rate using Program MARK, Version 5.1 (White and Burnham 1999, Rotella et al. 2004, Dinsmore and Dinsmore 2007). We used model selection methods (Burnham and Anderson 2002) to compare ten candidate models for nest daily survival rate of the two focal sparrow species. Parameters considered were: elevation, year (dummy coded), lay date, substrate (dummy coded), and nest height. Substrate was dummy coded as whether or not it was the most commonly used substrate by the species, which was chamise (*Adenostoma fasciculatum*) for Black-chinned Sparrows and cholla (*Cylindropuntia* spp.) for Black-throated Sparrows. To test for trends across species, we related the nest daily survival rate to elevation and compared slopes among chaparral and desert scrub species using a sign test. To test for the effect of elevation on nest survival across species, we compared logistic exposure models with and without elevation, controlling for year and species, and compared the slope and confidence interval for elevation between the two groups of species.

## RESULTS

As expected, higher-elevation chaparral sites were substantially wetter and cooler than lower-elevation desert scrub sites (Table 3.1). Across the three years (2006–2008), there was approximately 8.7 times more annual precipitation at the high end of the gradient (~1800 m) compared to the low end (~200 m). Mean maximum temperature (March to June) was lower by 22.5 °C while mean minimum temperature was lower by 15.7°C. All sites and years during the three-year study were below the 40-year precipitation means (Table 3.1). 2007 was near record drought conditions, while 2008 was closest to the 40-year mean. Average annual minimum and maximum temperatures tended to be negatively correlated with precipitation, and thus 2007 was also the warmest year.

Based on point-count estimates of abundance, 11 species were categorized as "chaparral" (more common at higher elevations with a lower distribution margin) and 11 species were categorized as "desert scrub" (more common at lower elevations with an upper distribution margin) (Table 3.2).

For most species, individual productivity increased with elevation, as seen by positive relationships between elevation and fledgling index when averaged across years (Table 3.2, sign test, $n = 22$, $P = 0.002$), with a slightly greater tendency by chaparral species to have positive relationships ($n = 11$, $P = 0.02$) compared to desert scrub species ($n = 11$, $P = 0.07$). For chaparral species, this relationship was in the expected direction, while for desert scrub species, it was opposite of the expected direction, with no effect of year (log-linear analysis on expected direction, species group $G^2 = 23.02$, df = 1, $P < 0.001$, year

$G^2$ = 0.06, df = 2, $P$ = 0.97, species group*year $G^2$ = 0.08, df = 2, $P$ = 0.96). However, the relationship between elevation and individual productivity varied among years for our two focal species (Fig. 3.1), and the total number of fledglings produced varied strongly among years with chaparral species producing twice as many fledglings in 2008 compared to 2007 (the two years with identical plot coverage), and desert species producing over six times as many fledglings in 2008 compared to 2007 (Table 3.2).

The number of nesting attempts varied among years, with 1.5 times as many nests found in 2008 compared to 2007 for chaparral species and almost twice as many nests found in 2008 compared to 2007 for desert scrub species (Table 3.2). This difference does not reflect differential nest-searching intensity—if anything, nest-searching was more intensive in the year in which fewer nests were found. There was no consistent directional relationship between elevation and nest survival rate across species (sign test, $n$ = 22, $P$ = 1.0), but nest sample size was low for most species (Table 3.2). Overall, the relationship between elevation and daily nest survival rate was weakly positive for both chaparral and desert scrub species when controlling for year and species, but there was no support for logistic exposure models with elevation added for chaparral species (Table 3.3) or for desert scrub species (Table 3.4). The confidence interval for the effect of elevation on a logit scale included zero, both for chaparral species ($\beta_{Elevation}$ = 0.20 x $10^{-3}$, SE = 0.76 x $10^{-3}$, 95% CI –1.3 x $10^{-3}$, 1.7 x $10^{-3}$), and for desert scrub species ($\beta_{Elevation}$ = 0.02 x $10^{-3}$, SE = –0.34 x $10^{-3}$, 95% CI –0.65 x $10^{-3}$, 0.69 x $10^{-3}$).

For our two focal species, there were differences both in the relationships between elevation and fledgling index (Fig. 3.1) and in the relationships between elevation and

nest survival (Fig. 3.2). Black-chinned Sparrows consistently had greater individual productivity in terms of fledgling index where birds were more abundant (at higher elevations), but with a slight improvement at lower elevations in 2008. Black-throated Sparrows, on the other hand, tended to have greater individual productivity where birds were *less* abundant (at higher elevations toward the distribution margin), and a stronger year effect with a large improvement in individual productivity at lower elevations in 2008 (Fig. 3.1). These trends in productivity were somewhat paralleled by nest survival, with little year effect for Black-chinned Sparrows, and a stronger interaction between year and elevation for Black-throated Sparrows with a reduction in nest survival rate at lower elevations in drier years (Fig. 3.2). However, the strong year effect in fledgling productivity of Black-throated Sparrows is better explained by nesting attempts than by nest survival. In the driest year of 2007, there was only a single nesting attempt at lower elevations where Black-throated Sparrows were most common, while 2008 had the greatest number of nesting attempts at lower elevations and earlier lay dates with a wider range (Fig. 3.3).

The differences in nest survival trends between the two species are corroborated by model selection results that show relatively low importance of elevation for nest survival of Black-chinned Sparrows with only the model including year+lay date slightly better supported than the null model (Table 3.5). In contrast, the substrate-only model received the best support for Black-throated Sparrows, but again, models including elevation performed poorly (Table 3.6).

For Black-chinned Sparrows, while lay date combined with year was relatively important for nest survival, there was also a suggestion of an interaction with year in terms of behavior. In the driest year of 2007, nesting shifted toward higher elevations compared to 2008, and lay dates were earlier at lower elevations in 2008 (Fig. 3.3). For both species, lay dates tended to be later at higher elevations, but that pattern was reversed for Black-chinned Sparrows in 2007 (Fig. 3.3). For Black-chinned Sparrows, breeding season length (lay-date range) appeared to be somewhat compressed at higher elevations, while for Black-throated Sparrows, breeding season length appeared to be compressed at lower elevations during drier years (Fig 3.3).

## DISCUSSION

For most species, individual productivity increased with elevation, which for chaparral species fit the expected pattern of niche-limited distributions with reduced breeding success toward the margin, but for desert scrub species was contrary to the expected pattern. However, productivity improved for desert scrub species at lower elevations during wetter years. Although nest survival somewhat paralleled productivity patterns, nest sample sizes were low for most species, and productivity appeared to have a stronger relationship with elevation than did nest survival. The relationship between elevation and nest survival was weak for our two focal species, Black-chinned and Black-throated sparrows. Differences in productivity were best explained by nest initiation rather than by

nest survival, especially for the Black-throated Sparrow, and lay date combined with year had some influence on nest survival of Black-chinned Sparrows.

The southern California desert regions are predicted to become warmer and drier over the next century, and variation in extreme events such as floods and droughts is expected to increase (Hayhoe et al. 2004). With these changes, upward shifts in elevational distributions of species are expected, but fine-scale studies of mechanisms along elevation gradients are needed (Sekercioglu et al. 2008). If breeding distributions are influenced by reproductive success, the greater productivity at higher elevations for both groups of species in this study and influence of year supports the prediction that upward elevational shifts will occur due to a warming and drying climate, with lower margins of chaparral species retracting and upper margins of desert scrub species expanding, and recent evidence suggests that such shifts are occurring in this system (Hargrove and Rotenberry in press).

Abundance patterns along elevation gradients have a long history of study (e.g., Whittaker 1967, Terborgh 1971), but few studies have included fitness parameters and fewer have attempted to link abundance patterns to fitness of populations at the margins of their distributions. Although abundance may not decline uniformly toward distribution margins across the entire range of a species (Sagarin and Gaines 2002), this is obviously scale-dependent, and declining abundance at margins may be more apparent where strong environmental gradients occur over short spatial gradients, such as along a steep elevational gradient. If distribution boundaries are mostly stochastic, or due to historical precedence, seasonal effects, dispersal limitation, or social effects independent of habitat

quality, then locations of distribution boundaries may be arbitrary with respect to adaptations. Alternatively, if distributions are niche-limited, then habitat quality should decline at the margin of a distribution, with associated reductions in fitness and abundance. Some examples of niche-limited margins have been previously documented, with a good example of marginal declines in both nest survival and productivity at both upper and lower elevation limits of Warbling Vireos (*Vireo gilvus*) in the Sierras (Purcell 2006), and declines in fitness toward margins of *Mimulus* in the Sierras (Angert and Schemske 2005). In the current study, abundance declined along the elevation gradient in opposite directions for chaparral and desert scrub species, but only chaparral species showed declines in productivity toward their margin. Along a desert elevation gradient, productivity may tend to be reduced at the lowest elevations for all species, which appeared to be the case in this study at least during dry years. In the Chihuahuan Desert, Pidgeon at el. (2003) also found that Black-throated Sparrows tended to have lower reproductive success at their lowest elevation sites where the birds were most common. Although this tendency could be reversed during cooler, wetter years, these findings support the prediction that distributions should tend to shift upward over time if the climate becomes warmer and drier, both for advancing and retreating margins (Thomas et al. 2006).

This study found that productivity tended to increase with elevation, regardless of adult abundance distribution along the gradient. This is contrary to other studies that found reduced productivity at higher elevations (e.g., Badyaev and Ghalambor 2001, Bears et al. 2009), but supports findings that productivity is reduced where conditions

become extremely arid (Tieleman et al. 2004). Since this study was along a relatively low elevation gradient, it suggests that birds at mesic mid-elevation sites (moderate climate) may tend to have the highest fecundity, which may also be associated with reduced adult survival and greater nest predation (Martin 1995). However, more studies are needed that relate marginal abundance patterns to trade-offs in fitness due to limiting environmental factors, and how those relationships change over time.

It is possible that high quality areas can have a surplus of adults, which would cause a decrease in the ratio of fledglings relative to adults. However, higher quality areas are still predicted to have greater fledgling ratios than marginal areas. For desert scrub species, no sites in this system had high territory density, and few unpaired birds were detected. For a few chaparral species, there were areas of high territory density and instances of unpaired birds. However, if this caused a reduction in the fledgling ratio, then our findings of marginal declines in fledgling ratio were even more strongly supported.

Nest predation is a key cause of nest failure for many passerines, so many studies focus on nest survival as a measure of reproductive success, yet this can be misleading in comparative studies (Murray 2000, Thompson et al. 2001), especially if nest attempts vary among compared study areas, species, treatments, or years. Nest attempts can be greatly reduced during drought years (e.g., Bolger et al. 2005), and could be an especially important source of variation in productivity at distribution margins, as found in this study. To adequately measure overall habitat quality and monitor how distribution limits may shift over time due to environmental change, multiple levels of measurement are

needed. Long-term intensive studies of individually-marked populations are especially valuable, but low-cost alternatives include territory-level estimates of reproductive success (Vickery et al. 1992) and fledgling indices (Buford and Capen 1999). Fledglings are highly detectable for many species, so the use of fledgling surveys as indices of productivity can be especially useful in systems where nests are difficult to locate or monitor. These alternative strategies may be especially useful in marginal systems and when combined with long-term monitoring of population abundance and environmental change.

Distribution margins have received relatively little study, but are likely to yield insights into distribution limits and the linkages between environmental change and distribution shifts (Thomas et al. 2001, Franco et al. 2006). In this system, individual productivity tended to increase with elevation regardless of the direction of the species' margin along the study gradient. These results support the prediction that upward elevational shifts will occur with increasing temperature and aridity, but long-term monitoring is needed.

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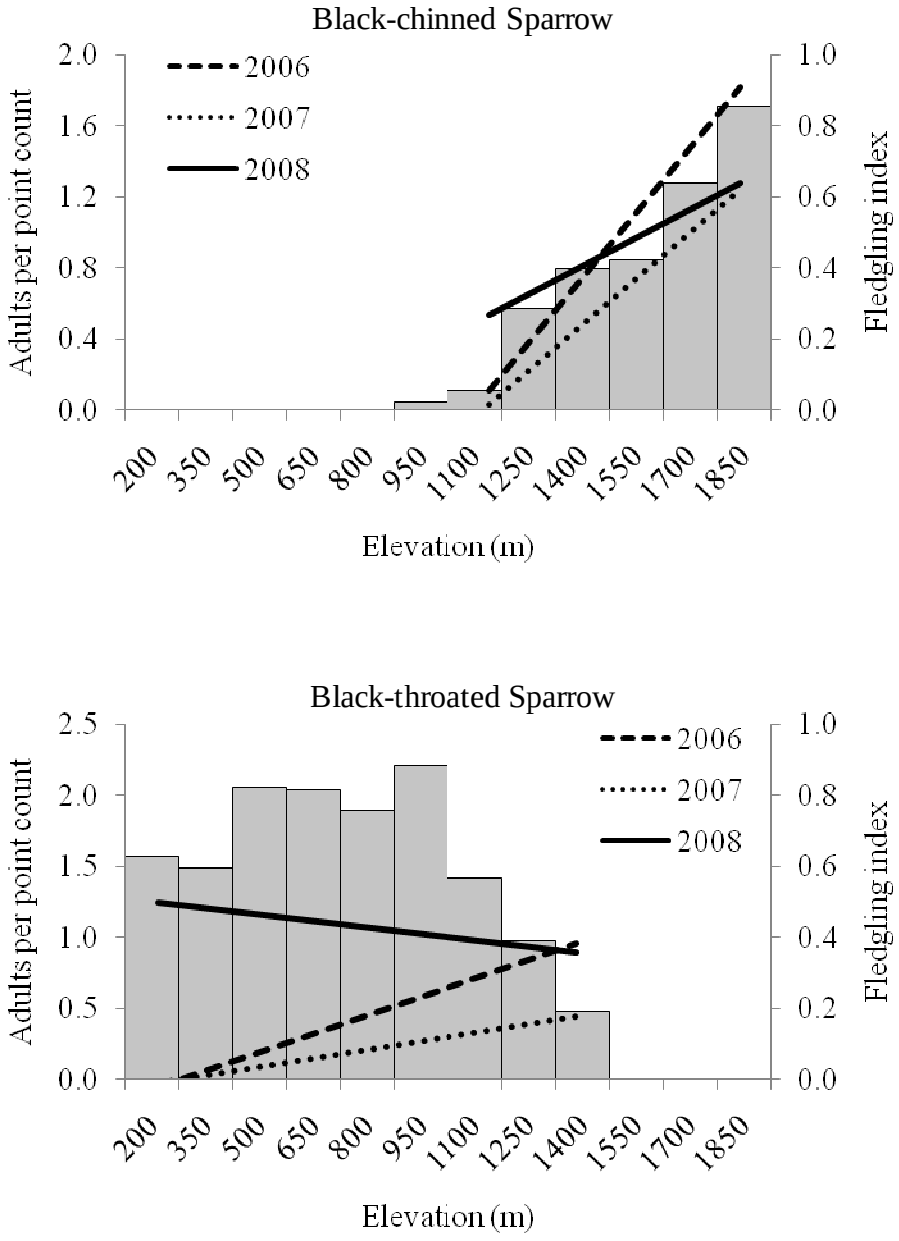


**Figure 3.1** Relationships between elevation, adult abundance (bars denote mean adults per point count, 2005–2008), and fledgling index (linear trends by year, 2006–2008) for Black-chinned Sparrows (top) and Black-throated Sparrows (bottom).

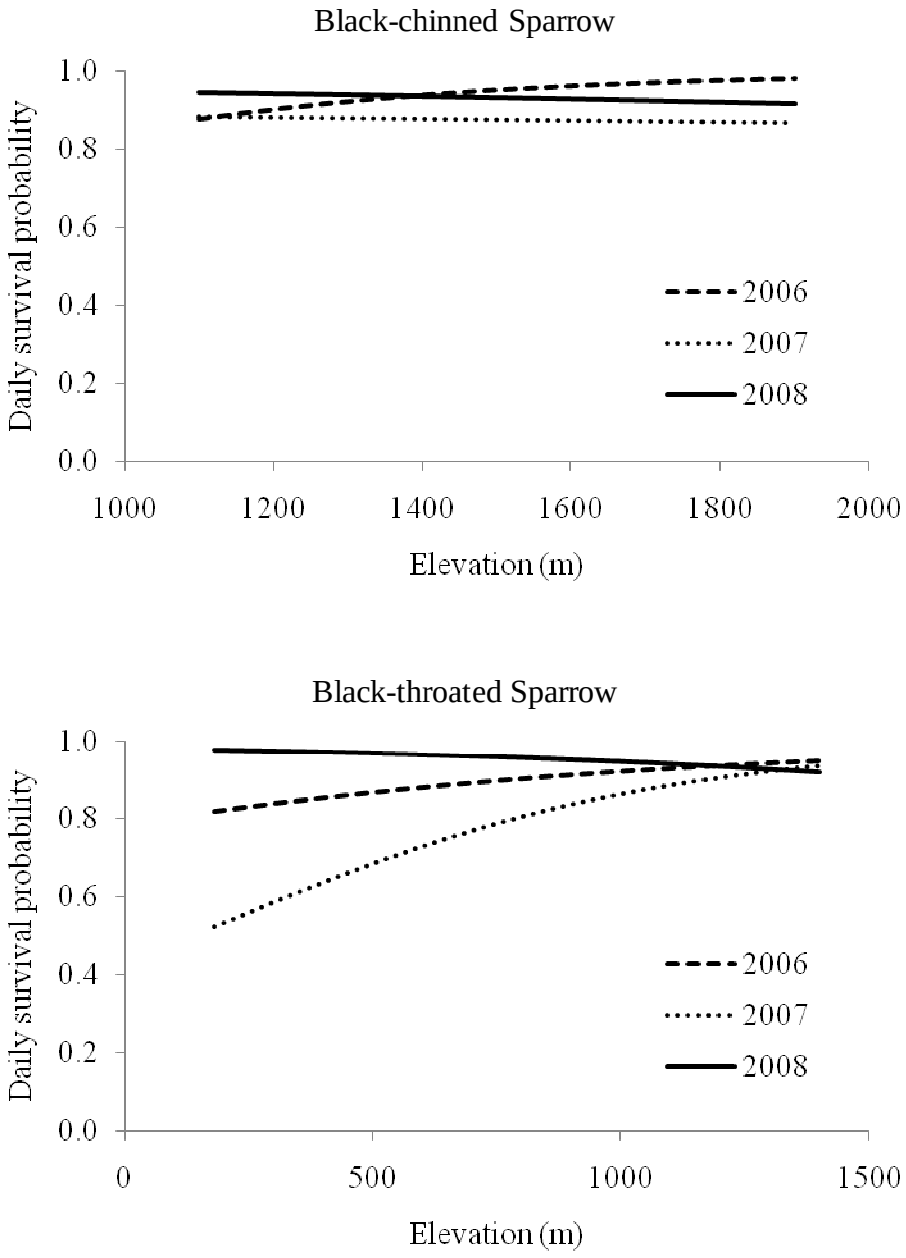


**Figure 3.2** Relationship between elevation and nest daily survival rate (logistic trends by year, 2006–2008) for Black-chinned Sparrows (top) and Black-throated Sparrows (bottom).

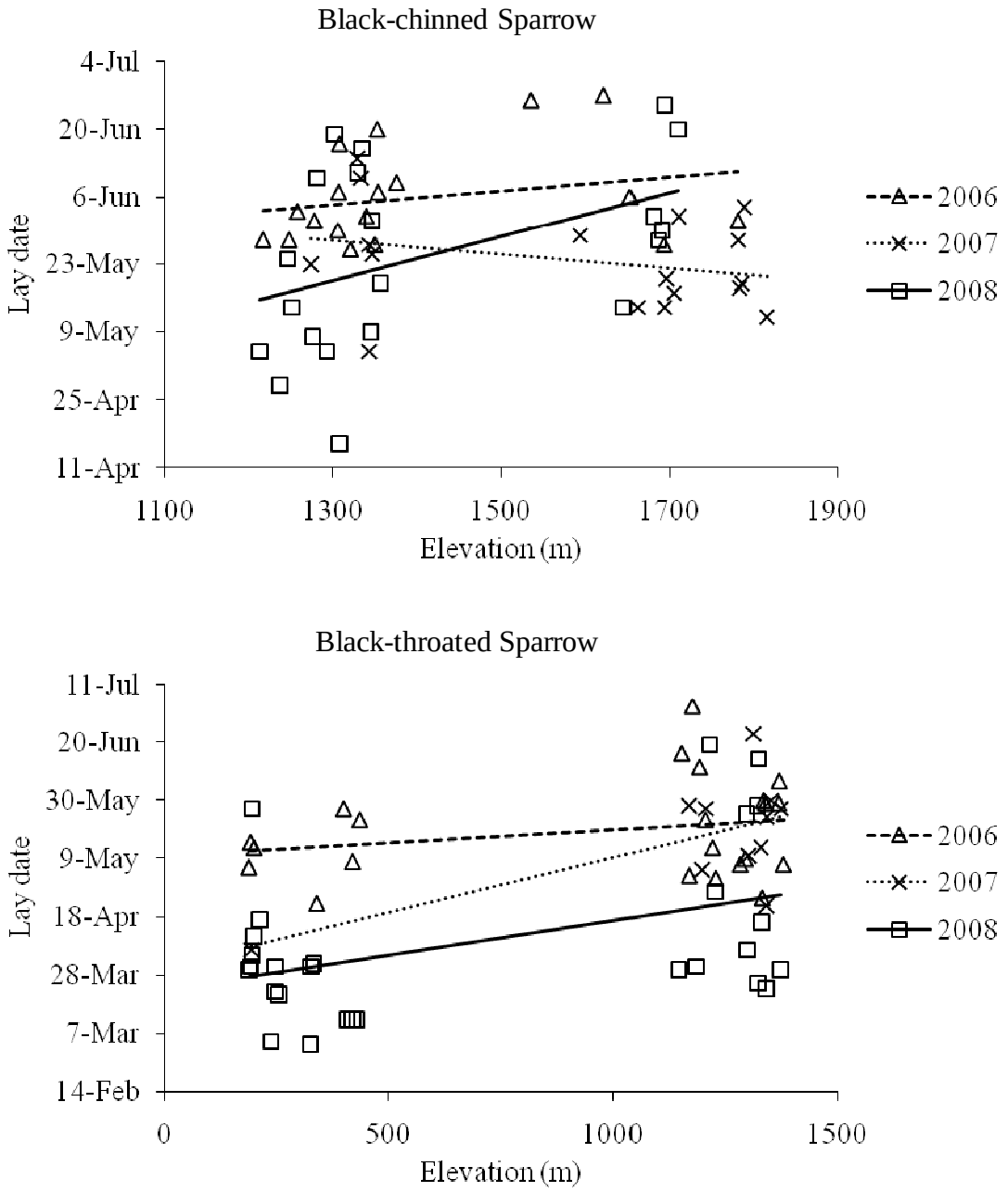


**Figure 3.3** Relationship between elevation and estimated lay date for Black-chinned Sparrows (top) and Black-throated Sparrows (bottom), 2006–2008.

**Table 3.1** Estimates of climatic conditions for both ends of the elevational gradient (1788 m and 228 m), comparing each of the three current survey years (2006-2008) to the 40-year means (1968-2008). Precipitation is the annual cumulative total from the previous July through June. Temperatures are monthly mean maximum and minimum, averaged over the months of March to June. (Data were obtained from PRISM Climate Group, Oregon State University, http://www.prismclimate.org, accessed 22 March 2009.)

| | Precipitation (mm) | | | | Maximum temperature (°C) | | | | Minimum temperature (°C) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Elev. (m) | 40-yr mean | 2006 | 2007 | 2008 | 40-yr mean | 2006 | 2007 | 2008 | 40-yr mean | 2006 | 2007 | 2008 |
| 1788 | 798 | 595 | 328 | 704 | 64.6 | 64.6 | 68.2 | 66.9 | 38.0 | 38.0 | 36.9 | 37.0 |
| 228 | 103 | 65 | 36 | 85 | 87.2 | 87.5 | 90.5 | 89.2 | 54.5 | 53.4 | 53.3 | 52.3 |

**Table 3.2** Relationships with elevation (positive or negative) for daily nest survival rates and fledgling indices of species with nests monitored or fledglings detected at a minimum of three study plots, 2006-2008. Species are listed in descending order by weighted mean elevation, and categorized into two groups: lower-elevation limited and upper-elevation limited. Not applicable ("na") refers to years in which there were fewer than three nests monitored or years in which there were fewer than two groups of fledglings detected.

| | Mean | 2006 | | | | 2007 | | | | 2008 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | elevation | Nests | | Fledglings | | Nests | | Fledglings | | Nests | | Fledglings | |
| Species | (m) | *n* | DSR | *n* | FI | *n* | DSR | *n* | FI | *n* | DSR | *n* | FI |
| Chaparral (lower-elevation limited) | | | | | | | | | | | | | |
| Black-headed Grosbeak *(Pheucticus melanocephalus)* | 1512 | 0 | na | 2 | + | 0 | na | 2 | + | 1 | na | 7 | + |
| Black-chinned Sparrow *(Spizella atrogularis)* | 1507 | 18 | + | 63 | + | 17 | – | 41 | + | 20 | – | 59 | + |
| Blue-gray Gnatcatcher *(Polioptila caerulea)* | 1499 | 2 | na | 3 | + | 2 | na | 0 | na | 6 | + | 2 | + |
| Oak Titmouse *(Baeolophus inornatus)* | 1487 | 1 | na | 1 | na | 1 | na | 4 | + | 1 | na | 10 | + |
| Spotted Towhee *(Pipilo maculatus)* | 1426 | 3 | + | 14 | + | 1 | na | 15 | + | 1 | na | 33 | + |
| Wrentit *(Chamaea fasciata)* | 1415 | 1 | na | 0 | na | 1 | na | 1 | na | 1 | na | 3 | + |
| Mountain Quail *(Oreortyx pictus)* | 1387 | 0 | na | 0 | na | 0 | na | 0 | na | 0 | na | 10 | + |
| Bushtit *(Psaltriparus minimus)* | 1377 | 3 | + | 46 | – | 5 | – | 70 | + | 7 | – | 33 | – |
| California Thrasher *(Toxostoma redivivum)* | 1348 | 0 | na | 4 | + | 0 | na | 0 | na | 2 | na | 5 | – |
| Western Scrub-Jay *(Aphelocoma californica)* | 1339 | 1 | na | 20 | + | 2 | na | 11 | + | 5 | – | 88 | + |
| California Towhee *(Pipilo crissalis)* | 1144 | 2 | na | 5 | + | 1 | na | 3 | + | 1 | na | 45 | + |

**Table 3.2** Continued.

| Species | Mean elevation (m) | 2006 Nests *n* | 2006 Nests DSR | 2006 Fledglings *n* | 2006 Fledglings FI | 2007 Nests *n* | 2007 Nests DSR | 2007 Fledglings *n* | 2007 Fledglings FI | 2008 Nests *n* | 2008 Nests DSR | 2008 Fledglings *n* | 2008 Fledglings FI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Desert scrub (upper-elevation limited) | | | | | | | | | | | | | |
| Scott's Oriole *(Icterus parisorum)* | 951 | 2 | na | 1 | na | 0 | na | 1 | na | 1 | na | 2 | + |
| California Quail *(Callipepla californica)* | 936 | 0 | na | 32 | + | 0 | na | 1 | na | 0 | na | 70 | + |
| Rock Wren *(Salpinctes obsoletus)* | 810 | 0 | na | 0 | na | 0 | na | 2 | + | 0 | na | 14 | + |
| Black-throated Sparrow *(Amphispiza bilineata)* | 754 | 22 | + | 23 | + | 11 | + | 14 | + | 35 | - | 91 | - |
| Costa's Hummingbird *(Calypte costae)* | 734 | 9 | - | 5 | - | 2 | na | 4 | - | 2 | na | 3 | - |
| Phainopepla *(Phainopepla nitens)* | 722 | 1 | na | 1 | na | 1 | na | 1 | na | 4 | + | 5 | + |
| Cactus Wren *(Campylor. brunneicapillus)* | 626 | 5 | + | 4 | + | 1 | na | 2 | + | 0 | na | 0 | na |
| Northern Mockingbird *(Mimus polyglottos)* | 530 | 0 | na | 0 | na | 0 | na | 1 | na | 4 | – | 8 | – |
| Loggerhead Shrike *(Lanius ludovicianus)* | 489 | 9 | - | 11 | + | 6 | - | 7 | + | 2 | na | 17 | + |
| Verdin *(Auriparus flaviceps)* | 397 | 0 | na | 8 | + | 3 | + | 3 | + | 1 | na | 13 | + |
| Black-tailed Gnatcatcher *(Polioptila melanura)* | 317 | 4 | - | 1 | na | 1 | na | 0 | na | 1 | na | 9 | + |

**Table 3.3** Results of model selection examining the effect of elevation on nest survival of chaparral species, 2006–2008. Species were included in the model if a total of at least five nests were monitored from at least three sites (Black-chinned Sparrow, Blue-Gray Gnatcatcher, Spotted Towhee, Bushtit, and Western Scrub-Jay).

| Model | Likelihood | *K* | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| Year, species | 1.00 | 7 | 0.00 | 0.67 |
| Elevation, year, species | 0.37 | 8 | 1.97 | 0.25 |
| Null | 0.12 | 1 | 4.21 | 0.08 |

**Table 3.4** Results of model selection examining the effect of elevation on nest survival of desert scrub species, 2006–2008. Species were included in the model if a total of at least five nests were monitored from at least three sites (Black-throated Sparrow, Costa's Hummingbird, Phainopepla, Cactus Wren, Loggerhead Shrike, and Black-tailed Gnatcatcher).

| Model | Likelihood | *K* | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| Year, species | 1.00 | 8 | 0.00 | 0.69 |
| Elevation, year, species | 0.37 | 9 | 2.02 | 0.25 |
| Null | 0.09 | 1 | 4.89 | 0.06 |

**Table 3.5** Results of model selection examining factors affecting nest survival of Black-chinned Sparrows, 2006–2008. Ten candidate models were considered.

| Model | Likelihood | *K* | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| Lay date, year | 1.00 | 4 | 0.00 | 0.17 |
| Null | 0.73 | 1 | 0.62 | 0.13 |
| Year | 0.73 | 3 | 0.63 | 0.13 |
| Nest height | 0.72 | 2 | 0.66 | 0.13 |
| Substrate | 0.59 | 2 | 1.05 | 0.10 |
| Substrate, nest height | 0.49 | 3 | 1.43 | 0.09 |
| Lay date | 0.46 | 2 | 1.57 | 0.08 |
| Elevation, lay date, year | 0.45 | 5 | 1.60 | 0.08 |
| Elevation | 0.31 | 2 | 2.36 | 0.05 |
| Elevation, year | 0.27 | 4 | 2.64 | 0.05 |

**Table 3.6** Results of model selection examining factors affecting nest survival of Black-throated Sparrows, 2006–2008. Ten candidate models were considered.

| Model | Likelihood | *K* | $\Delta AIC_c$ | $w_i$ |
|---|---|---|---|---|
| Substrate | 1.00 | 2 | 0.00 | 0.18 |
| Lay date | 0.97 | 2 | 0.06 | 0.17 |
| Year | 0.84 | 3 | 0.34 | 0.15 |
| Null | 0.64 | 1 | 0.90 | 0.11 |
| Substrate, nest height | 0.58 | 3 | 1.08 | 0.10 |
| Elevation | 0.47 | 2 | 1.52 | 0.08 |
| Nest height | 0.36 | 2 | 2.03 | 0.06 |
| Lay date, year | 0.33 | 4 | 2.21 | 0.06 |
| Elevation, year | 0.31 | 4 | 2.35 | 0.05 |
| Elevation, lay date, year | 0.13 | 5 | 4.15 | 0.02 |

## Chapter 4: Breeding Success at the Distribution Margin of a Desert Species: Potential for a Climate-induced Range Shift?


### ABSTRACT

The distribution and abundance of a species often vary along environmental gradients. If the breeding distribution of a species is limited by biotic or abiotic environmental factors along a gradient, then reduced breeding success is expected at distribution margins. However, if environmental conditions change at distribution margins so that they are no longer limiting, breeding success should improve and result in a range expansion. Over a three-year period, we measured breeding success of Black-throated Sparrows (*Amphispiza bilineata*) along an elevation gradient between the Peninsular Mountains and Colorado Desert (San Diego County, California) in a region with a gradual warming trend. We compared breeding success at marginal locations (higher-elevation chaparral sites) to more central locations (lower-elevation desert scrub sites). Breeding success was measured at the nest level, territory level, and population level. At each level measured, breeding success tended to be greater at higher-elevation chaparral sites at the distribution margin compared to lower-elevation sites where the bird was more common. Black-throated Sparrows had 100% reproductive failure at lower-elevation sites during the two driest years of our study (2006–2007), but did relatively well at higher-elevation sites. Only in a wetter year (2008) was breeding success

improved at lower-elevation sites. If the climate continues to become warmer and drier in this system as predicted, then the distribution boundary of this species is expected to track upward in elevation as a result of greater breeding success at higher-elevation sites. However, there has been little evidence of an upward shift over a 26-year period despite a clear warming trend. Greater territory density at lower-elevation sites with reproductive failure during dry years suggests the possibility of an ecological trap in this system, which could prevent or delay climate-induced range shifts. A common presumption has been that desert species will be relatively little-impacted by a warming climate, but it is possible that desert species are more likely to be at or near their temperature and aridity tolerance limits within their current range and shifts may not always be possible.

## INTRODUCTION

All species are limited to a particular geographic area, whether of great or small extent, by historical contingency and interactions between extrinsic biotic or abiotic environmental factors, and intrinsic dispersive and adaptive traits. Many range boundaries occur along ecological gradients and are presumed to mark the limits of habitat quality or "niche" to which a species is best adapted, beyond which fitness is reduced. If limiting environmental conditions change at a range margin, then distributions are expected to expand or retract in response to that change. However, despite the ecological and evolutionary significance of distribution margins, they have received relatively little study (Hoffman and Blows 1994, Parmesan et al. 2005).

Unless there is a geographic barrier or other limitation to dispersal, distributions are often assumed to be niche-limited such that poor quality habitat occurs at and beyond distribution margins. In comparing vertebrate distributions, Grinnell (1904, 1914) found a tendency for higher densities at distribution centers with gradual declines at margins, and attributed this pattern to two general causes: (1) favorable environmental conditions at distribution centers promoting a relatively high rate of reproduction, and (2) radial dispersal away from the population center due to intraspecific competition. Brown (1984) hypothesized that species are limited by multiple environmental variables that have some degree of stochasticity and are spatially correlated, so that the density distribution tends toward normal and approximates the adaptive niche (Brown et al. 1995). Both of these models suggest that overall habitat quality in terms of relative fitness should decline toward distribution limits. With the tendency for outward dispersal, one could distinguish between an empirical boundary, marking the absolute limit of occurrence, and a functional boundary, marking the limit of habitat suitability (Emlen et al. 1986, Pulliam 2000). In territorial species, individuals are expected to trade off higher quality habitat with higher density for lower quality habitat with lower density, and a fitness difference is expected in highly territorial species with a "despotic" distribution (Fretwell and Lucas 1970). However, at some point, lower density in the form of larger territory sizes no longer compensates for poor quality habitat. The occurrence of individuals in sink habitat at distribution margins may be most likely in territorial species, and this may be especially true for highly vagile organisms such as birds (Grinnell 1922, Brown et al.

1996, Pulliam 2000). Although many studies have attempted to link population density and habitat type to reproductive success, especially in birds (Bock and Jones 2004), few studies have focused on distribution margins where different limiting mechanisms may operate.

Many extrinsic biotic and abiotic factors have been identified that limit distributions (e.g., Andrewartha and Birch 1984, Parmesan et al. 2005) and the relative importance of such factors has long been debated. It has been suggested that biotic interactions limit distributions at lower latitudes while abiotic interactions limit distributions at higher latitudes (Dobzhansky 1950, MacArthur 1972), and this may apply to elevational and aridity gradients as well (Brown et al. 1996). Although biotic factors are predicted to limit desert species where conditions become more mesic, competition and predation alone are unlikely to explain distribution limits due to the overriding effects of dispersal (Pulliam 2000). In an unchanging environment, local expansion or contraction likely depends both on the strength of the environmental gradient relative to dispersal and the potential for adaptation (Kirkpatrick and Barton 1997).

Along an environmental gradient, there can be many interactions and trade-offs that affect reproductive performance (Badyaev and Ghalambor 2001). In passerines, habitat selection and territorial choices can be critical, both because nest predation is common (Martin 1992), and because a territorial pair and their offspring depend on local resources throughout the nesting cycle. Breeding success is determined by many biotic and abiotic factors that can exert a limiting influence on different stages of the nesting cycle (Fig.

4.1). Thus, to evaluate habitat quality and trade-offs affecting breeding birds, it is informative to examine multiple stages of the nesting cycle from territory and pair establishment, to nest attempts and timing, to clutch size and fledging success.

Our objective was to test whether habitat quality is reduced at the distribution margin of a desert passerine and link that to the potential for a climate-induced range shift. Along an arid elevation gradient, we compared the abundance and breeding success of the Black-throated Sparrow (*Amphispiza bilineata*) at its more mesic upper elevation limits to locations in desert habitat at lower elevations that it more typically occupies. We measured breeding success at the nest level, territory level, and population level across three years under differing climatic conditions. If niche-limited, for a stable or retracting range boundary we predict that marginal locations will have reduced habitat quality measured as breeding success.

## METHODS

### *Study system*

Our focal species was the Black-throated Sparrow (*Amphispiza bilineata*), which breeds throughout the desert southwest of the U.S. and northern Mexico (Johnson et al. 2002). The "Laguna" study area was located at a western distribution margin in San Diego County, California (Fig. A.1). In southern California, the Peninsular Mountains form a rain barrier to the Colorado Desert to the east. There is a strong ecological

gradient that varies with elevation along the eastern slope of the mountains, which is correlated with temperature and precipitation. In this area, Black-throated Sparrows are abundant in desert habitat east of the Peninsular Mountains, but are rare or absent at higher elevations and coastal areas (Unitt 2004). This boundary occurs at the transition between desert scrub and chaparral vegetation types.

To determine local distribution and abundance, we conducted point counts at 90 locations along the elevational gradient. Point counts were conducted during the 2005–2008 breeding seasons, and repeated 2–3 times per year by a single observer using distance sampling (Buckland et al. 2004). Preliminary surveys in 2005 showed no difference in Black-throated Sparrow detectability among habitat types using a duration time of 15 minutes per point count. The westernmost distribution limits for the Black-throated Sparrow in this system occurred at approximately 1450 m. To monitor breeding activity, we established 10 study sites along the margin of Black-throated Sparrow distribution limits at 1150–1450 m, and 6 study sites at lower-elevation desert scrub at 150–650 m. Mean distance between the desert scrub and chaparral sites was 13 km, and each study site was approximately 24 ha in area (1200 m x 200 m). At least one Black-throated Sparrow was found each year at each of the selected study sites.

Lower-elevation desert sites were characterized by Sonoran desert scrub while higher-elevation marginal sites were characterized by chaparral, but there was substantial variation in shrub composition and cover among sites (Fig. 4.2). Rocky outcrops and cacti were common at many of the sites in both elevation zones.

*Climate*

We used PRISM data (PRISM Group, Oregon State University, http://www.prismclimate.org, accessed 22 March 2009) to generate an approximation of climatic conditions during the three survey years, and compared them to 40-year means (1968–2008). For each site and year we calculated the cumulative precipitation during the July to June rain-year, and the mean monthly minimum and maximum temperatures.

*Breeding success*

We conducted weekly censuses and nest monitoring at each site throughout the breeding season from 2006–2008. Locations of all Black-throated Sparrow territories were mapped weekly, and we monitored each territory for evidence of breeding activity from vantage points that were unlikely to cause disturbance (Ralph et al. 1993). Nest checks were as brief and unobtrusive as possible, at intervals of 3–8 days, and we avoided approaching nests during construction or egg-laying.

We estimated bird abundance based on both point count surveys and mapped territory densities. Point count surveys were conducted at the 90 point count sites along the full elevation gradient while territory density estimates were based on the 16 study sites in desert scrub and chaparral zones. The relationship between mean birds per point count (square-root transformed) and elevation was compared among years by analysis of covariance after removing points above the highest elevation that birds were detected. To test for differences in territory density between desert scrub and chaparral sites and among years, we used a non-parametric 2-way analysis of variance with a site-type by year interaction term (Brunner et al. 2002, Shah and Madden 2004).

As an index of relative productivity, we calculated the fledgling ratio (proportion of fledglings relative to adults) based on total numbers of adults and fledglings estimated from weekly territory mapping. To test for differences in fledgling ratio between desert scrub and chaparral sites and interactions with year, we used a log-linear analysis (Zar 1999).

We measured breeding success by scoring each territory based on the highest stage of progression observed during the breeding season: (1) territorial male alone (observed over at least three weeks), (2) adult pair, (3) nest construction, (4) nest with eggs, (5) nest with nestlings, (6) fledglings, and (7) fledglings plus a second nest attempted (Vickery et al. 1992). To test for differences in territory scores between desert scrub and chaparral sites and interactions with year we used a nonparametric analysis of variance (PROC MIXED with anovaf, SAS 9.2).

To estimate mean clutch size, we only used nests for which final clutch size could be determined with certainty. To test for differences in clutch size between desert scrub and chaparral sites, we used a Mann-Whitney test for two-sample rank testing and adjustment for tied ranks (Zar 1999). To estimate daily nest survival probability, we only used nests for which final outcome was known and we considered nests within ~2 days of fledgling successful. We generated a maximum-likelihood estimate of daily nest survival probability assuming constant daily survival rate using Program MARK, Version 5.1 (White and Burnham 1999).

## RESULTS

### *Climate*

As expected, precipitation was substantially lower at the low-elevation desert scrub sites relative to higher-elevation chaparral sites (Fig. 4.3). Across the three years (2006–2008), desert scrub sites had 78% less precipitation than chaparral sites. All sites and years during the three-year study were below the 40-year precipitation means. 2007 was near record drought conditions, while 2008 was closest to the 40-year mean. Average annual minimum and maximum temperatures tended to be negatively correlated with precipitation.

### *Population-level*

Mean Black-throated Sparrow abundance measured by point counts declined toward the upper elevation margin (Fig. 4.4), and this pattern was maintained across 2005–2008 (ANCOVA, elevation $P < 0.001$, elevation*year $P = 0.60$), although abundance tended to decrease at all sites across the four years (year $P = 0.03$). Overall, abundance was 157% greater in the 150–650 m elevation range ("desert scrub" sites) than in the 1150–1450 elevation range ("chaparral" sites) at the distribution margin. Likewise territory density (2006–2008) was 81% greater at desert scrub sites than at chaparral sites at the distribution margin with a small effect of year (ANOVA-type statistic $B_{1,14} = 12.8$, habitat $P < 0.001$, year $P = 0.05$, habitat*year $P = 0.18$), which was seen in 2007, the driest year, where the difference was somewhat reduced (Table 4.1).

Across the three years, productivity (ratio of fledglings) was greater at chaparral sites than at desert scrub sites overall (Table 4.1) but there was both a strong year effect and interaction (log-linear analysis, habitat $G^2 = 7.84$, df = 1, $P = 0.005$, year $G^2 = 62.86$, df = 2, $P < 0.001$, habitat*year $G^2 = 7.48$, df = 2, $P = 0.02$). . At chaparral sites, the fledgling ratio varied strongly by year, with 2008 being the most productive year, followed by 2006, and 2007 was the least productive. At desert scrub sites, no fledglings were observed in both 2006 and 2007, so there appeared to be 100% reproductive failure at desert scrub sites during these two driest years of the study, despite the fact that territory density was greater. However, in 2008, the wetter year, the fledgling ratio was 0.72, which was equivalent to chaparral sites in 2008.

*Territory-level*

Breeding success measured at the territory level was significantly lower at desert scrub sites than at chaparral sites across the three years but there was a strong year effect and interaction (Fig. 4.5; ANOVA-type statistic $F_{1,103} = 12.62$, $P < 0.001$, year $F_{2,103} = 16.66$, $P < 0.001$, habitat*year $F_{2,103} = 11.02$, $P < 0.001$). For chaparral sites the three-year average was 4.0, indicating that the average territory got to the incubation stage. Although 2007 had a slightly lower average territory score at chaparral sites, the year effect was much more pronounced at desert scrub sites. For territories at desert scrub sites in 2006 and 2007, the two driest years, the average breeding index was 2.4 and 2.0, respectively, indicating that the average territory only had a pair present with no evidence of a nesting attempt. The breeding index rose to 5.1 for desert scrub sites in 2008, indicating that the average territory got to the nestling stage.

*Nest-level*

There were few nests at desert scrub sites in 2006 and 2007, and clutch size and daily survival probability could not be estimated in 2007 for desert scrub sites. However, the overall pattern was similar to other breeding success measures, with a suggestion of a reduction in both clutch size and nest survival probability at desert scrub sites in the two driest years (2006 and 2007), and a reversal in that pattern in 2008 with similar scores between desert scrub and chaparral sites (Table 4.1). Clutch size was significantly greater at chaparral sites than at desert scrub sites in 2006 ($P = 0.001$), but there was no difference in 2008 ($P > 0.20$; Mann-Whitney Test for two-sample rank testing).

## DISCUSSION

For a niche-limited static or retracting breeding distribution boundary, reduced breeding success is predicted at the distribution margin, but we found this not to be the case. More Black-throated Sparrows occurred at desert scrub sites than at chaparral sites at the upper elevation distribution margin with no evidence of an upward elevational shift across four years despite reduced breeding success at desert scrub sites. Overall, chaparral sites at the upper elevation distribution margins had relatively consistent breeding success across all years, whereas there was 100% reproductive failure at desert scrub sites during the two driest years of the study, 2006 and 2007. In 2008 all measures of breeding success became more equivalent between the two elevation zones.

*Abundance and breeding success at a distribution margin*

If breeding distributions are niche-limited, we expect that habitat quality will be reduced at distribution margins due to biotic or abiotic environmental factors, resulting in reduced breeding success. Our results were not consistent with this prediction, with marginal chaparral sites doing as well or better than desert scrub sites, especially in the two driest years of our study. In this arid system, cumulative precipitation is substantially greater at chaparral sites at the distribution margin, such that even during the dry years, it was still greater than the 40-year mean of desert scrub sites. Thus, drought conditions are more likely to have a greater impact at desert scrub sites. Black-throated Sparrows experienced 100% reproductive failure at desert scrub sites during the two driest years of our study, mostly due to failure to initiate nests. This suggests that the drought conditions removed the necessary behavioral or physiological cues needed to initiate nesting, presumably in the face of resource insufficiency. Black-throated Sparrows, like most passerines, are strongly dependent on insect prey during nesting, and droughts have been known to cause reproductive failure in arid environments (Bolger et al. 2005). Of the nests initiated in 2006, clutch size was substantially reduced, which was also likely due to the drought conditions. Food supplementation is known to increase clutch size in passerines (Nager et al. 1997), and water supplementation has also been shown to increase clutch size for this species (Coe and Rotenberry 2003). The strong differences in breeding success between 2006 and 2008 despite a precipitation difference of only 19% also suggests a possible threshold effect.

These results highlight the importance of considering territory-level and population-level measures of breeding success in addition to nest-level measures. Nest-level measures are frequently used in passerine studies due to the prevalence of nest predation, but are insufficient for measuring the impact of other limiting factors such as drought that reduce nest attempts.

*Is there potential for a climate-induced range shift?*

The desert regions of southern California are generally predicted to become warmer and drier over the next century, and variation in extreme events such as floods and droughts is expected to increase (e.g., Hayhoe et al. 2004, Seager et al. 2007, Christensen et al. 2007). If breeding success improves at a distribution margin, the expectation is that breeding distributions will expand at that margin. In this system, breeding success was greater at the margin, and it was likely that drought was the principal cause of that difference. However, Black-throated Sparrows showed little evidence of any upward shift in their elevational distribution. Abundance remained greater at desert scrub sites even during the driest years of the study, and the upper elevational limit did not shift during the four years of the study. Hargrove and Rotenberry (in press) found no upward elevational shift for the Black-throated Sparrow over a 26-year period at a similar study area just to the north despite a strong warming trend and drier conditions, although other desert species did show an upward shift. Many factors affect distribution structure and dynamics, and here we present three possible reasons for why the elevational distribution has not shifted upward in this system, despite the apparent strong potential for a climate-induced shift:

(1) Trade-offs such as increased survival at lower elevations could make overall fitness greater in desert scrub habitat. However, abundance tended to decrease at all sites over the four years of the study, and an inability to initiate nests should be correlated with reduced survivability. Over-winter survival could be an important factor, but Black-throated Sparrows do not remain territorial during the non-breeding season.

(2) The pattern could be reversed in wetter, cooler years so that overall fitness is greater in desert scrub over the long-term. Even if desert scrub habitat acts as a sink during drought years and abundance decreases, marginal chaparral habitat could act as a "refuge" source and help to repopulate desert scrub habitat. Although there was no evidence of a longer breeding season at desert scrub sites during this study, that could become an important factor during wetter years if Black-throated Sparrows are able to increase their number of clutches in desert scrub habitat during wetter years. However, with 100% reproductive failure in desert scrub habitat during the two dry years of this study and the close proximity of the more productive higher-elevation sites, the lack of at least a short-term elevational shift is surprising.

(3) If biotic and abiotic limiting factors are decoupled, at least in the short term, there could be a mismatch between habitat preference and habitat suitability. If desert scrub habitat had greater suitability historically, and Black-throated Sparrows evolved a preference for desert scrub vegetation over chaparral, this can cause a mismatch if suitability of abiotic conditions shifts more rapidly than vegetation cover. The current situation of greater density at sites with reduced reproductive success that are only a short distance apart from sites with lower density and greater reproductive success has the

appearance of an ecological trap. Ecological traps occur when low-quality habitat is preferred over available habitat of higher quality, and can drive a population to extinction (Kristan 2003, 2007; Battin 2004). On average, chaparral sites were 13 km from desert scrub sites, but are presumably less preferred given the evidence of lower density and marginal location. If this is only a local phenomenon, range-wide dynamics could swamp any local shifts. However, Pidgeon et al. 2003 found a possibly similar ecological trap for the Black-throated Sparrow in the Chihuahuan Desert, where at the lowest-elevation habitat type, nest success was lowest but abundance was highest. Thus, in both studies, density was inversely correlated with habitat quality in terms of reproductive success.

Mismatches between habitat choices and reproductive consequences have been described in other studies as well (e.g., Misenhelter and Rotenberry 2000), but ours is the first study to describe the phenomenon at a range margin with a possible link to climate change. Van Horne (1983) identified three likely reasons for a mismatch between density and habitat quality in a breeding range: (1) an overriding influence of winter habitat quality, (2) site tenacity combined with inter-annual variability, and (3) social interactions forcing surplus individuals into sink habitat. Here we suggest a fourth possible cause: If there has been a climatic shift such that marginal areas now have greater suitability, individuals may still have an inherited preference for less-suitable central habitat that was historically adaptive. This preference can prevent or delay a climate-induced range shift, especially if marginal areas represent a small proportion of the overall range.

There is strong evidence that climate change is causing northward range shifts and earlier spring arrival for numerous species (Walther et al. 2002, Root et al. 2003, Parmesan and Yohe 2003, Parmesan 2006), but there has been less evidence of elevational shifts. Species that are unable to shift could be subject to ecological traps (e.g., Both et al. 2006), and this may be more likely in systems with rapid change and along steep environmental gradients. Bird communities in the Sonoran and Mojave deserts have shown decreasing population trends from 1966 to 2007, including for the Black-throated Sparrow (Sauer et al. 2008), and evidence is lacking for northward shifts for desert birds including this species (La Sorte and Thompson 2007). A common presumption has been that desert species will be relatively little-impacted by a warming climate (e.g., Sala et al. 2000, Thomas et al. 2004), but it is possible that desert species are more likely to be at or near their temperature and aridity tolerance limits within their current range, and new areas are not necessarily suitable or available for occupation—especially if preferred habitat shifts more slowly than climate. Even when local expansion is possible, a large proportion of the current range can become unsuitable if tolerance limits are exceeded.

Climate change is often used as a basis to predict distribution changes (e.g., Pearson and Dawson 2003), but distribution stasis with either adaptation or extinction is also possible, while at the same time rapid distribution shifts can occur even in the absence of environmental change (e.g., Kirkpatrick and Barton 1997). A better understanding of local habitat relationships is needed before distributional shifts can be predicted. Local biotic interactions can outweigh the effects of climate change in predicting shifts (e.g.,

Preston et. al 2008), and the relative importance of limiting factors at distribution margins can be critical, but marginal areas are still rarely studied, especially at the trailing or rear edge (Hampe and Petit 2005). There can also be strong differences in responses among taxa and among species within taxa. In this system, there is evidence that some bird species, particularly desert species, have shifted upward in elevation (Hargrove and Rotenberry in press), and that plant species have also shifted upward, although to a lesser extent (Kelly and Goulden 2008) and this may be due primarily to low-elevation die-off (Miriti et al. 2007). There has also been evidence for upward shifts of bighorn sheep in the southern California desert region due to extinctions of populations at lower elevations (Epps et al. 2004). In the case of the Black-throated Sparrow, a climate-induced upward shift is expected due to greater breeding success at upper elevation limits related to climate, but no upward shift occurred. We do not know how Black-throated Sparrow distributions will respond to future changes in climate, but in this system at least over the short-term, there was a mismatch between density and habitat quality at the distribution margin with the appearance of a local ecological trap, which could prevent or delay a range expansion if conditions continue to become warmer and drier as predicted.

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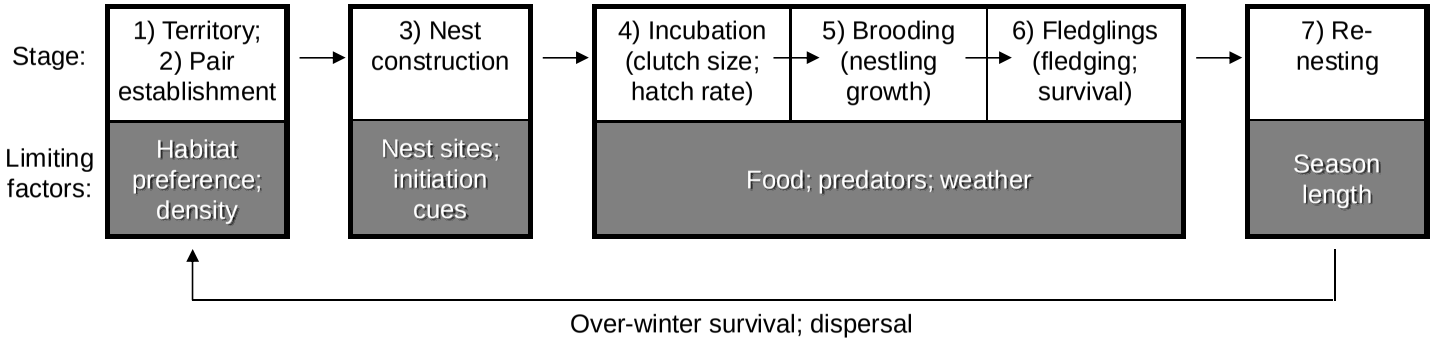
**Figure 4.1** Stages of the avian nesting cycle and the major limiting factors that determine breeding success.



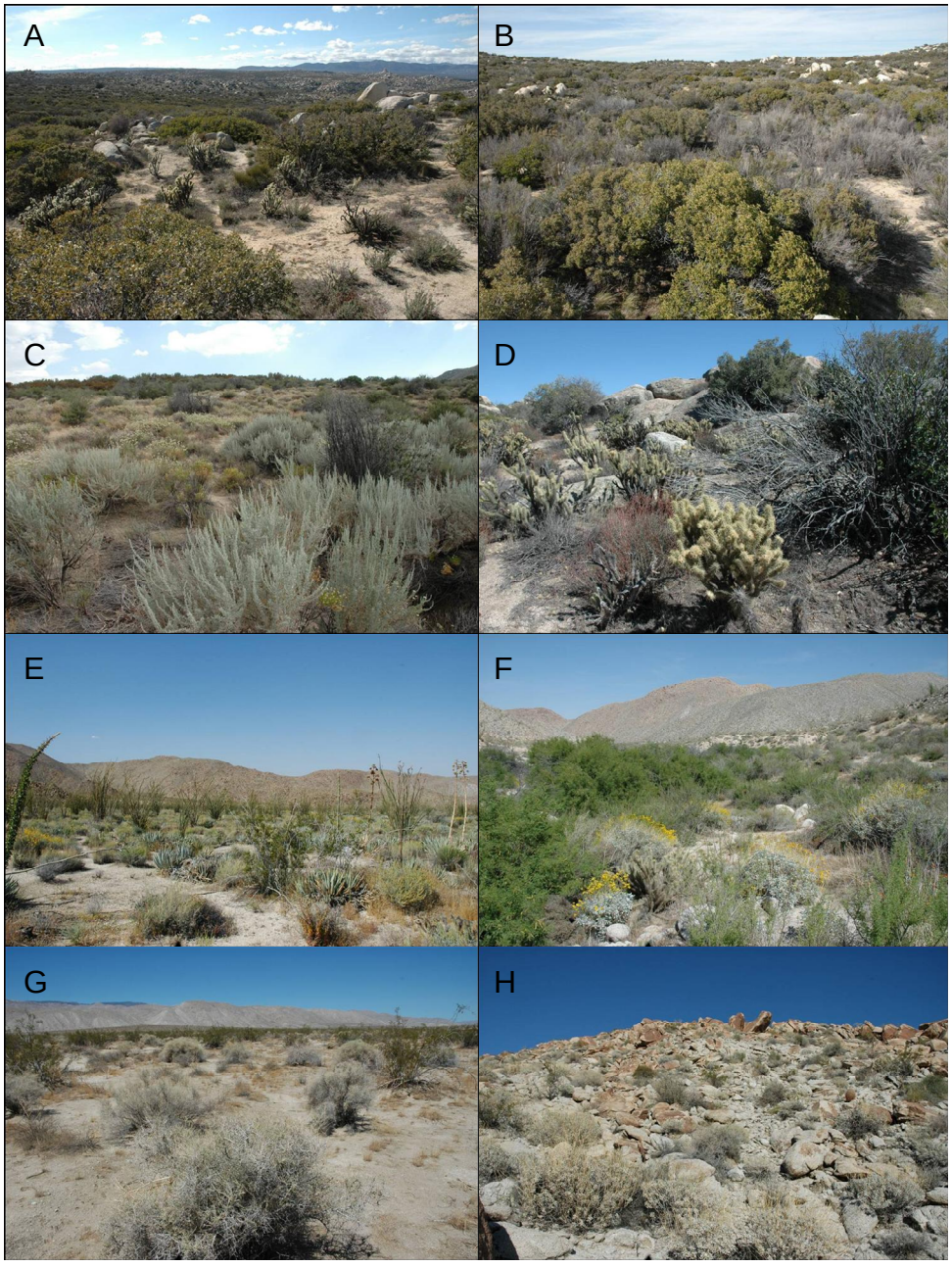



**Figure 4.2** Range of vegetation types at chaparral (A–D) and desert scrub (E–H) sites, San Diego County, California. Chaparral sites (elevation 1150–1450 m) included: (A) sugar bush (*Rhus ovata*) and sandy openings; (B) scrub oak (*Quercus berberidifolia*) and chamise (*Adenostoma fasciculatum*); (C) big sagebrush (*Artemisia tridentata*), California buckwheat (*Eriogonum fasciculatum*), interior goldenbush (*Ericameria linearifolia*), and desert ceanothus (*Ceanothus greggii*); (D) Gander's buckhorn cholla (*Cylindropuntia ganderi*) and rock outcrops. Desert scrub sites (elevation 150–650 m) included: (E) white bur-sage (*Ambrosia dumosa*), ocotillo (*Fouquieria splendens*), and desert agave (*Agave*

*deserti*); (F) catclaw acacia (*Acacia greggii*) and Gander's buckhorn cholla (*Cylindropuntia ganderi*); (G) desert saltbush (*Atriplex polycarpa*) and creosote bush (*Larrea tridentata*); (H) brittlebush (*Encelia farinosa*) and rock outcrops.

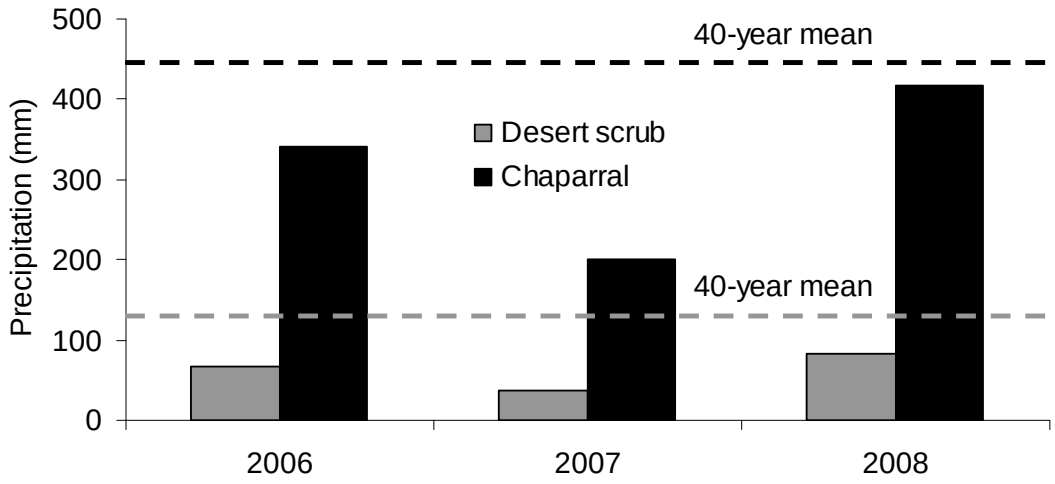



**Figure 4.3** Cumulative precipitation during July to June rain-year at desert scrub sites (mean elevation 300 m) and chaparral sites (mean elevation 1250 m), 2006–2008. The dashed lines represent the 40-year means for desert scrub (131 mm/year) and chaparral sites (444 mm/year), 1968–2008. (PRISM Group, Oregon State University, http://www.prismclimate.org, accessed 22 March 2009.)

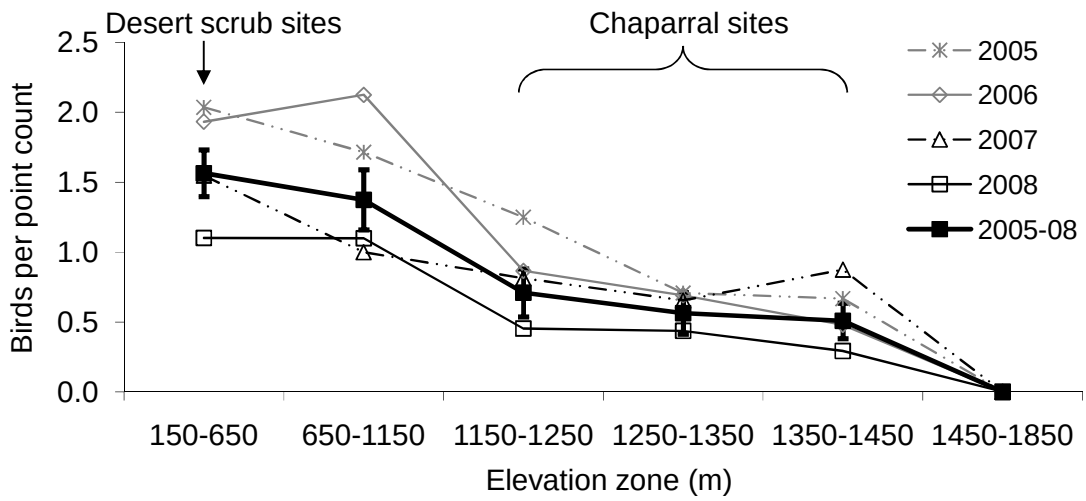



**Figure 4.4** Mean Black-throated Sparrow abundance along the elevation gradient (150–1850 m) based on a total of 542 point counts at 90 point locations, 2005–2008. "2005-08" represents the four-year average (± SE). Bins are based on equal survey effort. Note that desert scrub study sites were located within the 150–650 m elevation zone while chaparral sites were located within the 1150–1450 m elevation zone at the distribution margin.

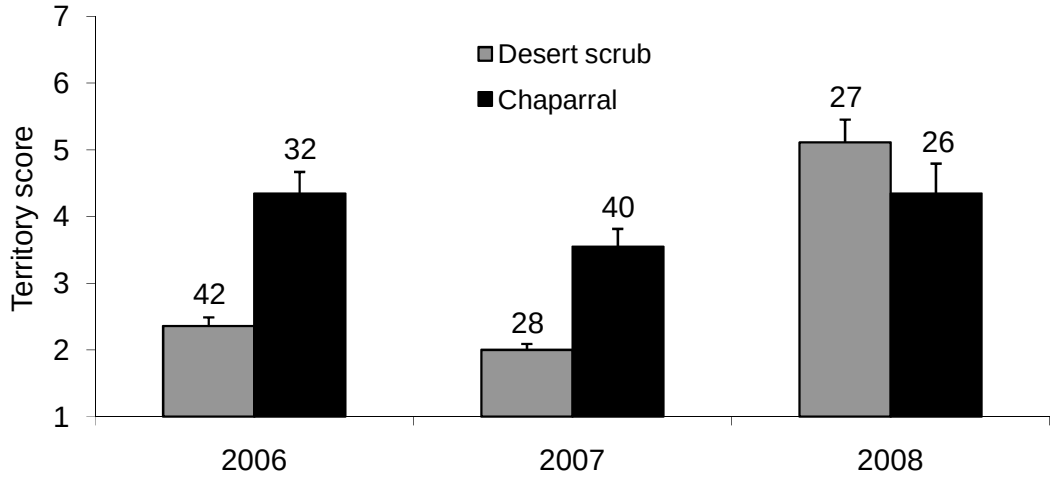



**Figure 4.5** Territory-level breeding success of Black-throated Sparrows at desert scrub and chaparral sites 2006–2008. Territory scores reflect the highest breeding stage observed, from territorial male alone (score of 1), to pair with fledglings also attempting a second nest (score of 7). Error bars indicate SE. Numbers above error bars represent sample sizes.

**Table 4.1** Population-level and nest-level attributes of Black-throated Sparrows at desert scrub and chaparral sites, 2006–2008. Values represent means ± SE, except adult-to-fledgling ratio, which is based on totals observed. Sample sizes for territory density are the number of sites (desert scrub $n = 6$ and chaparral $n = 10$, each year). Sample sizes for clutch size and daily survival probability are the number of nests for which the values could be determined with certainty (i.e., known clutch size and known nest outcome, respectively).

| Year | Habitat zone | Population-level | | Nest-level | |
|---|---|---|---|---|---|
| | | Territories / 40 ha | Adult : Fledgling | Clutch size | Daily survival probability |
| 2006 | desert scrub | 10.9 ± 1.7 | 1.00 : 0.00 | 2.0 ± 0.0 ($n$ = 4) | 0.84 ± 0.06 ($n$ = 7) |
| | chaparral | 4.6 ± 0.5 | 1.00 : 0.36 | 3.2 ± 0.1 ($n$ = 13) | 0.94 ± 0.02 ($n$ = 15) |
| 2007 | desert scrub | 7.5 ± 1.0 | 1.00 : 0.00 | — | — |
| | chaparral | 5.7 ± 0.8 | 1.00 : 0.14 | 2.6 ± 0.2 ($n$ = 9) | 0.92 ± 0.03 ($n$ = 10) |
| 2008 | desert scrub | 6.9 ± 1.3 | 1.00 : 0.73 | 3.9 ± 0.2 ($n$ = 16) | 0.98 ± 0.01 ($n$ = 16) |
| | chaparral | 4.1 ± 0.8 | 1.00 : 0.75 | 3.9 ± 0.1 ($n$ = 9) | 0.93 ± 0.03 ($n$ = 12) |

## Conclusion

Along an ecological gradient, species distributions can be limited by multiple interactive factors that define an adaptive "niche", and distribution limits are expected to shift in relation to environmental change. In Chapter One, we saw that breeding bird species had highly individualistic environmental associations along an arid scrub gradient, with strong differences in the relative importance of biotic and abiotic factors among species. Climate was relatively important in setting the lower-elevation limit of chaparral species, while for desert scrub species, environmental correlates were more variable. Although elevational distributions were remarkably static over a three-year period, we saw in Chapter Two that longer-term (26-year) shifts occurred in the expected upward direction given warmer, drier conditions. Within this broader-scale distribution context, we saw in Chapter Three that individual productivity tended to increase with elevation, regardless of the direction of the species' distribution margin. For a focal desert scrub species, the Black-throated Sparrow (*Amphispiza bilineata*), we saw in Chapter Four that this difference in productivity was primarily due to a lack of nesting attempts at lower elevations during the two drier years of the study (2006–2007), and that there was an improvement in productivity at lower elevations during the wetter year (2008), possibly due to a threshold effect.

There have been many illuminating studies of elevational diversity (e.g., Whittaker 1967, Terborgh 1971), avian-habitat relationships (e.g., Wiens and Rotenberry 1981, Bock and Jones 2004), and broad-scale limiting factors (e.g. Root 1988, Parmesan et al.

2005). Yet few studies have focused on distribution margins where limiting mechanisms can provide insights into broader-scale range dynamics (e.g., Thomas et al. 2001). This dissertation research was innovative in several ways, especially: (1) comparison of marginal structure and dynamics of species with a lower and upper elevation limit within the same system, (2) fine-scale sampling of a wide range of abundance and habitat conditions over a low-elevation desert scrub gradient, and (3) linkage of broader-scale distribution structure and dynamics to local-scale breeding success.

There are many environmental factors that can affect the distribution and abundance of species, and not all were measured in this study. Other important considerations that can influence marginal structure and dynamics include: survival, site fidelity, habitat preference, competition, and predation. However, if distributions are niche-limited, an overall decline in habitat quality is expected at distribution margins associated with reduced abundance and reduced fitness. This was found to be the case for chaparral species, but not for desert scrub species. These results support the prediction that distributions will shift upward in elevation with increases in temperature and aridity, both by retraction of lower-elevation limits and expansion of upper-elevation limits. Conclusions can also be greatly influenced by the spatial and temporal scale of study. Long-term monitoring of distribution limits is needed, ideally linking two levels of study: individual-level fitness measurements and population-level abundance patterns.

Although distributions are expected to shift in relation to environmental change, decoupling of factors can prevent or delay shifts. In the case of the Black-throated Sparrow, productivity was relatively good and more consistent at higher elevation sites at

the distribution margin, but the birds remained more common at low-elevation sites over the three-year period, presumably due to preference for desert scrub habitat. Even though there was an apparently strong selective pressure toward upward elevational shifts, there was no long-term upward shift over a 26-year period despite warmer, drier conditions. Along a gradient of habitat quality, habitat preference is unlikely to be ideal, and the evolution of habitat preference at a margin can be swamped by gene flow. Darwin noted: "Why are species not formed, during ascent of mountain or approach of desert? — because the crossing of species less altered prevents the complete adaptation which would ensue" (Darwin 1837-1838). Thus, just as gene flow prevents speciation, it can also prevent or delay adaptation in marginal areas within a species' range. Local expansion or contraction likely depends both on the strength of the environmental gradient relative to dispersal and the potential for adaptation (Kirkpatrick and Barton 1997), and the decoupling of environmental factors with respect to habitat preference can further delay shifts.

The causes and consequences of distribution limits involve a complex interplay among ecological, evolutionary, and behavioral processes. A better understanding of distribution limits and their dynamics is especially critical for conservation planning in the face of climate change. The study of local-scale processes at distribution margins helps to elucidate the nature of distribution limits, and can also provide important insights for understanding larger-scale range dynamics.

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## Endnotes

1. Nest success results for Black-throated Sparrows differ slightly between Chapter Three and Chapter Four because in Chapter Three data from all 26 plots were used in the analysis (where nests were found), while in Chapter Four, plots not surveyed all three years were excluded from the analysis.

2. Sites were occasionally referred to as “transition” to distinguish between higher-elevation chaparral and lower-elevation chaparral where it transitions into desert scrub. These same sites were referred to as “chaparral” in Chapter Four.

## Appendix: Additional Figures and Tables

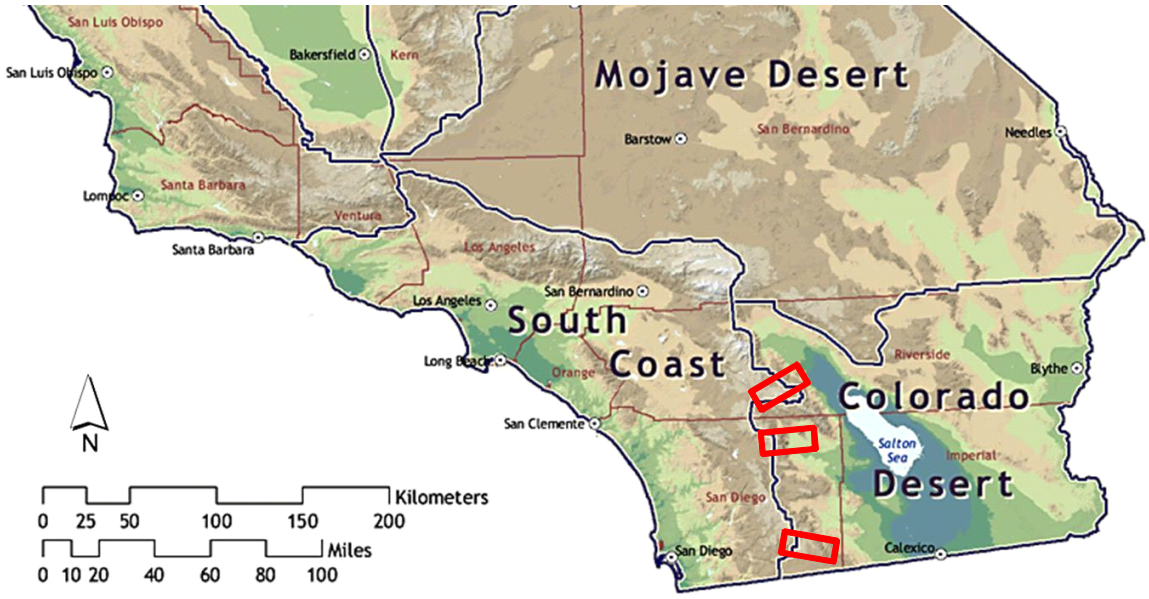


**Figure A.1** Location of three study areas (three rectangles) within southern California, each encompassing the transition between the South Coast Peninsular Ranges and the Colorado Desert. From north to south, the three study areas are: Deep Canyon, Hot Springs, and Laguna. (Map source: California Department of Fish and Game Wildlife Diversity Project 2005.)

**Table A.1** Results of principal components analysis of 10 habitat "structural" characteristics estimated within a 50-m radius centered on each point ($n$ = 159). Seven variables were estimated as the total proportion of area covered: trees (over 6 m tall,"Tree"), shrubs ("Shrub"), succulents ("Cactus"), grasses or annuals ("Herb"), rocks ("Rock"), open ground ("Open"), and leaf litter or other organic debris ("Litter"). Total counts were made of the number of large snags (dead trees or stems >10 dm in diameter, "LgSnag") and number of small snags (dead trees or stems <10 dm in diameter but large enough for a cavity nest, "SmSnag"). Shrub height was estimated as the average height of the tallest 10% of the shrub layer ("ShrubHt").

| | PC1 | PC2 |
|---|---|---|
| Factor loading | | |
| Tree | 0.661 | -0.581 |
| Shrub | 0.674 | 0.656 |
| Cactus | -0.545 | -0.379 |
| Herb | -0.095 | -0.125 |
| Rock | -0.314 | -0.170 |
| Open | -0.504 | -0.342 |
| Litter | 0.838 | 0.258 |
| LgSnag | 0.687 | -0.689 |
| SmSnag | 0.545 | -0.598 |
| ShrubHt | 0.447 | 0.183 |
| | | |
| Eigenvalue | 3.220 | 2.006 |
| % of variance | 32.2 | 20.1 |

**Table A.2** Results of detrended correspondence analysis of habitat "floristics" using estimates of total proportion of area covered by 39 plant species or groups within a 50-m radius centered on each point ($n$ = 159). Species are listed in order of mean elevation weighted by abundance. Total variance ("inertia") in the data was 7.48.

| | | Elev. (m) | DC1 | DC2 |
|---|---|---|---|---|
| Species scores | | | | |
| palo verde | *Cercidium floridum* | 244 | -0.68 | -0.38 |
| pencil cholla | *Cylindropuntia ramosissima* | 264 | -0.28 | -0.24 |
| smoketree | *Psorothamnus spinosus* | 267 | -0.38 | 1.29 |
| creosote | *Larrea tridentata* | 307 | -0.01 | 3.38 |
| saltbush | *Atriplex* spp. (mostly *polycarpa)* | 368 | 0.41 | 2.91 |
| white bur-sage | *Ambrosia dumosa* | 380 | 0.81 | 3.05 |
| teddy-bear cholla | *Cylindropuntia bigelovii* | 399 | 0.34 | 0.44 |
| indigo bush | *Psorothamnus schottii* | 404 | 0.45 | 0.45 |
| riparian shrubs (mostly willow, arrow weed, mule-fat, tamarisk) | (mostly *Salix* spp., *Pluchea sericea, Baccharis salicifolia, Tamarix* spp.) | 413 | 1.34 | 4.08 |
| mesquite | *Prosopis* spp. | 418 | 1.08 | 3.70 |
| ocotillo | *Fouquieria splendens* | 429 | 1.02 | 2.23 |
| desert-willow | *Chilopsis linearis* | 439 | 0.97 | -0.67 |
| desert-lavender | *Hyptis emoryi* | 458 | 0.94 | 0.03 |
| riparian trees (mostly cottonwood, sycamore, palms) | (mostly *Populus fremontii, Platanus racemosa, Washingtonia filifera)* | 463 | 1.65 | 3.96 |
| cheesebush | *Ambrosia salsola* | 542 | 1.49 | 0.03 |
| desert agave | *Agave deserti* | 711 | 2.38 | 1.19 |
| jojoba | *Simmondsia chinensis* | 721 | 2.28 | 2.73 |
| catclaw | *Acacia greggii* | 732 | 2.41 | 0.55 |
| brittlebush | *Encelia farinosa* | 732 | 2.21 | 2.04 |
| golden/silver cholla | *Cylindropuntia echinocarpa* and *ganderi* | 907 | 3.22 | 1.05 |
| ephedra | *Ephedra* spp. | 956 | 3.20 | 0.71 |
| California juniper | *Juniperus californica* | 1103 | 3.48 | 1.05 |
| bunch grass (includes galleta, needlegrass, deergrass) | (includes *Hilaria rigida, Nassella* spp., *Muhlenbergia rigens* ) | 1106 | 3.64 | 1.65 |

**Table A.2** Continued.

| | | Elev. (m) | DC1 | DC2 |
|---|---|---|---|---|
| prunus | *Prunus* spp. (mostly *ilicifolia and fremontii)* | 1120 | 3.87 | 2.81 |
| sugar bush | *Rhus ovata* | 1203 | 4.16 | 2.11 |
| big sagebrush | *Artemisia tridentata* | 1236 | 5.29 | 1.45 |
| California buckwheat | *Eriogonum fasciculatum* | 1238 | 4.39 | 1.77 |
| pinyon pine | *Pinus monophylla* and *quadrifolia* | 1279 | 4.08 | 1.09 |
| scrub oak | *Quercus berberidifolia, cornelius-mulleri* , and *wislizeni* | 1390 | 5.13 | 1.71 |
| chamise | *Adenostoma fasciculatum* | 1422 | 5.94 | 1.69 |
| yucca | *Yucca* spp. (*Hesperoyucca whipplei and Yucca schidigera)* | 1426 | 5.81 | 1.65 |
| mountain-mahogany | *Cercocarpus betuloides* | 1436 | 5.17 | 2.01 |
| red shank | *Adenostoma sparsifolium* | 1529 | 6.72 | 1.91 |
| desert ceanothus | *Ceanothus greggii* | 1581 | 6.11 | 1.77 |
| live oak | *Quercus agrifolia* and *chrysolepis* | 1616 | 8.04 | 1.89 |
| pine trees | *Pinus* spp. (mostly *jeffreyi* and *coulteri* ) | 1620 | 7.85 | 1.77 |
| chaparral whitethorn | *Ceanothus leucodermis* | 1635 | 7.22 | 1.80 |
| manzanita | *Arctostaphylos* spp. | 1657 | 7.05 | 1.82 |
| California black oak | *Quercus kelloggii* | 1713 | 8.54 | 1.75 |
| Eigenvalue | | | 0.849 | 0.399 |
| Length of gradient | | | 7.746 | 3.369 |

**Table A.3** Results of principal components analysis of mean maximum and minimum temperatures ($n$ = 159)

| | PC1 | PC2 |
|---|---|---|
| Factor loading | | |
| Maximum temperature | 0.972 | -0.233 |
| Minimum temperature | 0.972 | 0.233 |
| | | |
| Eigenvalue | 1.891 | 0.109 |
| % of variance | 94.6 | 5.4 |