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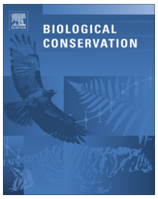

Special Issue Article: Tropical Insectivores

Absence of microclimate selectivity in insectivorous birds of the Neotropical forest understory

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ABSTRACT

Local abiotic conditions (microclimates) vary spatially and selection of favorable microclimates within a habitat can influence an animal's energy budgets, behavior, and ultimately, fitness. Insectivorous birds that inhabit the understory of tropical forests may be especially sensitive to environmental variation and may select habitat based on microclimatic (e.g. temperature, humidity, light) conditions. Sensitivity to microclimate could contribute to the population declines of understory insectivores in response to forest fragmentation or degradation, which changes the physical structure of the forest, thereby increasing light intensity and temperature and decreasing humidity. To understand the role of microclimates in the habitat selection of understory insectivores, we characterized the microclimatic associations of nine species of understory insectivores at three sites along a precipitation gradient and across seasons in central Panama. We compared the distributions of microclimates selected by birds with microclimates at randomly chosen points within their home ranges to test for microclimate selectivity. We predicted that: (1) birds would select microclimates that are more humid, cooler, and less bright than random microclimates, (2) selectivity would be greater in hotter, drier habitats and (3) selectivity would be greatest in the dry season. We found no evidence of selectivity for the nine species we sampled on a seasonal or spatial basis. Microclimate variation was minimal in the forest understory at all sites, particularly in the wet season. Understory insectivores did not use microhabitats characterized by high light intensity, and may be sensitive to light, though the mechanism remains unclear. The lack of microclimate variation in the understory of tropical forests may have serious fitness consequences for understory insectivores due to increasing temperatures associated with climate change coupled with a lack of thermal refugia.

1. Introduction

Maintaining energy balance is a primary challenge for all organisms (Piersma and van Gils, 2010) and the fitness consequences of persisting in energetically demanding habitats can be substantial (Bakken, 1976; Huey, 1991). The energetic costs associated with unsuitable environmental conditions can govern macroecological patterns such as species' geographic range limits (Root, 1988; Brown et al., 1996) and can also have profound effects on behavior and habitat use on a local scale (Adolph, 1990; Hertz, 1992; Huey et al., 2012). Within a habitat, spatial variation in solar radiation, wind speed, air temperature and humidity creates a mosaic of local abiotic conditions (hereafter microclimates, sensu Angilletta, 2009) that can influence behavior, energy budgets and ultimately, fitness (Huey, 1991). For example, selection of favorable microclimates can enhance an organism's ability to escape from predators (Hertz et al., 1983; Carrascal et al., 1992), improve foraging efficiency (du Plessis et al., 2012), reduce costs of thermoregulation (Buttemer, 1985; Jenni, 1991; Wiersma and Piersma, 1994; Cooper, 1999) and even increase survival (Huey et al., 1989; Dawson et al., 2005) and reproductive success (Martin, 1998; Jones and Reichert, 2008). Previous research on the physiological consequences of habitat selection, however, has focused largely on ectotherms (Huey, 1991) because they are predominantly "thermoconformers" and are therefore more directly dependent on ambient temperature (Angilletta, 2009; Somero, 2010).

The role of microclimates in the habitat selection of endotherms such as birds remains relatively unexplored. Microclimatic conditions can influence energy budgets in endotherms, but most sampling has been limited to fixed locations such as roost sites

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(e.g. Buttemer, 1985) and nest sites (e.g. Gloutney and Clark, 1997; Martin, 1998). Daily patterns of microclimate selection, particularly in birds, have received less attention but are equally important to understand given that habitat selection is a dynamic process that also occurs during an animal's active phase (Walsberg, 1993). For example, in arid regions of the southwest U.S., birds avoided foraging in microclimates characterized by high ambient temperatures and light intensity (Walsberg, 1993), resulting in substantial energy savings (Wolf and Walsberg, 1996). Similarly, Karr and Freemark (1983) suggested that tropical forest bird species moved seasonally to track microclimatic optima within their home ranges. In a changing world, understanding how birds respond to microclimate variation within their habitats is emerging as an important conservation issue because microclimatic heterogeneity may provide important thermal refugia and mitigate the negative impacts of climate change (Bonebrake and Deutsch, 2012).

Understory insectivorous birds of Neotropical forests are characterized by low dispersal capabilities (Moore et al., 2008; Tarwater, 2012; Woltmann et al., 2012a), specialized foraging habits (Sherry, 1984; Marra and Remsen, 1997; Şekercioğlu et al., 2002; Walther, 2002a, 2002b) and narrow niche breadth (Marra and Remsen, 1997; Stratford and Stouffer, 2013). Understory insectivores are also especially sensitive to anthropogenic disturbance, experiencing population declines and local extirpation in response to habitat loss and fragmentation (Bierregaard and Lovejoy, 1989; Stouffer and Bierregaard, 1995; Canaday, 1997; Şekercioğlu et al., 2002; Sigel et al., 2006; Sigel et al., 2010; Cordeiro et al., 2015). The mechanistic underpinnings of these declines, however, are unclear (Powell et al., 2015-b). One possibility is that understory insectivores are particularly sensitive to the altered environmental conditions that result from forest fragmentation (Stratford and Robinson, 2005; Robinson and Sherry, 2012; Stratford and Stouffer, 2015). The understory of tropical forests is characterized by relatively low environmental variability on both ecological (Didham and Lawton, 1999) and evolutionary time scales (Janzen, 1967). Constancy in environmental conditions is hypothesized to promote physiological specialization (Janzen, 1967), including in understory insectivores (Robinson and Sherry, 2012). The microclimate hypothesis (Stratford and Robinson, 2005; Robinson and Sherry, 2012) posits that by altering the distribution of microclimates within a forest (Didham and Lawton, 1999; Laurance et al., 2002) habitat fragmentation introduces novel abiotic conditions that may physiologically challenge understory insectivores and contribute to their population declines.

A tenet of the microclimate hypothesis is that understory insectivores are sensitive to local abiotic environmental variation, and there is evidence supporting this idea. Activity and local abundances of certain understory insectivorous species in central Panama declined in xeric areas within individual home ranges during the tropical dry season (Karr and Freemark, 1983), suggesting that habitat selection is at least partially a function of microclimatic conditions. Similarly, a study across a precipitation gradient in central Panama found that Song Wren (*Cyphorhinus phaeocephalus*) individuals from drier forests had poorer mean body condition and abnormally low hematocrit values (Busch et al., 2011). Along this gradient, the species richness and abundance of understory insectivores declines with decreasing precipitation (Rompre et al., 2007). The limited evidence suggests that understory insectivores are sensitive to low humidity and high temperature, but plausible alternatives (e.g. responses to variation in food resources) exist (Robinson and Sherry, 2012). More detailed studies of the microclimatic associations of understory insectivores are needed to determine the role of microclimate variation in their habitat selection.

Light intensity is another microclimatic variable that may influence the habitat selection of understory insectivores and their sensitivity to fragmentation. For example, species from Neotropical forests that occupied low-light environments (e.g. understory insectivores) exhibited the greatest negative population trends and propensity for local extirpation (Patten and Smith-Patten, 2012). Similarly, high sensitivity to light may restrict movements of understory insectivores throughout a landscape matrix (Develey and Stouffer, 2001; Laurance et al., 2004; Stratford and Robinson, 2005) and could explain their low dispersal capabilities (Moore et al., 2008; Burney and Brumfield, 2009; Salisbury et al., 2012; Tarwater, 2012; Woltmann et al., 2012a) relative to other guilds. Habitat loss and fragmentation reduces connectivity (Andren, 1994) and may impede understory insectivores from recolonizing fragments (Powell et al., 2013), turning them into population sinks (Robinson et al., 1995). Sensitivity to light may therefore contribute to the population declines of understory insectivores (Stratford and Robinson, 2005; Robinson and Sherry, 2012) and could also be an important factor in their selection of microclimates.

To understand how understory insectivorous birds respond to variation in abiotic conditions within their home ranges, we assessed microclimate selectivity in a suite of nine understory insectivorous species in central Panama. Previous studies of avian microclimatic associations have relied on indirect sampling methods such as mist-nets (Karr and Freemark, 1983; Champlin et al., 2009) or point-counts (Patten and Smith-Patten, 2012), which do not allow for direct observation of the microhabitats used by birds. We adopted a novel approach by intensively sampling radio-tagged individuals of focal species within their own home ranges to characterize their microclimatic associations (light, temperature and humidity). We then compared distributions of bird microhabitat points with randomly selected points within the bird's home range to test for selectivity (i.e. to determine if birds were selecting microclimates within their home range that differed from microclimates at random points). Selectivity should be greater where environmental conditions are more challenging (e.g. Walsberg, 1993). Therefore, we sampled along a precipitation gradient, where intensity of the dry season decreases and annual rainfall increases with distance from the Pacific coast of Panama (Condit et al., 2000; Van Bael et al., 2004), to examine microclimate selectivity across differing environmental regimes. We predicted that understory insectivores would: (1) exhibit microclimate selectivity (i.e. select microclimates with significantly different humidity, temperature, and light intensity distributions than random), (2) exhibit greater microclimate selectivity in hotter, drier environments compared to cooler and more humid habitats, and (3) exhibit greater microclimate selectivity within localities during the dry season when humidity is lower and more variable than in the wet season.

2. Methods

2.1. Study sites

We sampled microclimates at three sites along the Isthmus of Panama (Fig. 1) between the months of February–July from 2012 to 2013. The three sites (Table 1) differ substantially in annual precipitation and degree of seasonality (Fig. 2). The driest site, Metropolitano Natural Park (Metropolitano hereafter), is a 232-ha fragment of semi-deciduous secondary tropical dry forest on the Pacific coast located within Panama City that receives 1800 mm annual rainfall and has a pronounced dry season (Van Bael et al., 2004). Metropolitano is surrounded on all sides by urban areas and is one of the only remaining tracts of dry forest left along the Pacific coast of Panama. The wet site, "Limbo", is a 104-ha study plot of old secondary and some primary (300–400 years old) tropical moist forest located within the 22,000-ha Soberanía National Park that receives 2600 mm annual rainfall and has a moderate dry season (Robinson et al., 2000). Limbo is deep within contiguous forest and is situated at least 3.5 km from the nearest forest edge. A narrow