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

Henry S. Pollock^{a,*}, Zachary A. Cheviron^{a,b}, T.J. Agin^d, Jeffrey D. Brawn^{a,c}^a Program in Ecology, Evolution, and Conservation Biology, University of Illinois at Urbana-Champaign, 505 S. Goodwin Ave., Champaign, IL 61801, USA^b Department of Animal Biology, University of Illinois at Urbana-Champaign, 505 S. Goodwin Ave., Champaign, IL 61801, USA^c Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, 1102 S. Goodwin Ave., Champaign, IL 61801, USA^d Department of Biology, University of South Dakota, 414 E. Clark St., Vermilion, SD 57069, USA¹

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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.

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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 (Buttner, 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

* Corresponding author. Tel.: +1 217 621 6007.

E-mail address: hpollock@illinois.edu (H.S. Pollock).¹ Present address.

(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., this issue](#)). The mechanistic underpinnings of these declines, however, are unclear ([Powell et al., this issue-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, this issue](#)). 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, Metropolitan 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](#)). Metropolitan 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

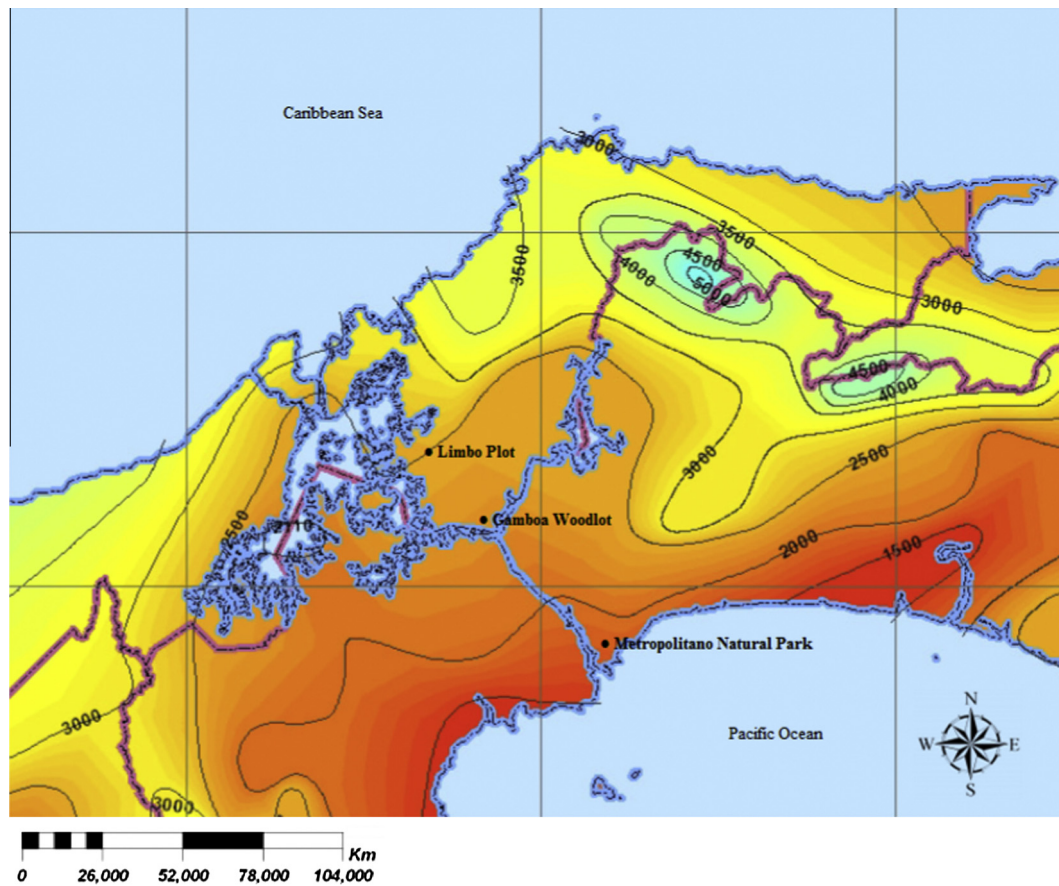


Fig. 1. Map of the study sites across the isthmus of Panama; numbers indicate annual rainfall in millimeters (adapted with permission from www.hidromet.com.pa).

Table 1

Characteristics of the three study sites (data from [Robinson et al., 2000](#); [Van Bael et al., 2004](#)).

Site	GPS coordinates	Annual rainfall (mm)	Forest age (years)	Canopy height (m)
Wet (Limbo)	9°9'N, 79°44'W	2600	60–120	30–40
Mesic (Gamboa)	9°7'N, 79°41'W	2100	60–70	20–30
Dry (Metropolitano)	8°59'N, 79°33'W	1800	90	20–35

(~5 m) gravel road runs through the center of the plot, but the canopy is closed over most of its length and it does not create enough edge to attract second-growth species ([Robinson et al., 2000](#)). The mesic site, the Gamboa Woodlot (Gamboa hereafter), is a 22-ha lowland secondary moist forest fragment located 6.9 km southwest of Limbo that receives 2100 mm of annual rainfall and also has a moderate dry season ([Robinson et al., 2000](#)). Gamboa is separated from the closest contiguous forest (Soberanía National Park) by a 100-m wide grassy field. We did not consider degree of fragmentation as a confounding factor since we sampled a variety of species (see Section 2.2) in both edge and interior habitats at all sites.

2.2. Focal species

We sampled nine understory insectivorous species (Table 2) representing six different avian families, with varying habitat preferences and sensitivities to anthropogenic disturbance (i.e. propensity to decline in abundance or disappear from disturbed habitats).

2.3. Radio-tracking understory insectivores

We sampled the microclimatic associations of individual birds within their home ranges using radio-telemetry. We sampled

during the dry season (February–April) and the wet season (May–August) to investigate potential seasonal differences in the degree of microclimate selectivity. We captured birds in mist-nets (12 × 2.6 m; 36-mm mesh) set at ground level. Upon capture, we placed birds in cloth bags and weighed them to the nearest 0.5 g. We then attached radio-transmitters (0.5–0.9 g: BD-2 model, Holo-hil Systems, Inc.) to birds with 1 mm beading cord using the leg harness method ([Rappole and Tipton, 1991](#)). Transmitters always weighed <5% of the bird's body mass to minimize adverse effects on behavior and fitness. We observed focal individuals for 5 min to ensure that the bird was able to move normally. All focal birds were given ≥24-h to acclimate to the radio-transmitters before observation took place.

We followed radio-tagged individuals of focal species using handheld VHF radio-telemetry to localize focal individuals. We recorded an average of 21.4 microhabitat points per individual ($n = 58$ individuals, $sd = 6.90$, range = 9–50 microhabitat points) and followed focal birds for an average of 3.78 days ($n = 58$ individuals, $sd = 3.23$, range = 1–14 days). Once a bird was visually located, we recorded behavior, time of day and amount of time spent at the microhabitat point. Once the bird vacated the point, we marked the precise location where the bird was observed with flagging tape and georeferenced the position using a handheld GPS unit (Garmin

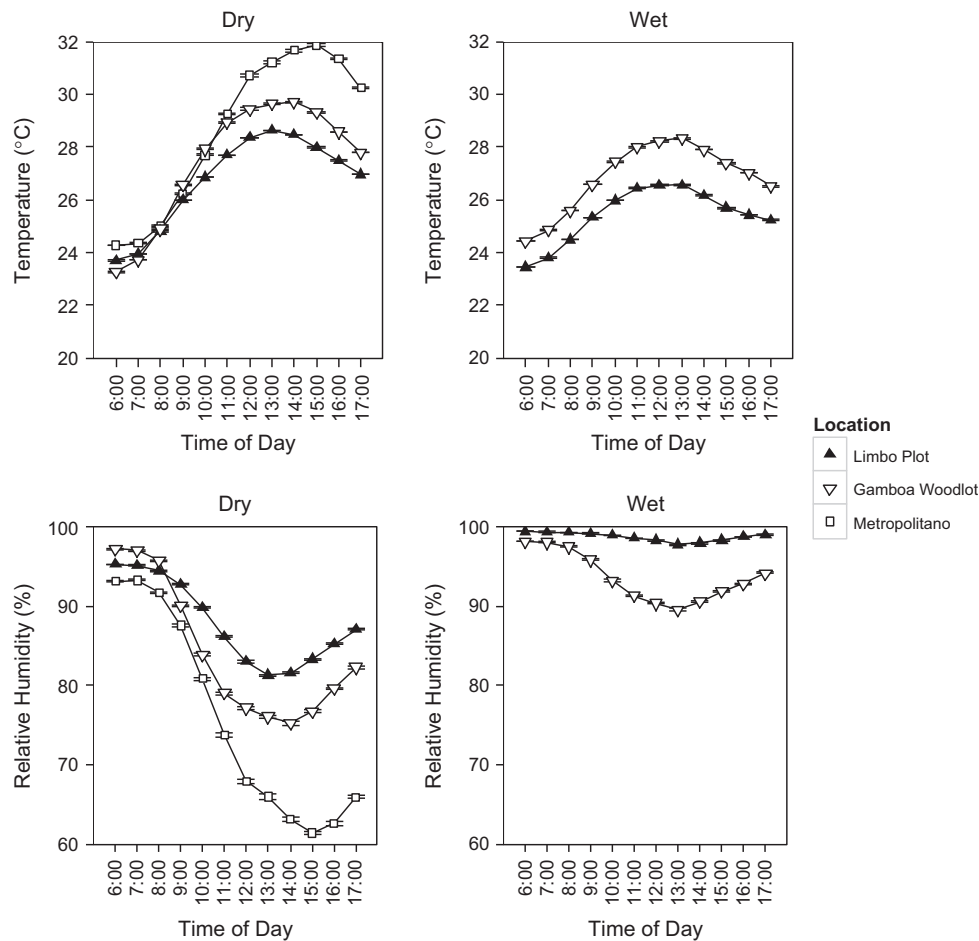


Fig. 2. Hourly diurnal variation in temperature and humidity by season collected at the study sites between 2012 and 2013 (mean \pm SE). Data include bird microhabitat points and random microhabitat points and represent a characterization of the understory abiotic environment at each site. No wet season data were collected in Metropolitan.

Table 2

Characteristics of study species and samples sizes of radio-tracked individuals per site (data from Parker et al., 1996; Woltmann et al., 2012b).

Species (scientific name)	Family	Mass (g)	Habitat preference	Sensitivity to disturbance	Wet ^a	Mesic ^b	Dry ^c
Scaly-throated Leaf-tosser (<i>Sclerurus guatemalensis</i>)	Furnariidae	34	Primary forest	High	5	–	–
Chestnut-backed Antbird (<i>Myrmeciza exsul</i>)	Thamnophilidae	28	Primary forest	Low	4	2	1
White-bellied Antbird (<i>Myrmeciza longipes</i>)	Thamnophilidae	28	Secondary forest	Low	–	8	2
Spotted Antbird (<i>Hylophylax naevioides</i>)	Thamnophilidae	17	Primary forest	Moderate	4	–	–
Streak-chested Antpitta (<i>Hyllopezus perspicillatus</i>)	Grallariidae	46	Primary forest	High	5	–	–
Rufous-and-white Wren (<i>Thryophilus rufalbus</i>)	Troglodytidae	28	Secondary forest	Low	–	2	5
Song Wren (<i>Cyphorhinus phaeocephalus</i>)	Troglodytidae	25	Primary forest	High	8	6	–
Red-throated Ant-tanager (<i>Habia fuscicauda</i>)	Cardinalidae	42	Secondary forest	Low	–	2	2
Orange-billed Sparrow (<i>Arremon aurantiirostris</i>)	Emberizidae	34	Secondary forest	Low	–	1	1
Total					26	21	11

^a Limbo Plot.

^b Gamboa Woodlot.

^c Metropolitan.

60CSx). Successive microhabitat points were separated by ≥ 15 m and/or 30 m, allowing birds to re-locate to an independent microhabitat point in an effort to control for spatial and temporal autocorrelation in microclimate (Swihart and Slade, 1985). We only investigated microclimates at microhabitat points where focal individuals spent ≥ 5 min to ensure that birds were not transiently passing through the microhabitat. We conducted preliminary trials to determine the appropriate distances (between 5 and 15 m, depending on the species) between observer and birds to minimize the effect of human disturbance on birds and maintained these dis-

tances throughout sampling. Any observations with abnormal behavior (e.g. rapid movements, alarm vocalizations, etc.) induced by human proximity were discarded.

2.4. Temperature, relative humidity and light measurements

We measured three environmental variables: temperature, relative humidity (RH hereafter), and light intensity. At each microhabitat point, we deployed stainless steel Hygrochron iButtons (Embedded Data Systems, Inc.), which recorded temperature ($^{\circ}$ C)

and RH (%) at 10-min intervals (temperature precision: ± 0.0625 °C, RH precision: ± 0.04 RH) for 2–5 days. All iButtons were calibrated against a mercury thermometer (model T6000, Miller & Weber, Inc.) with standards traceable to the U.S. National Bureau of Standards prior to use. We deployed iButtons with a protective plastic cover painted flat white to prevent solar radiation and precipitation from biasing temperature and humidity measurements (iButtons exposed to direct solar radiation and precipitation can yield spurious data). We measured light intensity (kLux) at each point after the bird departed using an Extech® EasyView EA30 digital light meter. The light meter reading was allowed to stabilize for 1 min and then light intensity was recorded. We measured light within 1 min of the bird's departure from the microhabitat point.

2.5. Selection of random points

At each microhabitat point, we designated a corresponding random point using a random-number generator to choose a cardinal direction (N, E, S, W) and distance (15–30 m) from the microhabitat point. We deployed and recovered iButtons simultaneously at microhabitat points and random points, allowing for direct comparisons between the two point types on the home range level. We placed iButtons at the same height at the random point at which the bird was observed at the microhabitat point. We measured light at each random point within 5 min of the light measurement at the corresponding microhabitat point.

2.6. Statistical analyses

We measured temperature and humidity at 10-min intervals for 2–5 days at microhabitat points within each individual bird's home range, but we restricted analyses to the temperature and humidity values that corresponded to when birds were observed at a given microhabitat point. Similarly, for random points, we used only the temperature and humidity values recorded at the same time of day when the bird was present at its corresponding microhabitat point to detect whether or not the bird was selecting a non-random subset of microclimates at that particular time of day. We first compared microhabitat points with random points on the level of individual home range. For each individual, we used the ks.test function in R (R Development Core Team, 2013) to compare the distribution of temperature, humidity and light intensity values of microhabitat points to the corresponding distribution of random points using nonparametric Kolmogorov–Smirnov (KS) two-sample tests with the null hypothesis that the microhabitat and random distributions are similar. To assess microclimate selectivity for understory insectivores as a guild, we took two approaches for each of the three microclimatic variables: (1) We pooled the results of all individual KS tests and performed a Fisher's combined probability test using the function combined.test from the package survcomp in R, which combined the results from the independent KS tests to generate a χ^2 distribution to test the null hypothesis that all of the individual null hypotheses were true; (2) we pooled all data and conducted two-sample permutation tests with 10,000 permutations. Each permutation combined the values of microhabitat and random points and then generated two distributions from the pooled data. The *p*-value was calculated as the proportion of sampled permutations where the difference in means was greater than or equal to the original mean difference between microhabitat and random points. To investigate whether selectivity was occurring on a seasonal basis, we pooled data from all species into either the dry season (February 1–May 15) or wet season (May 16–August 30), and conducted separate two-sample permutation tests with 10,000 permutations for each season for temperature, humidity and light intensity values. Although the exact date of the transition between dry and wet season varies annually (Fu and Li, 2004), and simplifying a continuous

variable (day of year) into a categorical variable (wet vs. dry season) may be problematic in some cases, only six individuals were not able to be placed unambiguously in either season. Additionally, we conducted all analyses on this subset of six individuals and obtained similar results and therefore deemed our seasonal classification to be adequate. To investigate whether level of selectivity varied across sites, we pooled data from all species and conducted separate two-sample permutation tests with 10,000 permutations for each site for temperature, humidity and light intensity values.

3. Results

We found little evidence of microclimate selectivity for any species. After pooling all individuals of each species across sites, temperature (Fig. 3), humidity (Fig. 4) and light intensity (Fig. 5) distributions were similar between microhabitat points and their paired random points. Only 1 of 58 comparisons at the individual level was significant ($D = 1$, $p = .029$; *C. phaeocephalus*, dry season 2013) for humidity and none was significant for temperature or light intensity. Overall, understory insectivores as a whole showed no evidence of microclimate selectivity for temperature (Fisher's combined probability test, $\chi^2 = 11.46$, $df = 116$, $p = 1$), humidity (Fisher's combined probability test, $\chi^2 = 25.73$, $df = 116$, $p = 1$), or light intensity (Fisher's combined probability test, $\chi^2 = 78.09$, $df = 116$, $p = 0.997$). The two-sample permutation test indicated no significant differences between random points and microhabitat points with respect to temperature ($Z = 0.01$, $p = 0.99$), humidity ($Z = -0.30$, $p = 0.76$), or light intensity ($Z = -0.27$, $p = 0.79$).

We also did not observe variation in microclimate selectivity on a seasonal basis, despite the fact that environmental conditions varied seasonally at all study sites (Fig. 2). Temperature did not differ between microhabitat and random points in the wet season ($Z = -0.40$, $p = 0.69$) or dry season ($Z = -1.38$, $p = 0.17$). Similarly, humidity did not differ between microhabitat and random points in the wet season ($Z = 0.39$, $p = 0.70$) or dry season ($Z = 0.76$, $p = 0.45$). Lastly, light intensity did not differ between microhabitat and random points in the wet season ($Z = -0.81$, $p = 0.42$) or dry season ($Z = -1.31$, $p = 0.20$).

Despite the observed variation in temperature and humidity regimes among our sampling sites (Fig. 2), we did not observe microclimate selectivity at the site level. Temperatures did not differ between microhabitat and random points at Limbo ($Z = 0.34$, $p = 0.72$), Metropolitanano, ($Z = -0.69$, $p = 0.49$) or Gamboa ($Z = 0.36$, $p = 0.72$). Similarly, humidity did not differ between microhabitat and random points at Limbo ($Z = -0.28$, $p = 0.78$), Metropolitanano ($Z = 0.32$, $p = 0.75$) or Gamboa ($Z = -0.19$, $p = 0.85$). Lastly, light intensity did not differ between microhabitat and random points at Limbo ($Z = 0.18$, $p = 0.86$), Metropolitanano ($Z = -0.57$, $p = 0.57$) or Gamboa ($Z = 0.41$, $p = 0.68$).

4. Discussion

Our study is the first to document microclimatic associations of understory insectivores using focal observations of individual birds. Despite their putative sensitivity to humidity (Karr and Freemark, 1983) and light (Patten and Smith-Patten, 2012), we found no evidence of microclimate selectivity on the home range level across seasons or among sites distributed across a pronounced precipitation gradient in Panama. These results were consistent across nine species that show considerable variation in habitat preferences and sensitivity to anthropogenic disturbance, suggesting that lack of microclimate selectivity on the level of the home range is a general pattern in this guild.

A central assumption of the microclimates hypothesis (Stratford and Robinson, 2005; Robinson and Sherry, 2012) is that understory

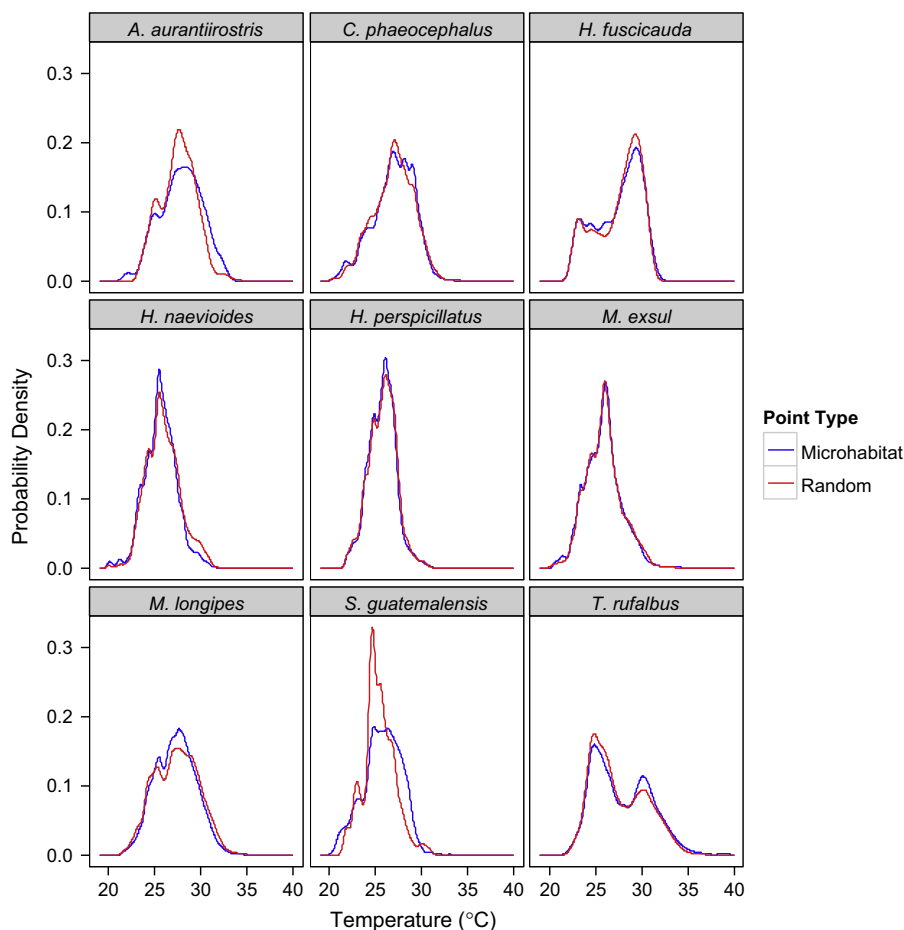


Fig. 3. Probability density functions of temperature at microhabitat and random points of focal species (data for each species pooled across sites).

insectivores are sensitive to local environmental variation, which may underlie their population declines in response to the altered environmental conditions associated with forest fragmentation (Laurance et al., 2002). We tested this assumption in both contiguous forest and forest fragments and found no evidence of sensitivity to environmental variation, at least in terms of microclimate use. However, we only sampled birds at three sites, all of which were older secondary forests. The microclimatic effects of fragmentation on understory insectivores may only occur early on during forest regeneration, when edge effects are most severe (Laurance and Yensen, 1991). Alternatively, the degree of microclimate selectivity may depend on fragment size (e.g. understory insectivores only exhibit sensitivity to local environmental variation in very small fragments). Future research should compare the microclimate associations of understory insectivores in forest fragments of different size and age in contiguous forest to test the generalizability of our results.

Perhaps the most unexpected result was the lack of microclimate selectivity across three sites with substantially different precipitation regimes and across seasons. We originally predicted that selectivity would be greater (i.e. distributions of bird microhabitat and random points would be more dissimilar) at hotter, drier sites and during the dry season, when environmental conditions are more challenging (Williams and Middleton, 2008). The apparent lack of microclimate selectivity at drier sites and in the dry season ostensibly suggests that individuals of our focal species are insensitive to microclimate variation within their home ranges, at least within the levels of variation to which they were exposed at our field sites in Panama.

Within each sampling site at a given time of year, there was little variation in temperature and humidity in the forest understory. Uniformity in the understory environment was especially apparent at our contiguous wet forest site (Limbo), where in the wet season (May–August), relative humidity remained close to 100% and daily temperature varied by as little as 3 °C over a 24-h time period. Low variability in environmental conditions in the forest understory corroborates previous studies of forest microclimate (Ewers and Banks-Leite, 2013) and differs from conclusions drawn by Karr and Freemark (1983), who reported substantial microclimate variation at locations sampled within Limbo. The lack of microclimate selectivity, therefore, might simply be attributed to a general lack of microclimate variation for understory insectivores to select.

Similar to temperature and humidity, light intensity was relatively uniform throughout the forest understory at all sites. The low (0–2 kLux) mean light intensity and low light variability that we found in the understories of all of our forest sites corroborate previous results from other tropical forest sites. Only a small fraction (0.5–5%) of incident light reaches the understory of closed-canopy tropical forests (Chazdon and Pearcy, 1991) and diurnal and seasonal variability of light intensity is low in forest understory relative to other environments (Chazdon and Fetcher, 1984).

In our focal observations, we noticed that understory insectivores appeared to avoid microhabitats such as canopy gaps. Light intensity in gaps can reach 120 kLux on sunny days (H.S. Pollock, unpublished data), two orders of magnitude greater than the light intensity encountered in shaded forest understory. These microhabitats were rare within individual territories, but were actively avoided when encountered by a variety of understory insectivore

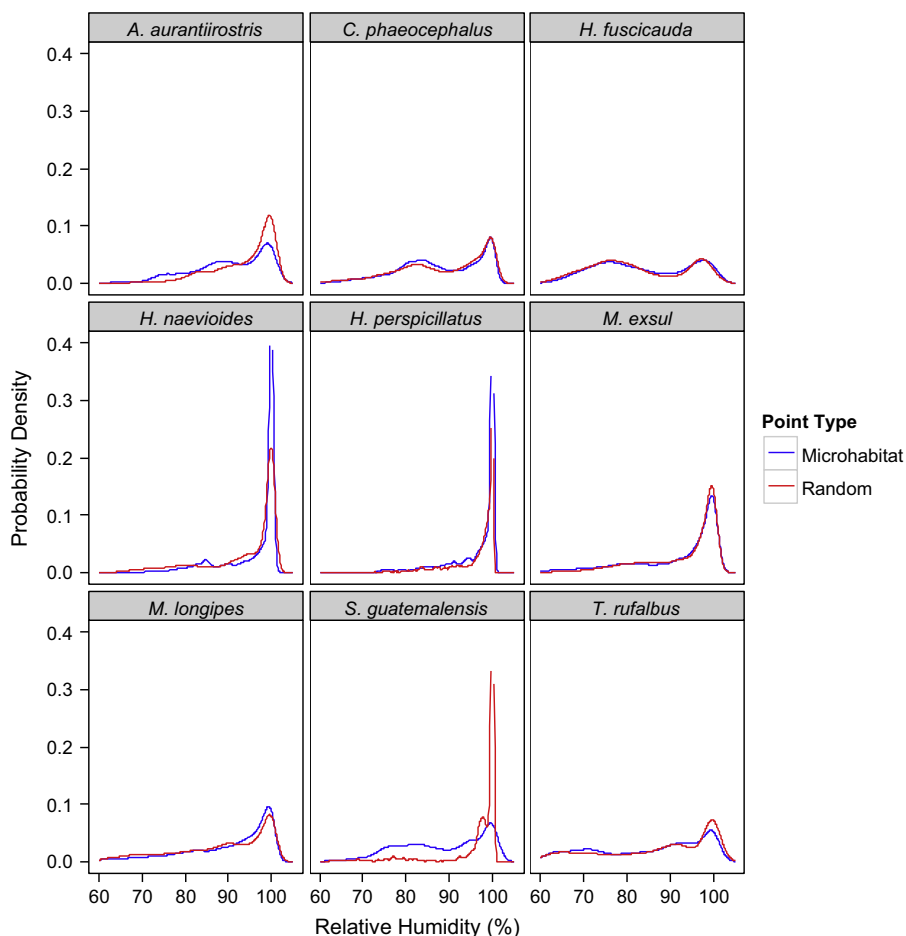


Fig. 4. Probability density functions of humidity at microhabitat and random points of focal species (data for each species pooled across sites).

species (H.S. Pollock, personal observation). Many tropical forest bird species exhibit a marked preference for either closed-canopy forest or gap habitats (Schemske and Brokaw, 1981), and the avoidance of microhabitats with high light intensity corroborates patterns recently reported for other understory insectivores (e.g. Patten and Smith-Patten, 2012). Inability or unwillingness to use areas with high light intensity may be due to physiological sensitivity to the light itself (e.g. understory insectivores may have evolved eyes specialized to low-light environments to detect their cryptic arthropod prey), to the higher temperature and lower humidity associated with high light intensity, or to another proximate factor (e.g. reduced predation risk, increased prey availability, etc.). The high light intensity environments associated with fragmentation could make habitats physiologically unsuitable for understory insectivores (e.g. Robinson and Sherry, 2012), or could limit movements between habitats (e.g. Gillies and St. Clair, 2010; Powell et al., this issue-a), both of which could contribute to the population declines of understory insectivores in response to forest fragmentation. Given the increasing rates of deforestation and fragmentation in the Neotropics (Achard et al., 2002), understanding the mechanism of sensitivity to light in understory insectivores should be made a research priority in Neotropical avian conservation.

Despite the lack of observed microclimate selectivity across species, sites, and seasons, there were several limitations to our sampling design that could be improved upon in future research efforts. One drawback of our study is that we were only able to sample larger-bodied insectivore species (range: 17–46 g) due to time constraints and equipment limitations. Many understory insectivore species (e.g. Dot-winged Antwren (*Microrhopias quixen-*

sis; 9 g), White-flanked Antwren (*Myrmotherula axillaris*; 8 g), Golden-crowned Spadebill (*Playtrinchus coronatus*; 9 g), Ruddy-tailed Flycatcher (*Terenotriccus erythrurus*; 7 g) were too small to attach radio-transmitters without affecting behavior and mobility (H.S. Pollock, personal observation). These smaller-bodied species are especially vulnerable to forest fragmentation (Sigel et al., 2006, 2010), possibly due to increased sensitivity to local environmental variation, and may exhibit microclimate selectivity, in contrast to their larger-bodied counterparts. Future studies should expand sampling to include smaller-bodied species to account for the possibility of microclimate selectivity occurring in this subset of understory insectivores.

The spatial and temporal extent of our sampling efforts was also quite limited. Temporally, our data were collected in only two sampling years (2012–2013), both of which were characterized by mild dry seasons (Panama Canal Authority, unpublished data), and it is possible that we did not observe microclimate selectivity because it is only manifested during periods of severe environmental stress. The abundance of cool, dark, humid microclimates in the understory of closed-canopy forest may act as a buffer for understory insectivores and preclude their need for microclimate selectivity except under extreme environmental conditions. Intensity and length of the dry season varies substantially from year to year and can have strong effects on population dynamics (Sillett et al., 2000; Williams and Middleton, 2008) and behavior (W.A. Boyle, personal communication) of tropical birds. It would be informative to examine microclimate use on a longer temporal scale to determine whether or not understory insectivores exhibit selectivity in drier years.

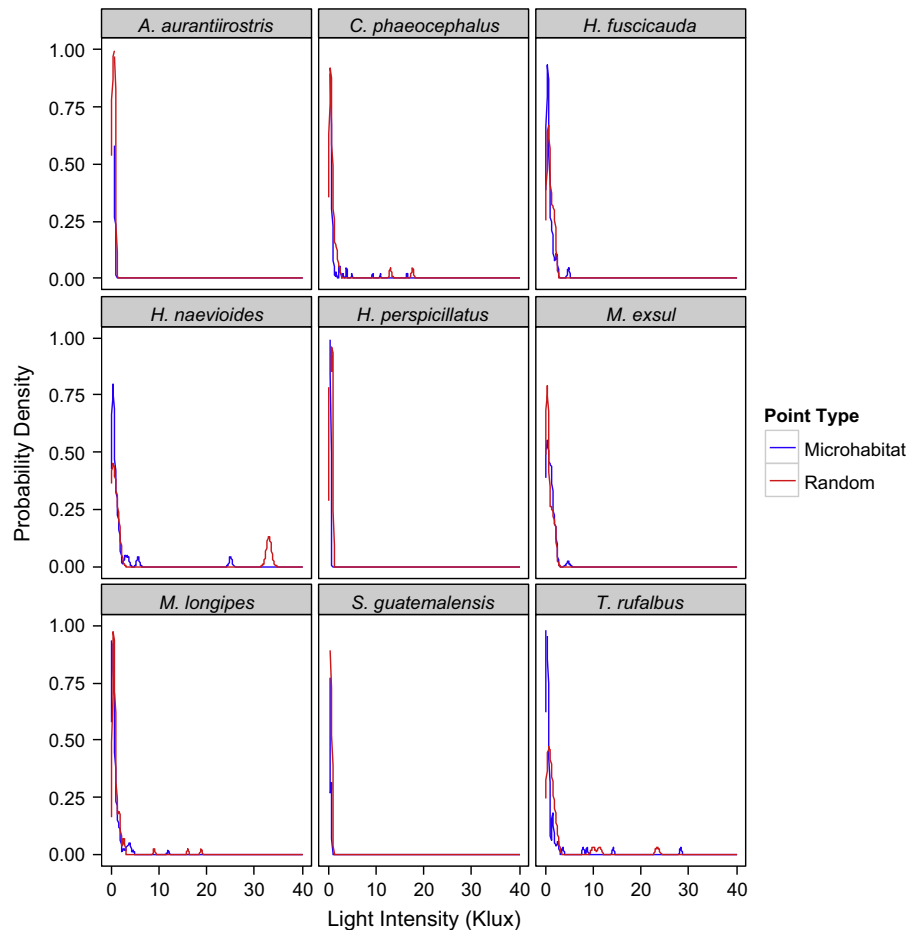


Fig. 5. Probability density functions of light intensity at microhabitat and random points of focal species (data for each species pooled across sites).

Our spatial scale was also restricted to comparing bird microclimate points with randomly selected points within each bird's home-range, and therefore, we did not quantify all of the microclimates "available" to each bird (i.e. microclimates outside of the bird's home-range, or even microclimates within the bird's home-range that it does not use, such as gaps). Therefore, we were unable to compare microclimates used by birds with all microclimates "available" to birds (sensu Jones, 2001), and birds may actually be exhibiting microclimate selectivity on a larger spatial scale (i.e. between home-ranges) or even within their home-ranges by avoiding gaps. Future research should attempt to quantify all microclimates available to birds to determine whether understory insectivorous birds exhibit selectivity on a larger spatial scale or via gap avoidance.

Alternatively, understory insectivores may exhibit sensitivity to environmental variation on a geographic scale, coping with ambient environmental conditions until an environmental threshold is reached, which limits species' distributions. Although within-site microclimate variation was low at any given time, variation among sites was substantial. For example, the driest site, Metropolitan, routinely experienced temperature ranges 4 °C greater and humidity ranges 20% greater than the wettest site, Limbo. Many species present at Limbo and Gamboa were either present in very low abundances or completely absent from the dry forest site, Metropolitan (e.g. Song Wren, Streak-chested Antpitta, Scaly-throated Leaf-tosser, Spotted Antbird, Chestnut-backed Antbird). Sensitivity to microclimate variation could explain the declines of these species across the precipitation gradient and their absence from the drier and hotter Metropolitan. Thus, despite the lack of microcli-

mate selectivity within habitats, environmental variation on a larger spatial scale may limit the distribution of understory insectivores (Rompere et al., 2007), though the mechanism (e.g. food limitation, direct sensitivity to climate) remains unclear (Williams and Middleton, 2008; Busch et al., 2011; Robinson and Sherry, 2012).

The lack of environmental variation in tropical forest understory is troubling in light of recent climate change. If environmental conditions exceed the physiological tolerances of understory insectivores, they will not be able to rely on local microclimatic heterogeneity to escape physiological stress (e.g. Walsberg, 1993) and may experience severe fitness costs. Nonetheless, vagile animals such as birds can also take advantage of large-scale spatial heterogeneity (i.e. between habitat patches) in environmental conditions to mitigate the effects of climate change (Bonebrake and Deutsch, 2012). However, the lowland tropics are characterized by shallow latitudinal temperature gradients, meaning that many understory insectivorous birds may have to travel large distances to find suitable habitat in response to increasing temperatures (Wright et al., 2009). Finding thermal refugia will be exacerbated by increasing habitat fragmentation (Achar et al., 2002) coupled with the low dispersal abilities of understory insectivores (Moore et al., 2008; Woltmann et al., 2012a) and their avoidance of habitats characterized by high light intensity (Schemske and Brokaw, 1981; Patten and Smith-Patten, 2012, this paper). The potential synergistic effects of climate change with habitat fragmentation have received little attention in the literature and will be an important aspect of predicting the impacts of anthropogenic change on tropical bird populations. In addition, tropical organisms in general

are predicted to have narrow physiological tolerances (Janzen, 1967) and low physiological flexibility (Bozinovic et al., 2011), yet the physiological tolerances of tropical understory insectivores are not known (Robinson and Sherry, 2012). Direct measurements of the physiological tolerances to temperature and humidity of understory insectivores and further investigation of the mechanism of light avoidance will be a crucial first step towards predicting responses to climate change and forest fragmentation in these species.

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