

Research article

Thermoregulation of understory birds in lowland Amazonia

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Subject Editor: Jiri Reif Editor-in-Chief: Dries Bonte Accepted 5 April 2024 Understanding the capacity for thermoregulation is critical for predicting organismal vulnerability to climate change, especially in lowland tropical rainforests, where warming conditions combine with high humidity and limited elevational or latitudinal refugia. Here, I focused on nine species of ground-foraging insectivorous birds in the genus Myrmoderus, Myrmornis, Hylopezus, Myrmothera, Formicarius and Sclerurus – sensitive forest specialists characterized by recently documented population declines in both disturbed and undisturbed forests. Using high-resolution data from loggers deployed on birds and their environment, I examined whether and how birds used thermoregulation and whether ambient water provided cooling opportunities. Variation in the rate of temperature change over the diel cycle suggested that all species employed behavioral and physiological thermoregulation, but some patterns differed by species' phylogenetic relatedness. All species warmed hours before their environment at sunrise, then experienced lower temperature increases at midday relative to the ambient thermal flux. These morning warming periods peaked around sunrise for all but Sclerurus rufigularis and constituted the diel temperature change maxima for five of the nine species. Six species exhibited pronounced oscillations in temperature change consistent with regular bathing around sunset, possibly for thermoregulatory or other purposes. This oscillation was the most prominent feature in the diel thermal flux for all three Sclerurus species and, to a lesser extent, for Myrmoderus ferrugineus, Myrmornis torquata and Myrmothera campanisona. Local rainfall reduced ambient temperatures, and birds experienced stronger cooling in the wet season and with higher rainfall intensity. However, rain-induced cooling events were markedly absent in all three *Sclerurus* spp. These results highlight the fundamental role of water in avian thermoregulation and suggest that terrestrial insectivores attempt to maintain thermal homeostasis throughout the diel cycle. The observed thermoregulatory behaviors highlight a potentially critical aspect of their vulnerability - thermal regimes are profoundly altered by forest disturbance, climate change, and their combination.

Keywords: Amazonian avifauna, behavioral thermoregulation, climate change, microclimate refugia, physiological thermoregulation, terrestrial insectivores



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Introduction

Global climate change has raised concerns regarding the loss of species in lowland tropical rainforests. Organisms in these biodiversity hotspots may be particularly vulnerable to warming because they have adapted to low climatic variations (Janzen 1967, Ghalambor et al. 2006, Huey et al. 2012, Pollock et al. 2021, Bennett et al. 2021), occupy hot environments that are rapidly changing (Mora et al. 2013, Bathiany et al. 2018), and cannot easily track their thermal niche via elevational or latitudinal shifts (Colwell et al. 2008, Wright et al. 2009). These concerns stem primarily from theory because monitoring responses of tropical biota to climate change inherently requires long-term datasets limited to a few locations and taxa. The Neotropical avifauna is among the best-surveyed groups (Lees et al. 2020), but only a handful of sites (in Ecuador, Brazil and Panama) have reported on temporal abundance trends within undisturbed rainforests (Stouffer et al. 2021, Pollock et al. 2022, Blake and Loiselle 2024). These studies show shifts in community structure, largely marked by declines in understory and terrestrial insectivores, with climate change as the suspected cause (but see a resurvey in Peru reporting no change, Martínez et al. 2023). Two of these sites have examined climate specifically and found that more extreme dry seasons decreased population growth rates (Brawn et al. 2017) and even body size of birds (Jirinec et al. 2021a). Although broad patterns have emerged, their mechanisms remain unclear. Linking patterns to processes is impeded by limited data on species-specific responses to varying abiotic conditions in the Neotropics (Lees et al. 2020, Soares et al. 2023).

Behavioral and physiological thermoregulation are crucial adaptations for coping with environmental variation and are key processes for mitigating the effects of climate change (Huey et al. 2012). To maintain thermal homeostasis, birds regulate their body temperature via several physiological pathways, including heat dissipation through the bill, skin, gular flutter, hyperthermia, and evaporative water loss (McKechnie and Wolf 2019). The role of evaporative water loss (EWL) has been underscored by studies on aridzone birds that occupy characteristically hot and dry environments (McKechnie et al. 2016, 2021, Smit et al. 2018), but strategies of avifauna from these regions may not match the tropics where high humidity significantly constrains its potential (Powers 1992, Weathers 1997, Gerson et al. 2014, van Dyk et al. 2019). In addition, the gamut of behavioral thermoregulation options in the lowland tropics is limited, particularly for terrestrial species that occupy the coolest microclimates near the forest floor (Stratford and Robinson 2005, Nunes et al. 2022, Pollock et al. 2023, Xing et al. 2023). In fact, studies at the Brazil site show that terrestrial insectivores seek microclimate refugia, particularly during periods associated with high ambient temperatures (Jirinec et al. 2022a, b). Strong ties to certain microclimates may explain why this ecological guild declined following forest disturbance (Stouffer and Bierregaard 1995, Canaday 1996, Stratford and Stouffer 1999, Canaday and Rivadeneyra 2001) as well as in undisturbed forests under climate change (Stouffer et al. 2021, Pollock et al. 2022, Blake and Loiselle 2024) – both processes linked to shifts in abiotic conditions (Jirinec et al. 2022a, Nunes et al. 2022). The capacity of sensitive understory species to maintain thermal homeostasis thus remains a crucial data gap with implications for hundreds of species in vast tropical regions experiencing environmental changes.

Water access contributes to thermoregulatory capacity of tropical avifauna in several ways. Water intake through drinking is required for physiological heat dissipation (the supply for EWL); however, ambient water may also be a source of direct, rapid cooling through conductive and evaporative heat loss. Cooling may occur inadvertently when birds are exposed to rainfall or deliberately through bathing. Bathing behavior may include substantial soaking of feathers in water, for which birds use streams, puddles, tree cavities, or leaves (Slessers 1970, Jullien and Thiollay 1998, Delgado-Martínez et al. 2022), and some species intentionally bathe in rain or rain-soaked foliage (Slessers 1970). Although bathing is often associated with hygiene, observations of bathing at higher rates at higher temperatures also suggest a thermoregulatory function (Slessers 1970, Jullien and Thiollay 1998, Oswald et al. 2008). However, excessive water can also be detrimental as acute exposure might lead to hypothermia, prolonged and severe rainfall constrains foraging opportunities (Nowack et al. 2015), and high humidity blunts EWL by reducing the organism-environment gradient (van Dyk et al. 2019). The hygric niche concept proposes the existence of rainfall optima for tropical endotherms (Boyle et al. 2020), and access and exposure to water thus present both challenges and opportunities for birds in the context of thermoregulation.

The Biological Dynamics of Forest Fragments Project (BDFFP) near Manaus, Brazil, offers an opportunity to study the response of sensitive species to local variation in abiotic conditions (Stouffer 2020). The BDFFP reported loss of avian terrestrial insectivores in areas free from human disturbance over an interval marked by progressively hotter, drier dry seasons and hotter, wetter wet seasons (Stouffer et al. 2021, Jirinec et al. 2022a). Using standardized data collected by loggers placed on terrestrial insectivores and their environments, I addressed two general aims. First, I aimed to determine whether and how birds use thermoregulation by comparing the diel rates of temperature change (referred to as 'thermal flux') between bird and ambient loggers. Second, through testing for relationships between local rainfall intensity and cooling events experienced by birds, I aimed to determine whether ambient water affects avian thermoregulation. The results reveal novel insights into the thermal ecology of these enigmatic rainforest species and present implications for their persistence under climate change.

Material and methods

Study area and study sites

Field data were collected near Cabo Frio and Camp 41, two study sites at the BDFFP (Fig. 1). Despite its name, the BDFFP has remained more than 90% forested since its inception in 1979, and vast tracts of primary forests remain to this day (Rutt et al. 2019a). Conditions are warm and humid throughout the year, but a single wet-dry cycle reduces rainfall by ~ 50% during the dry season from June to November (Jirinec et al. 2022a). Typical of the Guiana Shield region, the topography is reticulated, with plateaus bisected by streams that are sometimes > 100 m downslope (Tomasella et al. 2008, Jirinec et al. 2022a). Temperature and water availability vary seasonally across this elevational gradient - soil moisture is lower during the dry season and lowest on plateaus, whereas temperature varies little with elevation during the wet season and increases with elevation during the hotter dry season (Jirinec et al. 2022a). Across this landscape, terrestrial insectivores were captured and fitted with loggers that measured the temperature changes birds experienced. Ambient loggers measured environmental conditions concurrently with animal-borne sensors to assess bird response to shifts in weather across daily and seasonal cycles.

Measuring ambient conditions

Ambient conditions were quantified by measuring understory air temperature (T_{air}) between 8 June 2017 and 11 September 2019, soil temperature (T_{soil}) and soil moisture (*SM*) between 3 June 2017 and 13 September 2019, and ambient water temperature (T_{water}) between June 21 and 14 September 2019. Ambient measurements overlapped spatiotemporally with bird measurements (Supporting information).

Understory T_{air} was sampled every 15 min at 0.125°C resolution and 0.5°C accuracy using Intigeo-P65B1-11T-20deg loggers (Migrate Technology). These matched devices that were placed on birds, but ambient T_{air} loggers were positioned near the forest floor in the vicinity of capture locations (Fig. 1). T_{air} loggers (n=6) were systematically placed across a range of elevations and away from treefall gaps, with a final



Figure 1. Study area and sampling locations. The research was conducted at two sites (Cabo Frio, Camp 41) at the Biological Dynamics of Forest Fragments Project (BDFFP), located ~ 60 km north of Manaus, Brazil. Thirty-two individuals of nine species of terrestrial insectivorous birds were captured in continuous forest and tracked with temperature loggers (T_{tag}). Ambient air temperature (T_{air}) was measured with identical loggers placed in the understory (squares), while rainfall (soil moisture, *SM*) and soil temperatures (T_{soil}) were sampled by nine weather stations (crosses) across three transects. Blue dots denote temperature measurements (T_{water}) within water bodies (streams, seeps, puddles, cavities, palm bracts). Green shading represents forest canopy height in 2019 (light 0 m, dark ~ 35 m) from Potapov et al. (2021).

location offset by 3 m at a random bearing. PVC stakes (~ 10 cm) held T_{air} loggers above the soil, facing upward to reflect animal-borne loggers.

To study the impact of ambient water on local temperature and bird cooling, weather stations were installed and ambient water temperature was manually measured. T_{water} was obtained from opportunistic measurements (CH-103 thermometer; Walcom International Industry) at 73 locations during daylight hours in the 2019 dry season (Fig. 1). These measurements came predominantly from streams and seeps but also included puddles (n=10), pools (n=5), tree cavities (n=4), and palm bracts (n=3). To track rainfall events, nine weather stations were placed across the two study sites (Fig. 1). Stations comprised of one logger (TrueLog100) and one sensor (SMT100; T_{soil} and SM measurement capabilities), both manufactured by Truebner. Stations were set to measure T_{soil} (0.2°C accuracy) and soil moisture as percent volumetric water content (3% accuracy) at 10-min intervals for ~ 2.3 years. Readings were taken synchronously starting on the hour along the sensor blade fully inserted into the ground, thus reflecting conditions in the upper ~ 11 cm of the soil. Although precipitation is usually measured directly via rain gauges, soil moisture is a more reliable proxy given that stations were exposed to harsh conditions (heat, humidity, wildlife and litterfall) and operated for up to nine months between checks. Stations were arranged in three transects running approximately north to south (Fig. 1). Because rainfall in this environment can be localized, and winds generally carry precipitation from east to west (Anselmo et al. 2020), the design adequately linked rainfall events with conditions experienced by birds in the two study sites (Supporting information). Two transects were placed at Cabo Frio (lengths 585 and 488 m), where the study birds aligned more along the north-south axis, and one transect at Camp 41 (647 m).

 $T_{\rm air}$ loggers and weather stations functioned over various intervals because of moisture ingression and wildlife disturbances (Supporting information). At least one $T_{\rm air}$ logger operated throughout the entire bird tracking period (Supporting information). Loggers obtained a total of 187 120 $T_{\rm air}$

measurements. Weather stations functioned throughout the bird tracking period, but short data gaps developed at three stations in Cabo Frio when rodents severed sensor cables. Weather stations obtained a total of $1\,005\,677$ of both *SM* and $T_{\rm soil}$ measurements.

Bird temperature

This study comprises nine species of terrestrial insectivores tracked in the primary forest of the BDFFP (Table 1) and represents nearly all of the 10 species in the guild examined by Stouffer et al. (2021) to estimate population trends. I do not include *Grallaria varia* and *Cyphorhinus arada* but add a new species *Myrmothera campanisona*. The focal species here contain antbirds (*Myrmorderus* and *Myrmornis* spp.), antpittas (*Hylopezus* and *Myrmorthera* spp.), antthrushes (*Formicarius* spp.), and leaftossers (*Sclerurus* spp.) – six genera that reflect diverse body size, nesting strategy, and locomotion.

Birds were fitted with temperature loggers to quantify the avian thermal flux. Loggers (Intigeo-P65B1-11T-20deg) were attached via a backpack-style harness and weighed approximately 1 g, representing $\leq 5\%$ of bird body mass (Jirinec et al. 2021b). This configuration appeared to have no adverse effects on the study individuals (Jirinec et al. 2021b). Loggers measured temperature atop a stalk positioned 9 mm above logger base, which was flush with the bird's skin. Logger readings were thus influenced by heat radiating from bird bodies, whose internal temperature averages between 40.5 and \geq 43.0°C depending on species (Jirinec et al. 2022b), as well as ambient temperature on the forest floor, which averaged between 23.0 and 28.0°C depending on diel and seasonal cycles (Jirinec et al. 2022a). Here, bird logger temperature is denoted T_{tag} . As in T_{air} , T_{tag} loggers sampled temperature every 15 min. To eliminate any potential influence of handling on bird behavior, only tag measurements taken after midnight local time following the day of capture and up to three hours before recapture were considered. Methods pertaining to bird capture are described in more detail in Jirinec et al. (2022b).

Table 1. Study species sample size, body size, and timing of ΔT thresholds from generalized additive models (Fig. 3). Times are local times within the diel cycle, starting at midnight: warming start (first instance of positive ΔT), max ΔT , cooling start (following morning warming, the first instance of negative ΔT), min ΔT . Brief fluctuations between warming and cooling in the afternoons and evenings for some species are not considered here. a) Mean mass per species from Jirinec et al. (2021a), except for *M. campanisona*, for which mass represents individuals captured in this study. Mass sample size mean and range are 103 (4–265) individuals. b) Time at which tag temperature change matches air temperature change ($\Delta T tag = \Delta T air$). That is, intersection of tag and air curves in Fig. 3. c) Proportion of days where individuals experienced at least one major cooling event ($\geq 5^{\circ}$ C drop in 15 min) likely caused by contact with water, either through bathing or rainfall exposure.

Species	n	Mass (g) ^a	Warming start	$Max\ \Delta T$	Cooling start	$Min\ \Delta T$	Morning equilibrium ^b	Cool days ^c
Myrmoderus ferrugineus	4	23.3	02:51	05:56	13:02	17:12	06:47	0.48
Myrmornis torquata	3	43.8	03:54	18:07	12:20	17:29	06:58	0.33
Hylopezus macularius	4	42.1	03:58	05:24	12:45	18:57	06:46	0.21
Myrmothera campanisona	4	48.2	02:16	05:34	12:56	18:57	07:02	0.16
Formicarius colma	5	45.8	03:46	06:00	12:49	17:48	06:46	0.30
Formicarius analis	5	61.8	04:12	06:06	12:53	17:37	06:51	0.32
Sclerurus obscurior	3	25.2	04:45	18:31	13:14	17:41	06:55	0.83
Sclerurus rufigularis	1	20.9	04:48	18:24	12:27	17:31	07:29	0.85
Sclerurus caudacutus	3	39.1	03:34	18:31	12:28	17:42	06:41	0.87
Mean	3.6	38.9	03:47	11:24	12:46	17:53	06:55	0.48

Loggers were deployed on 70 individuals, and 32 individuals from nine species were recovered between 2017 and 2019 (Supporting information). The recovered T_{tag} sample size ranged from one to five per species and temperature readings ranged from 1941 to 66 709 per individual (961 371 in total).

Statistical analysis

Diel thermal flux

The rates of temperature change (ΔT) were computed from ambient loggers and bird tags to represent the diel thermal flux for comparison. Time of day is used throughout the analysis because this equatorial region has relatively consistent sunrise (~ 06:00) and sunset (~ 18:00) timings throughout the year (Jirinec et al. 2022a). ΔT was calculated between adjacent time steps as T at time of interest (Tt_0) minus T15 min prior (Tt_{-1}). That is, ΔT is the temperature change at lag 1. This allows standardized quantification of warming (positive ΔT) and cooling (negative ΔT), along with magnitude, for ambient loggers and bird tags. ΔT_{soil} at lag 1 is also presented to show the thermal flux in the soil, a buffered environment that is more resistant to sun flecks.

Generalized additive models (GAMs) were used to estimate the diel thermal flux in all cases. GAMs were fitted with the R package 'mgcv' ver. 1.8-41 (Wood 2017, 2022). mgcv's *bam()* function was used to model ΔT as the sum of two smooths: decimal time of day (0–23.99) using the cyclic cubic regression spline basis function (bs='cc', k=50), the index of sequential observation per logger (2 to n) with the Gaussian process basis (bs='gp', k=50) to help account for autocorrelation, and a grouping term (bs='re') to account for clustered data (species, ΔT_{air} logger, weather station). The GAM structure for *Sclerurus rufigularis* did not include a group term because only one logger was recovered for this species. All models assumed a Gaussian error distribution and were fit using the restricted maximum likelihood.

Cooling effects of rainfall

To determine whether and how local rainfall affected avian thermal flux and ambient temperature, $\Delta T_{\rm tag}$, $T_{\rm soil}$, and rainfall were related on a per-date basis in each study site. A change in soil moisture at lag 1 (ΔSM) at each station was used to represent rainfall, similar to the approach in calculating ΔT . A positive ΔSM (i.e. increasing soil moisture) thus indicates a rain event at that time and location, with the magnitude of ΔSM proportional to its intensity (Supporting information). The maximum T_{soil} and maximum ΔSM for each date per region were then calculated. That is, for each date in the 2017-2019 study interval, the highest change in SM and highest $T_{\rm soil}$ for Cabo Frio (maximum ΔSM and $T_{\rm soil}$ of six weather stations) and Camp 41 (maximum of three weather stations) were calculated. Similarly, the minimum ΔT_{tag} for each bird and date was then computed. In other words, these were the largest temperature drops birds experienced (per 15 min) on each date. Finally, these cooling events were joined with ΔSM and $T_{\rm soil}$ maxima by date and the site in which birds were captured.

Analyses involving rainfall were conducted in R package 'glmmTMB' ver. 1.1.8 (Brooks et al. 2017). To examine the effect of rainfall intensity on local temperature (Supporting information), a generalized linear model (GLM) was used to model maximum daily temperature (max T_{soil}) as a function of maximum daily rainfall intensity (max ΔSM). To determine the effect of season on avian cooling (Supporting information), a generalized linear mixed model (GLMM) was used to model daily minimum temperature change experienced by birds (min ΔT_{tag}) as a function of season (wet: December–May, dry: June–November). This model allowed both intercept and slope to vary across species and individuals. To examine the effect of rainfall intensity on avian cooling overall (Supporting information), a GLMM was used to model daily minimum temperature change experienced by birds (min ΔT_{rae}) as a function of maximum daily rainfall intensity (max ΔSM). This model allowed both intercept and slope to vary across species and individuals. Lastly, to determine species-specific effects of rainfall intensity on cooling, GLMMs were used for each species individually (Supporting information). These modeled daily min ΔT_{tag} as a function of daily max ΔSM and allowed intercepts to vary across individuals. An exception was the model for S. rufigularis – a GLM was used because the data comprised a single individual (Supporting information).

Model fit evaluation and error distribution selection were based on trials using the R package 'DHARMa' ver. 0.4.6 (Hartig and Lohse 2022). All models assumed student-t error distribution and were fit using restricted maximum likelihood. The final model results were summarized and plotted using the R package 'sjPlot' ver. 2.8.15 (Lüdecke et al. 2023). Analyses were conducted using R ver. 4.3.2 (www.r-project. org), and datasets were archived at Dryad (Jirinec 2024).

Results

Ambient conditions

Ambient thermal flux (ΔT_{air} , ΔT_{soil}) indicated that temperature increased from sunrise to approximately midday (Fig. 2). ΔT_{air} and ΔT_{soil} were positive at 06:07–13:05 and 07:02– 14:54 h, respectively, with maxima at 08:55 and 10:27 h and minima at 18:06 and 18:59 h. Ambient water temperature (mean \pm SD, range) averaged 24.7 \pm 1.5°C (22.4–35.2°C).

Rainfall reduced local temperature by up to ~ 1.5° C (Fig. 2). Daily maximum T_{soil} was negatively associated with daily maximum ΔSM in both Cabo Frio and Camp 41 (Supporting information).

Bird behavior

Comparing avian thermal flux (ΔT_{tag}) and ambient thermal flux (ΔT_{air}) indicated that birds regulated their temperature exposure throughout the diel cycle (Fig. 3, Supporting information). All species showed periods of warming that were initiated hours before sunrise (mean start at 03:47, Table 1).



Figure 2. Ambient conditions available for terrestrial insectivorous birds. (a–b) show thermal flux in the air and soil, respectively, measured as temperature change (ΔT) per 15 min and 10 min. Thick curves are generalized additive mixed models (gray ribbons=95% CIs) of ΔT for all loggers per group, colored by the direction of temperature change (warm colors=warming; cool colors=cooling). Thin gray curves are generalized additive models for individual loggers. Teal horizontal lines denote the threshold between cooling ($\Delta T < 0$) and warming ($\Delta T > 0$) and yellow shading approximates the daylight period. (c) shows the effect of maximum daily rainfall intensity, measured as the change in soil moisture (percent volumetric water content) per 10 min, on maximum daily soil temperature.

These morning warming periods peaked around sunrise for all but *S. rufigularis* and constituted the diel maxima for five of the nine species (Table 1). During morning warm-ups, the average time of ΔT_{tag} and ΔT_{air} equilibrium was 06:55 (Table 1). Following morning ΔT_{tag} peaks, all nine species experienced lower rates of warming than their environment until midday, when birds began to cool together with ΔT_{air} (Fig. 3). Additionally, six species demonstrated a pronounced oscillation in ΔT_{tag} (up to $\pm \sim 1.5^{\circ}$ C) around sunset. This oscillation was the most prominent feature in the diel thermal flux for all three *Sclerurus* spp., and to a lesser extent for *Myrmorderus ferrugineus*, *Myrmornis torquata* and *M. campanisona*.

All species experienced cooling likely related to water exposure through bathing or rainfall (Fig. 4, Table 1, Supporting information). Overall, birds experienced stronger cooling in the wet season ($\beta_{wet} = -0.42 \pm 0.09$ SE, z = -4.55, p < 0.001) and stronger cooling with higher rainfall intensity $(\beta = -0.11 \pm 0.03 \text{ SE}, z = -3.33, p < 0.001)$. However, individual models suggested that these responses are species-specific: higher rainfall intensity resulted in the strongest cooling for Hylopezus macularius and no cooling for all three Sclerurus spp. (Fig. 5). In fact, Sclerurus obscurior experienced less cooling with higher rainfall intensity, though this relationship was weak (Supporting information). Proportion of days with at least one cooling event of $\geq 5^{\circ}$ C equaled 0.48 across all species, with *M. campanisona* experiencing the fewest (0.16) and Sclerurus caudacutus the most (0.87) days on which these cooling events occurred (Table 1).

Discussion

I analyzed more than three million measurements representing local weather and its effects on nine species of terrestrial insectivores – rainforest specialists thought to be sensitive to microclimate variation (Powell et al. 2015, Ausprey et al. 2021, Sherry 2021, Jirinec et al. 2022a, b). Comparing the thermal flux representing avian and ambient sensors revealed a striking consistency in responses to ambient changes as well as endogenous behavior. As expected, local rainfall cooled birds in general (Fig. 4). Still, the rainfall effect was markedly absent in *Sclerurus*, three species whose thermal flux also indicated a regular bathing schedule around sunset independently of rainfall events (Fig. 3, 5).

Birds maintain thermal homeostasis

All species initiated warming before ambient temperature increased around sunrise (Fig. 3). Whereas the warming threshold for ΔT_{air} formed at 06:07, matching the local sunrise timing, the mean warming start for birds occurred more than 2 h earlier, at 03:47 (Table 1). Myrmothera campanisona, the species with the earliest threshold, shifted to warming approximately 4 h before sunrise. The period immediately preceding sunrise is the coldest time on the forest floor, falling to ~ 23° C regardless of the season (Jirinec et al. 2022a). $T_{\rm air}$ began to rise at the time corresponding to sunrise and increased until midday (12:00-13:00 h; Fig. 2), reaching ~ 26 and ~28°C in the wet and dry seasons, respectively (Jirinec et al. 2022a). The contrast between the ambient and bird thermal flux suggests that birds warmed up quickly before sunrise and then experienced lower ΔT_{tag} increases than ΔT_{air} (Fig. 3). In an analysis of thermal niches of these species, Jirinec et al. (2022b) reported that diel oscillations in \overline{T}_{tag} and \overline{T}_{air} span approximately the same breadth (~ 3–4 °C), although T_{tag} can be ~ 10°C higher due to body heat, which averages between 40.5 and 43.0°C, depending on species. During morning warming, the average time at which ΔT_{tag} and ΔT_{air} equalized (i.e. curve intersections in Fig. 3) occurred at 06:55 (Table 1). This period corresponds to $T_{air} = 22.8^{\circ}C$

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Figure 3. Diel thermal flux of terrestrial insectivorous birds in relation to their environment. y-axes indicate the rate of temperature change per 15 min (ΔT) for loggers placed on birds (red) and their habitat in the forest understory (black). Curves are generalized additive mixed models of ΔT with 95% CIs (gray ribbon), except for *Sclerurus rufigularis* where a generalized additive model was more appropriate for the single recaptured individual. Note that the gray CI ribbons are often barely noticeable due to a combination of large datasets and behavioral consistency. Teal horizontal lines denote the threshold between cooling ($\Delta T < 0$) and warming ($\Delta T > 0$) and yellow shading approximates the daylight period. Bird illustrations © Lynx Edicions.

(Jirinec et al. 2022b), suggesting that this could be the optimal T_{air} for terrestrial insectivores in the rainforest understory. Together, the ambient and avian thermal flux indicate that birds attempted to maintain thermal stability by warming during the coldest periods and moderating ΔT_{tag} increases during the highest ΔT_{air} . Here I show results for terrestrial insectivores that occupy a relatively warm, humid, and aseasonal environment. These sensitive habitat specialists are thought to be particularly invested in defending against environmental fluctuations (Sherry 2021). However, it is also possible that the broad thermoregulatory pattern presented here (particularly pre-dawn warming) are intrinsic to birds in general – especially those in environments with strong diel temperature oscillations. This question deserves further investigation.

However, thermal physiology data are needed to define when thermoregulation should occur. One important factor is body size, which was shown to correlate with heat tolerance in desert birds (Whitfield et al. 2015). Here I did not see an effect of size – *Myrmoderus ferrugineus* is about half the mass of *M. torquata* (Table 1), its sister species in this dataset (Jirinec et al. 2022b), yet the thermal fluxes of these two species were very similar (Fig. 3). Although warming started for *M. ferrugineus* an hour before *M. torquata*, as expected given thermal inertia, the earliest warming threshold occurred in the second largest species *M. campanisona*.





Figure 4. Cooling effects of rainfall for terrestrial insectivorous birds. Left panel shows the estimated marginal means from a model examining the effect of season (wet: December–May, dry: June–November) on the daily minimum temperature change (per 15 min) recorded by loggers placed on birds (min ΔT_{tag}). Birds experienced stronger cooling events in the rainier wet season. Right panel shows the estimated marginal means from a model examining the effect of rainfall intensity (daily maximum soil moisture change per 10 min in percent volumetric water content), recorded by nearby weather stations, on daily minimum ΔT_{tag} . Birds experienced stronger cooling events with higher local rainfall intensity. Models are generalized linear mixed models and shading represents 95% CIs. Bird illustrations © Lynx Edicions.

Another critical piece of information is the boundaries of the thermoneutral zone, the lower and upper critical T_{air} , which define the range of $T_{\rm air}$ that allows maintenance of basal metabolic rate without the need for metabolic warming or cooling, respectively (Scholander et al. 1950, Huey et al. 2012). However, thermal physiology data for these species and tropical birds in general are limited. Pollock et al. (2021) reported an upper critical temperature for a community of rainforest birds in Panama (37.6°C), including Formicarius analis (36.8 \pm 1.0°C; mean \pm SD). In a separate study, Pollock et al. (2023) found little evidence that thermal physiology traits varied with habitat type or vertical stratum. However, these studies used birds in experimental chambers filled with dry air (~ 30% relative humidity), cautioning that the upper critical $T_{\rm air}$ may be lower under higher humidities. Indeed, humidity strongly affects avian thermal physiology (Gerson et al. 2014, van Dyk et al. 2019, McKechnie and Wolf 2019), and relative humidity in lowland tropics often exceeds 90% (Aleixo et al. 2019), particularly near the ground of primary forests (Kapos 1989, Xing et al. 2023). Thus, natural settings likely pose greater thermal challenges for terrestrial insectivores than available experimental data suggest, especially given our limited understanding of how metabolic heat produced by normal activities such as flight contributes to constraints imposed by $T_{\rm air}$ and relative humidity. GPS data for this population of free-ranging *Formicarius analis* suggest that understory T_{air} (or its correlate, such as light intensity) may substantially restrict bird activity even at 28°C (Jirinec et al. 2022a). Disentangling the interplay between body heat, body size, activity, ambient humidity, and T_{air} in the context of thermoregulation is difficult. Indeed, animals occupy complex thermal environments where T_{air} is but a part of the equation. Operative temperature

(Bakken 1976, 1992, Huey et al. 2012), which incorporates humidity, radiation, evaporation, and metabolism, is a superior but onerous metric to obtain, especially for elusive rainforest birds. Regardless, here I show how unrestrained birds, tracked over long intervals, generally respond to changes in their thermal environment.

Water availability contributes to thermoregulation

Six of the nine species displayed evidence of behavior consistent with bathing (Fig. 3). A single oscillation in ΔT_{tag} of up to ~ 1.5°C revealed brief cooling events around sunset, particularly in Sclerurus spp., but also in M. ferrugineus, M. torquata and M. campanisona. The oscillation indicated that T_{tag} dropped rapidly and then quickly rebounded to the previous T_{tag} , a pattern consistent with birds deliberately bathing themselves in ambient water bodies. At an average of 24.7°C, $T_{\rm water}$ was > 15°C lower in the dry season than the average body temperature of these species (Jirinec et al. 2022b); thus, water bodies offer opportunities for rapid cooling. Alternative explanations for the ΔT_{tag} oscillation seem less plausible, as the oscillation did not match a corresponding dip in light intensity (Jirinec et al. 2022b), as would be expected if birds entered microclimate refugia such as burrows or cavities. Although I did not witness bathing behavior due to the very elusive habits of these species, direct observations of regular bathing schedules are available for several understory species in French Guiana, where birds bathed predominately in the late afternoon but also during midday heat (Jullien and Thiollay 1998).

Several compatible motivations are possible for these bathing events late in the day. First, bathing could help remove



Figure 5. Cooling effects of rainfall varied in species-specific models. Points are estimates for the effect of rainfall intensity (daily maximum soil moisture change) recorded by nearby weather stations on daily minimum temperature change experienced by birds (min ΔT_{tag}). Rainfall intensity was associated with stronger cooling (lower min ΔT_{tag}) for six species, especially *Hylopezus macularius*, but was not associated with cooling for all three *Sclerurus* spp. Models are generalized linear mixed models separate for each species, except for *Sclerurus rufigularis* represented by a generalized linear model for a single individual. Shading denotes 95% CIs. Entirely negative CIs (significant cooling effects of rainfall intensity) are denoted in orange, CIs overlapping zero (no statistical association) in black, and entirely positive CIs (higher min ΔT_{tag} with higher rainfall intensity) in blue. Bird illustrations © Lynx Edicions.

parasites, and doing so around sunset might reduce the likelihood of infestation overnight when birds are less active and more vulnerable to pests (Proctor et al. 2000). Second, bathing at dusk could reduce predation risk as reduced visibility can offer a safer window for bathing (Lima and Dill 1990). Third, bathing cools birds and might reduce heat stress – although ΔT_{tag} oscillations did not match the highest ΔT_{air} or peak T_{air} , bathing in the evening is likely to help birds manage cumulative heat load after exposure to earlier high temperature and humidity levels. Such heat dumping before roosting ensures that birds enter cooler night periods with reduced body temperature, metabolic rate, and associated energy costs (McKechnie et al. 2023). Fourth, bathing aids feather health, including cleaning, realigning, and enhancing the waterproofing and insulating properties before nocturnal cooling and possible rainfall at exposed roosts (Jirinec et al. 2018).

Although rainfall poses thermoregulatory challenges, it did not affect all species equally. Relative to the dry season, the wet season rainfall at the BDFFP is more than doubled (Jirinec et al. 2022a). Correspondingly, birds experienced stronger cooling in the wet season (Fig. 4), but the absence of rainfall effect in *Sclerurus* indicates that these species have the preference and ability to avoid rain (Fig. 5). Indeed, scant literature has reported that *Sclerurus* spp. dig underground burrows and roost propped against vertical substrates (Skutch 1969, van Els and Whitney 2011) – behaviors that may enable *Sclerurus* spp. to shelter from rain when needed. Rainfall intensity indicated the strongest cooling effect for *Hylopezus macularius*, but a relatively weak impact on *M*. *campanisona* (Fig. 4), which also experienced the fewest days with at least one ΔT_{tag} drop of $\geq 5^{\circ}$ C (Table 1). This is consistent with the notion that this species – an exception in terrestrial insectivores – is relatively resilient to landscape and climate disturbances: *Myrmothera campanisona* can tolerate altered forest (Stratford and Stouffer 2013) and warmer microclimates (Jirinec et al. 2022b). Resistance to rainfall may be beneficial given the increasing trend in wet season precipitation (Jirinec et al. 2021a, 2022a), as wet season rain can be torrential and thus likely detrimental. Similar to optima in T_{air} (i.e. the thermoneutral zone), optima in precipitation may be crucial for tropical endotherms and contribute to their thermoregulatory budgets (Boyle et al. 2020).

Behavioral versus physiological thermoregulation

Terrestrial insectivores seem to modulate their thermal status through both behavior and physiology. Although rain avoidance and bathing clearly manifest through behavior, warming thresholds in the early morning are likely a consequence of bird physiology. Rutt et al. (2019b) recorded the mean onset of dawn song, a measure of physical activity initiation, for the BDFFP avifauna, including six species tracked here. Myrmoderus ferrugineus, M. torquata, Formicarius colma and Sclerurus obscurior initiated dawn song within 10 min of sunrise, while Hylopezus macularius and M. campanisona were among the earliest singers, at ~ 20 min before sunrise. Similarly, analysis of BDFFP capture times in understory mist nets suggested that terrestrial insectivores are first to become mobile, peaking their movements 65 min after sunrise (Rutt et al. 2023). However, birds sing and fall into nets substantially later than the empirical warming thresholds observed here, and thus, these warm-ups are unlikely the result of birds actively moving around in complete darkness. Rather, warming might have occurred metabolically through shivering or non-shivering thermogenesis (Bicudo et al. 2001), or birds might have erected feathers to boost insulation (Morris 1956) and thus immerse the temperature sensor. Regardless of the mechanism, the presence of warming thresholds substantially earlier than local sunrise is consistent with physiological defenses against the lowest T_{air} in the diel cycle. The mechanisms of post-sunrise mediation of ΔT_{tag} are more challenging to identify because birds have a variety of behavioral and physiological mechanisms at their disposal (McKechnie and Wolf 2019). Previous studies reporting the selection of dark microclimates and cover for these species suggest that behavior is at least part of the strategy (Jirinec et al. 2022a, b).

One potential explanation for pre-dawn warming is torpor. Tropical birds, traditionally considered to maintain constant body temperatures due to the warm, stable climates of their environments, are increasingly reported to exhibit a physiological state of reduced metabolic rate and lower body temperature that mitigates metabolic costs associated with nocturnal temperature drops (McKechnie et al. 2023). This nocturnal hypothermia was observed in Costa Rica where montane birds reduced their nocturnal body temperatures by up to ~ 6 °C (Burnett et al. 2019), but also at lower elevations in Puerto Rico, where *Todus mexicanus* reduced its body temperature by as much as 11° C (Merola-Zwartjes and Ligon 2000). Similarly, in the lowland tropical forest of Panama, *Ceratopipra mentalis* and *Manacus vitellinus* reduced nighttime body temperatures by up to ~ 11° C (Bartholomew et al. 1983). If terrestrial insectivores also enter torpor, subsequent returns to active phase body temperature – providing that these occur pre-dawn – could explain the morning warming patterns observed in this study.

Conservation implications

The 'Bogert effect' refers to the capacity of behavior to buffer against environmental change and thus evade the force of selection but progressing climate change may eventually overwhelm this capacity (Huey et al. 2003, 2012). Emerging research has shown that changes in abiotic regimes affect demographic parameters in tropical birds (Brawn et al. 2017, Neate-Clegg et al. 2021). Although demography was not incorporated here, the study was motivated by enigmatic declines in terrestrial insectivores in pristine rainforests at this and other sites (Stouffer et al. 2021, Pollock et al. 2022, Blake and Loiselle 2024). Together, the avian and ambient thermal flux suggest that birds may prefer and track temperatures around 22.8°C – near the coolest temperatures available in the rainforest understory throughout the year (Jirinec et al. 2022a). Moreover, species that are best equipped to defend against thermoregulatory challenges posed by rain (Sclerurus spp.) appear to keep dry. It is worth comparing these patterns with climate trends at the BDFFP: since 1981, average T_{air} has increased ~ 1.3 and ~ 0.6° C in the dry and wet seasons, respectively (Jirinec et al. 2022a), and while wet season rainfall seems to be increasing, dry season rainfall has dropped by ~ 21% (Jirinec et al. 2022a). Moreover, T_{air} sharply increases near edges following forest fragmentation (Nunes et al. 2022). Even if behavioral and physiological thermoregulation buffers birds from these changes, mounting constraints on activity and increased energetic costs associated with thermoregulation may eventually lead to negative fitness consequences. In summary, results in this study support the notion that terrestrial insectivores are sensitive to shifts in abiotic conditions manifested through forest disturbance and climate change, linking these factors to population declines in both contexts. Although further investigation is warranted, the evidence unmistakably indicates that landcover and climate change in the central Amazon basin have altered ambient conditions, steering them away from the stable, relatively cool environments favored by terrestrial insectivores.

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Author contributions

Vitek Jirinec: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (supporting); Investigation (lead); Methodology (lead); Project administration (supporting); Resources (supporting); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xd2547dr3 (Jirinec 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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