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Research article

Long-term capture data uncover shifts in the daily activity patterns of Amazonian birds

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Although the duration of biological rhythms varies from milliseconds to decades, daily cycles are especially widespread for individual organisms. These circadian rhythms are synchronized by light–dark cycles, which govern predictable changes in other microclimate variables. Despite the fixed, regular nature of these abiotic cycles at low latitudes, little is known about how different animals structure activity along these gradients. We used 25 years of capture–recapture data and ~ 25 000 unique captures to characterize 'activity' (time of capture) for 65 species of Amazonian birds in the lowest forest stratum (0–2.5 m). To quantify vertical niche breadths, we also measured foraging heights for these same species in the field. Activity peaked within the first two hours after sunrise for most species (71%), while others peaked 1–3 h later (29%). This difference was associated with an apparent preference for specific vertical strata, as terrestrial and near-ground birds peaked ~ 1 h after sunrise, while birds from higher strata delayed their first bouts of activity in the lower understory (by an average of 40–100 min). Peak capture times also correlated with long-term abundance trends, as only species with the earliest capture times showed strong declines, suggesting that associations with mid- or late morning microclimates may contribute to resiliency in birds typical of higher strata. Because arboreal species largely avoid the lower understory in the early morning, when terrestrial birds are active, we infer that they are poorly adapted to low light environments. However, with their broad vertical niches and reliance on brighter microhabitats, we suggest that an arboreal lifestyle diminishes specialization and may increase the capacity to cope with a wider range of daily microclimate conditions. We predict that subtle, but important, shifts in daily activity patterns would materialize if other biodiversity-monitoring programs could analyze similar temporal datasets.

Keywords: capture–recapture data, circadian rhythms, microclimate, Neotropics, rainforest, specialization, temporal gradients, vertical stratification

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Introduction

Although biological rhythms track timescales from milliseconds to decades, daily rhythms are especially widespread in nature (Aschoff 1981, Merrow et al. 2005). In animals, these range from what is probably the largest migration on the planet – the daily ascent and descent of oceanic zooplankton (Hays 2003) – to subterranean African mole-rats, which are still able to synchronize their activity patterns to external light, even though they may never encounter direct sunlight (Oosthuizen et al. 2003). These daily (or circadian) rhythms can be lost in continuous lighting conditions, such as arctic summers and winters in the case of the reindeer (van Oort et al. 2005). For birds, internal rhythms such as body temperature, metabolic rate, and activity levels translate into daily patterns of behavior (Gill 2007), such as the timing of peak vocal activity (Blake 1992, Staicer et al. 1996).

Circadian rhythms are synchronized by light-dark cycles, and these solar cycles drive predictable rhythms in microclimate. Each day, light intensity changes by orders of magnitude near dawn and dusk (Chazdon and Fetcher 1984, Endler 1993, Ausprey et al. 2021). This sharp increase in morning sunlight causes a series of microclimate variables to shift in response, resulting in increasing temperature, decreasing relative humidity, and increasing wind speed. Simultaneously, across a vertical instead of temporal axis, another similar microclimate gradient exists inside forests, with the strength of that gradient increasing during sunny afternoons (Parker 1995, Scheffers et al. 2013, Zellweger et al. 2019). In tall lowland rainforests with complex layers of vegetation, these vertical microclimate gradients extend from the forest floor to the forest canopy. In Manaus, Brazil, for example, only ~ 1% of solar radiation penetrates to the forest floor (Shuttleworth et al. 1984). This attenuation in light corresponds to cooler and more humid conditions – and, thus, smaller diurnal swings – with decreasing height in the forest (Fetcher et al. 1985, Stratford and Robinson 2005, Scheffers et al. 2013). Remarkably, these vertical forest gradients can be steeper than climatic gradients across hundreds of meters of elevation and hundreds of kilometers of latitude (Scheffers et al. 2013, Thiel et al. 2021).

Despite the fixed nature of these daily cycles at low latitudes, little is known about the daily rhythms of tropical animals along recurring temporal and vertical gradients. Compared to their temperate counterparts, tropical forest birds are more highly specialized, selecting more restricted microhabitats and foraging heights – together, this horizontal and vertical specialization results in reduced niche breadth (Marra and Remsen 1997). Although vertical stratification has been described for forest birds around the world (Orians 1969, Pearson 1971, Cody 1974, Pearson 1977, Terborgh 1980, Bell 1982, Fitzgerald et al. 1989, Walther 2002, Chmel et al. 2016, Chmel et al. 2021), the tall rainforests of the tropics are widely believed to have the greatest vertical stratification (Allee et al. 1949, MacArthur et al. 1966, Smith 1973). Within these finely subdivided forests, birds that forage on or near the ground have the narrowest bands of vertical activity (Orians 1969, Cody 1974, Terborgh 1980). As such, these birds may be fine-tuned to the specific abiotic properties of their microhabitat (Terborgh 1980, Sherry 2021). Therefore, denizens of the rainforest understory provide a rare opportunity to explore how temporal and vertical microclimate gradients shape their daily activity patterns.

To compare avian activity in the lowest, most buffered stratum of the forest (0–2.5 m, using mist nets to capture birds), we harnessed the time of ~ 25 000 unique capture events in the Amazon Rainforest. For birds that are routinely captured in the lower understory, we first used foraging observations to characterize their preferred vertical stratum, as many of these birds routinely forage above mist-net-level height (> 2.5 m). We then asked whether this vertical stratification determines the onset and relative duration of mist-net-level 'activity' throughout the morning, using daily temporal gradients to infer associations with the microclimate at the time of capture. We predict that birds residing in the lowest stratum – terrestrial and near-ground birds – would be the first to become active, as they are exclusively exposed to the environmental conditions of the lower understory (e.g. relatively dark, cool, and humid). If the daily activity patterns of these groups suggest some form of microclimate specialization, it could help to explain their recent declines in Amazonian primary rainforest (Stouffer et al. 2021). In that case, we would hypothesize that timing of activity might also correspond with long-term abundance trends, which could shed light on the directional changes of Amazonian bird abundances. The results of this synthesis and exploration lay the groundwork for future, more nuanced studies about the biotic and abiotic drivers of daily activity patterns.

Material and methods

Microclimate gradients

To chronicle the temporal progression of local microclimate gradients, we acquired temperature data from a nearby meteorological tower, employing temperature as a proxy for the suite of microclimate variables (including light) that change in concert throughout the day. The K34 micrometeorological tower (02°36′S, 60°12′W), ~ 40 km southwest of the Biological Dynamics of Forest Fragments Project (BDFFP) in the central Amazon of Brazil (02°20′S, 60°W), records temperature every 30 min at three strata relevant to forest birds: understory (5.2 m), midstory (15.6 m), and canopy (28.0 m). Enlisting two years of data (2016–2017), this allowed us to characterize both temporal and vertical microclimate gradients within local terra firme rainforest (Fig. 1, Supporting information). We generated three temperature curves, one for each stratum, using cyclic cubic regression splines and generalized additive models (GAMs) in the R package 'mgcv' (Wood 2021). However, to ensure equal comparisons among strata (i.e. same dates and times), we eliminated all rows that contained missing data (totaling ~ four months), whenever just one of the three sensors failed.

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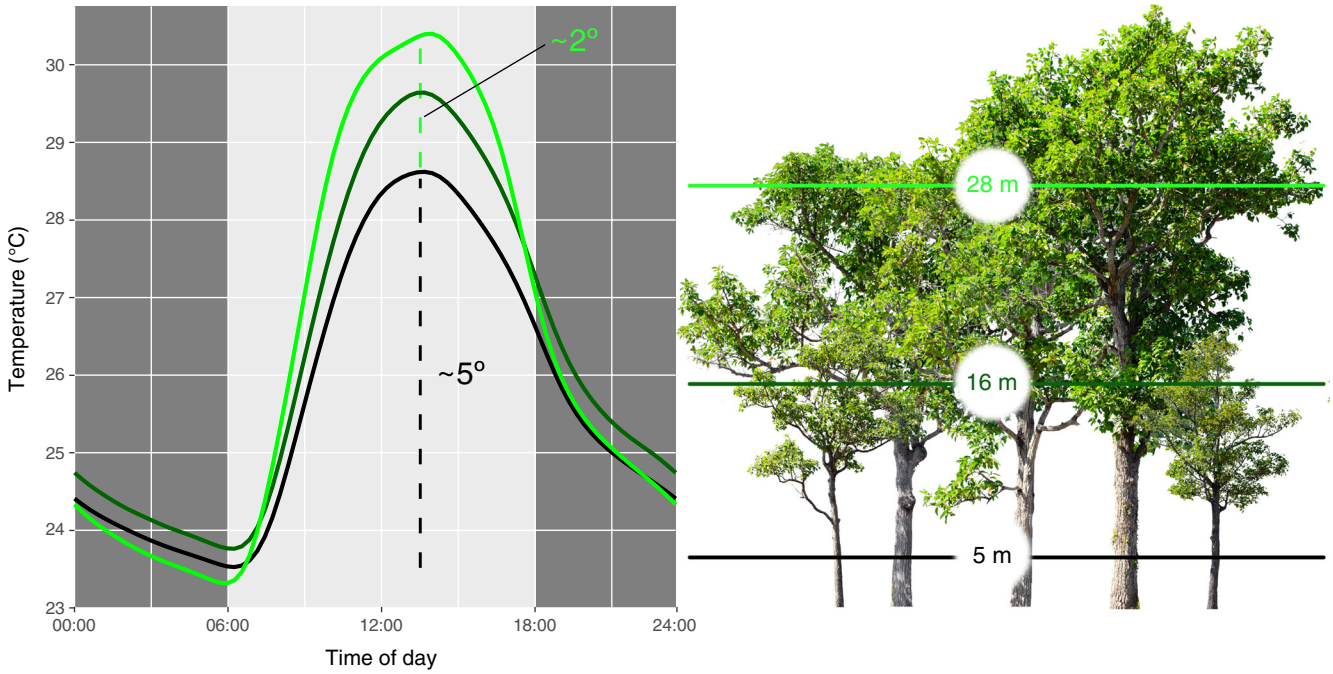

Figure 1 . Temporal and vertical microclimate gradients in local terra firme rainforest of the central Amazon, represented here by temperature. Lines are color-coded according to the vertical stratum of each temperature sensor along the K34 micrometeorological tower, as illustrated by the forest schematic at right: understory (5.2 m), midstory (15.6 m), and canopy (28.0 m). Note that temporal gradients are larger (~5°C within the understory) than vertical gradients (~7° – ~5° = ~2°C). Trees from ©pngtree.com.

Although daily lows were similar for all three strata (within ~ 0.5°C at sunrise), daily highs were separated by ~ 2°C in the early afternoon (Fig. 1), revealing warmer daytime temperatures and thus larger microclimate fluctuations with increasing forest height (canopy > midstory > understory). Within the understory (5.2 m), the daily temporal gradient spans roughly 5°C (23.5–28.5°C), indicating that temporal gradients are larger than vertical gradients.

Bird foraging heights

To determine the vertical range of species that use the lower understory, and thus their availability for mist-net capture, we measured foraging heights for the majority of the 65 species in this study. Without using playback, BRA and CLR opportunistically recorded or calculated the vertical positions of free-flying birds using a laser rangefinder (heights < 6 m had to be estimated by eye). For any given species, we considered observations to be independent if at least 10 min had passed between successive height measurements. By excluding roosts, song outposts, and display sites, we assumed all observations represented either foraging locations or sites interspersed between foraging bouts. During three years of fieldwork (2016–2018), we compiled 1429 foraging height measurements for 83% of study species (n = 54). However, because sample sizes differed greatly among species (median = 6.5; range = 1–144), we randomly subsampled 10 observations for species with larger sample sizes (> 10), resulting in a total of 341 measurements (Supporting information). We then binned species into four well-established categories for vertical stratification (Supporting information, Stouffer et al. 2021). Altogether, this included height data for 88% of our terrestrial birds (32 observations of seven species), 69% of near-ground birds (46 observations of 11 species), 86% of understory birds (124 observations of 18 species), and 90% of midstory birds (139 observations of 18 species). Unsurprisingly, lower-strata birds displayed much lower means than higher-strata birds and also much less variation around those means (Fig. 2): terrestrial ($\bar{x} = 0.13$ m; SD = 0.34 m) and near-ground species ($\bar{x} = 0.63$ m; SD = 0.83 m) versus understory ($\bar{x} = 7.3$ m; SD = 4.6 m) and midstory species ($\bar{x} = 10.8$ m; SD = 5.3 m). For lower-strata birds, 99% of observations were below mist-net-level height (n = 1 observation at 3 m) whereas most observations (87%) of higher-strata birds were above mist-net-level height, indicating that captures for these birds occurred during relatively uncommon forays into the lower understory. In contrast to the full vertical breadth of microclimate data (above), we were unable to evaluate canopy birds due to their infrequent occurrence in ground-level mist nets.

Bird capture data

Next, we extracted capture times from a long-term program of capture–recapture data at the BDFFP. Constant-effort passive mist-netting began in 1979 and has continued intermittently through 2017 (Stouffer 2020). Across these four decades, the mist nets themselves (ATX, 12 × 2.6 m, 36 mm

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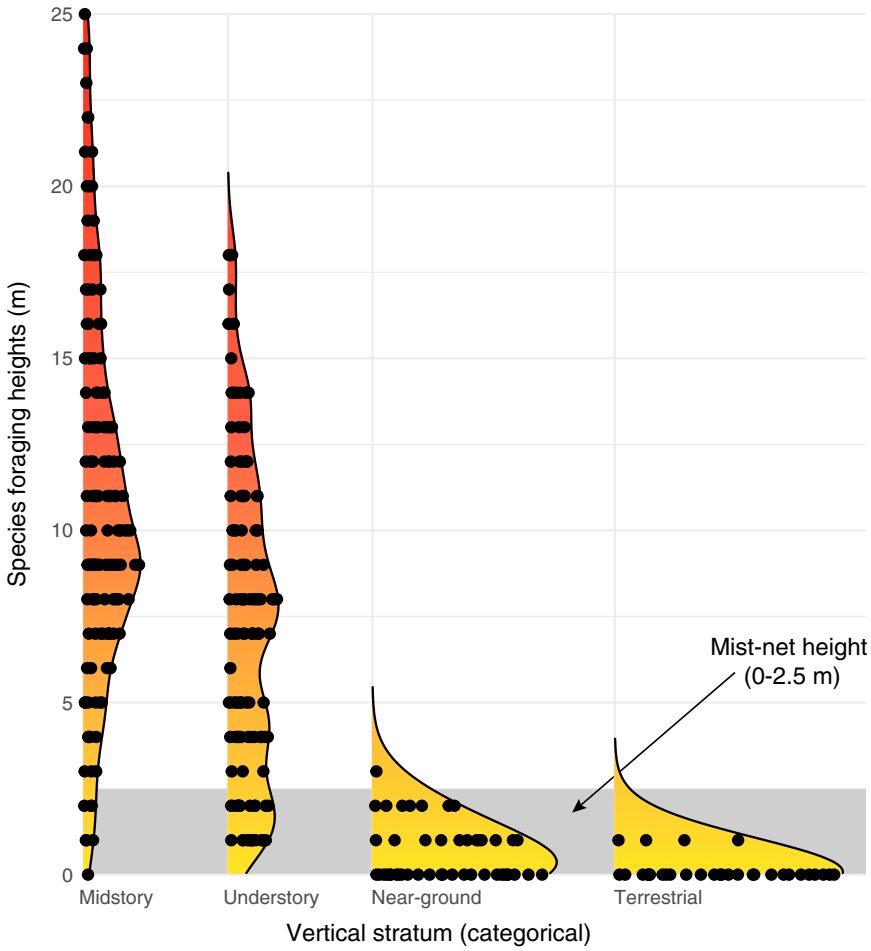

Figure 2. Kernel density plots reveal stark differences between the foraging heights and ranges of lower- and higher-strata species. Terrestrial and near-ground birds exhibit remarkably narrow vertical foraging breadths, with 99% of observations falling within the vertical range of mist nets (shaded in gray). Jittered dots represent the underlying height measurements. Data from 54 of the 65 species (83%) are shown here.

black nylon mesh), effort (from ~ 06:00 to 14:00 h), and protocols (e.g. with the bottom of the net set at ground level) have remained constant (Bierregaard and Stouffer 1997, Stouffer et al. 2006). Although mist-net sampling occurred in a variety of forest types (Gascon and Bierregaard 2001), we restricted our focus to the least disturbed sites: the interiors of 100 ha fragments and continuous primary rainforest. Some species may be absent or less common in 100 ha fragments (Stouffer et al. 2006, 2011); however, because we are only interested in within-species capture times, we only evaluated a species where it was present. It is important to note that the way in which birds were processed has changed over time at the BDFFP, with implications for how capture times were recorded. Historically (before 2000), capture time was recorded when a bird was processed, which was typically at the net at the time of extraction, whereas in subsequent decades, capture time denoted the time of in situ extraction, as birds were processed later at a more remote banding station. However, because this is a systemic change, it should not disproportionately affect any one species. Finally, because nets were checked at relatively long intervals (~ 45 min), capture times represent time-lagged activity patterns, but this bias applies equally to all species.

We further cleaned the database to remove any days with atypical effort and added daily sunrise times to each capture occasion. Although mist-netting protocols remained constant, there was still unwanted, residual variation in opening and (especially) closing times. We therefore removed any days when nets were opened before 05:40 or after 06:10 h and when operators began closing nets before 13:00 h, as well as all captures after 13:00 h, even though daily effort usually extended beyond 13:40 h. We also eliminated all same-day recaptures, as a capture event inevitably disrupts an individual's daily schedule, and it was impossible to determine when a previously captured bird had subsequently resumed normal activity patterns. We recognize, however, that this skews the dataset towards earlier capture times by excluding a later, unknown subset of natural recapture events. With the exception of hummingbirds, which were never banded, we also eliminated any individual that was not uniquely identifiable (i.e. banded, with band number recorded). We retained only those species (n = 65) that had more than 50 independent

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captures in our finalized dataset, although many species had much larger sample sizes (median = 230 captures). Finally, we added daily sunrise times to each capture occasion, which allowed us to generate our variable of interest (deviation from sunrise; hereafter 'capture time'). We downloaded daily sunrise times from the Astronomical Applications Dept of the US Naval Observatory (http://aa.usno.navy.mil) for a single leap year (2016) at the following coordinates (02°24′S, 59°53′W). Throughout the year, daily sunrise times ranged from 05:37 to 06:08 h (31 min), with an average value of 05:56 h (Supporting information). This timespan mirrors when nets were opened each morning, such that only six captures were registered before local, daily sunrise (minimum = −11 min). After filtering, the resulting dataset contained 24 561 independent captures and constituted 35% of the BDFFP capture–recapture database (see the Supporting information for summary depictions of the dataset). In all, captures spanned 25 years (1979–1993 and 2007–2017, excluding 2014), although 70% of these data stemmed from 1980–1987.

Statistical analysis

To quantify daily activity in the lower understory, we constructed individual distributions of capture times for each of the 65 species, which we further organized by foraging guild and vertical strata. Using kernel density estimation in the R 'stats' package (www.r-project.org), we generated smoothed curves for the probability distribution of each species, which formed the foundation for subsequent analyses. To characterize species-specific activity patterns, we derived two features from each species' density function: the time associated with the maximum density (peak capture time) and the maximum density value itself (a proxy for activity length). See the Supporting information for an illustrative graphic. A species with a tall peak (large density value) indicates that its bout of first activity is more restricted than a species with a short peak, which remains active for longer (Fig. 3). We then combined species that shared life history strategies (guild, strata) by averaging their species-specific density curves. Guild designations generally coupled vertical stratum and diet (e.g. near-ground insectivore), except when trumped by sociality (e.g. army-ant follower), and largely followed those of Stouffer et al. (2021; see the Supporting information for all guild and strata assignments).

To compare capture times among groups, we ran generalized linear mixed models (GLMMs) in the package 'lme4' (Bates et al. 2015). After shifting all capture times to positive integers (by adding 12 min), we modeled capture time as a function of guild or stratum, treating species as a random effect. We accounted for overdispersion in Poisson models by fitting negative binomial error distributions with a log link function. To infer 'significant' differences between the means of any two groups, we used non-overlapping 95% confidence intervals, even though this approach is overly conservative for group comparisons (Goldstein and Healy 1995). Finally, if group daily activity patterns imply microclimate specialization, then a species' degree of specialization could help to explain their decline or increase at the BDFFP. We therefore ran an exploratory linear model to test whether peak capture

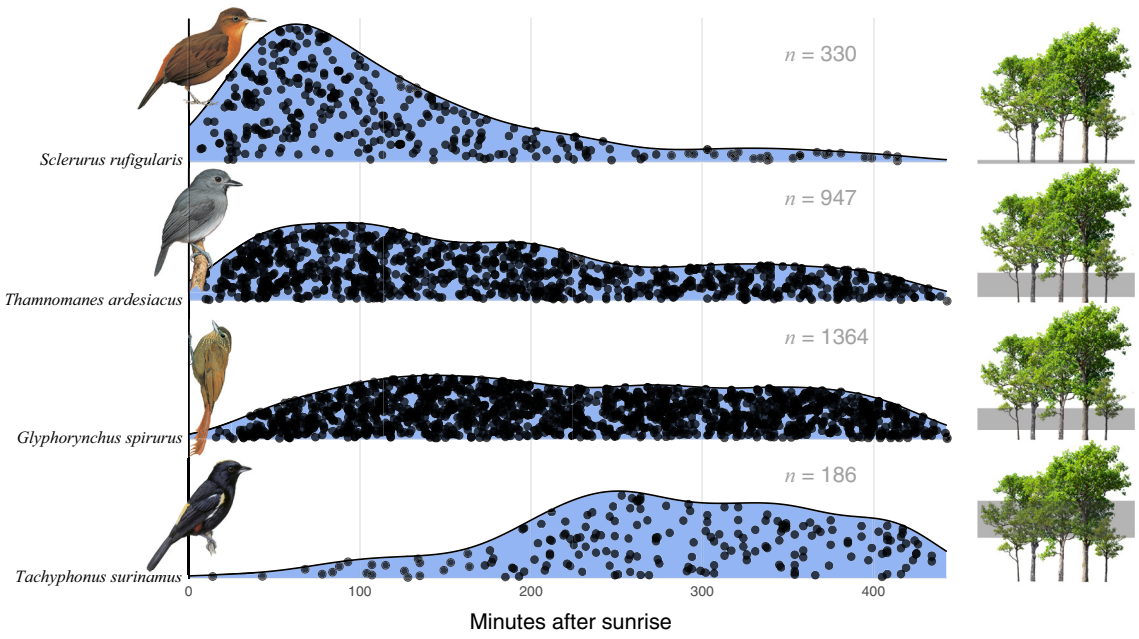

Figure 3. Representative probability distributions of capture times in the lower understory, illustrating four different responses. The time and height of each species' peak capture time were used to characterize species-specific activity patterns (see the Supporting information for details). Although all arboreal species we evaluated at least occasionally descend into the lower understory, translucent gray bands on the right depict the preferred vertical stratum for each of these species. Tree illustrations from ©pngtree.com. Bird illustrations from ©Lynx Edicions. Black dots portray underlying capture data from ground-level mist nets.

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times correlated with long-term abundance trends. However, because closely related species may share similar activity patterns, we accounted for phylogeny by building a maximum clade credibility tree with the TreeAnnotator tool ver. 1.10.4 in BEAST (Suchard et al. 2018), using 1000 pseudoposterior trees downloaded from Jetz et al. (2012), constrained by the Hackett et al. (2008) backbone. With this phylogenetic hypothesis, we compared abundance trends and peak capture times using phylogenetic generalized least-squares (PGLS) in the package 'caper' (Orme et al. 2018). Abundance trends in continuous primary forest were derived from the slopes in Fig. 2a of Stouffer et al. (2021).

Results

After estimating probability density functions for each species, we found a diversity of species-specific activity patterns (Fig. 4, Supporting information). In the lower understory, activity for most species (71%) peaked within the first two hours after sunrise (median = 96.3 min), led by *Myrmornis torquata*, the earliest species to peak (at 49.3 min or ~ 06:45 h; Supporting information). On the other hand, 19 species (29%) peaked between 2 and 5.5 h after sunrise, the last of which was *Rhynchocyclus olivaceus* (324.4 min or ~ 11:20 h). Figure 4 illustrates that most species had activity patterns that were right-skewed (positive skewness), with relatively early peaks followed by long tails drawn out to the right. Importantly, no species peaked close to the right boundary (within ~ 100 min of 13:00 h), suggesting that we had adequately characterized each of these species' peak activity bouts at mist-net-level height. Peak density (a proxy for activity length) was inversely correlated with peak capture time (Fig. 5). For instance, the peak density values for the 10 earliest species ($\bar{x} = 0.0059$) were 64% larger than those of the 10 latest species ($\bar{x} = 0.0036$), indicating that early species had narrower bouts of peak activity than late species (Supporting information). As further evidence of this inverse relationship, the species with the tallest peak *Sclerurus rufigularis* had the fourth-earliest peak capture time, whereas the species with the shortest peak *Thamnophilus murinus* was positioned among the last third of all species (45/65).

The diversity of species-specific responses was united by vertical strata (Fig. 4) and foraging guild (Supporting information). Insectivorous guilds that foraged on or near the ground (< 3 m) all peaked sharply about an hour after sunrise (Supporting information): terrestrial (65 min) and near-ground (68 min) insectivores peaked first, followed by army-ant followers (80 min). At the other extreme, the average hummingbird (168 min), midstory insectivore (202 min), and midstory frugivore (223 min) all showcased low, flat peaks, largely plateauing throughout the mid- to late morning. Across the full breadth of capture times, results from the guild GLMM revealed significant differences between pairs of many groups (Supporting information). This temporal sequence of guilds, however, largely followed vertical stratification, beginning with terrestrial species and progressing up through midstory birds. In contrast to terrestrial and near-ground species, most birds from higher strata (understory and midstory) were not sampled in the lower understory until later in the morning (Supporting information). For example, the average peak capture time (Supporting information) for species in each stratum group were as follows: terrestrial (67 min), near-ground (78 min), understory (113 min), and midstory (173 min). With the exception of midstory species, which showed a wide range of variable responses, species-specific curves for each stratum were remarkably uniform (Fig. 4).

Lastly, in our exploratory linear model, species-specific capture times correlated with local, long-term abundance trends. Although the regression did not fit the data particularly well (adjusted $R^2 = 0.08$), the PGLS model produced a significant, positive relationship between a species' peak capture time and its change in local abundance (Fig. 6; $F = 6.4$, $df = 1.61$, $p = 0.01$). Thus, after accounting for phylogenetic nonindependence (Pagel's $\lambda = 0.60$), species that had earlier bouts of peak activity tended to decline more strongly in primary forest over the past ~ 30 years (median: 1982–2012).

Discussion

This novel adaptation of capture–recapture data illuminates the importance of preferred vertical stratum on the activity patterns of tropical organisms. In the darkest, lowest stratum of the rainforest, birds that forage on or near the ground display remarkably narrow vertical foraging breadths and similarly narrow bouts of peak mist-net activity shortly after sunrise. In contrast, with much broader vertical niche breadths, birds from higher strata postpone their first bouts of lower understory activity until later in the morning, when the lower understory is brighter. We might even consider terrestrial and arboreal birds to represent two ends of a continuum from vertical specialists (low heights and narrow ranges) to vertical generalists (higher heights and broad ranges), with the behavior of each group leading to distinct signatures of temporal activity. Further, these temporal signatures correlated with vulnerable and resilient species – as evidenced by local, long-term abundance trends (Stouffer et al. 2021) – suggesting that associations with certain microclimates may contribute to resiliency or vulnerability.

Ground-level mist nets are an imperfect tool to holistically describe avian activity patterns. However, capture data can reveal two distinct characteristics about bird movement: general activity (that a bird is moving and not stationary) and localized activity (general activity within the vertical range of the nets). In this study, we primarily employ capture data from ground-level mist nets to indicate when species first become active in the lower understory (in essence, when this stratum becomes available to them). This is because subsequent attenuations in 'activity' (i.e. a reduction in captures) could be caused by an unknown combination of increased net visibility (i.e. net avoidance), behavioral adjustments (e.g. fewer flights, a reduction in activity), and/or upward shifts

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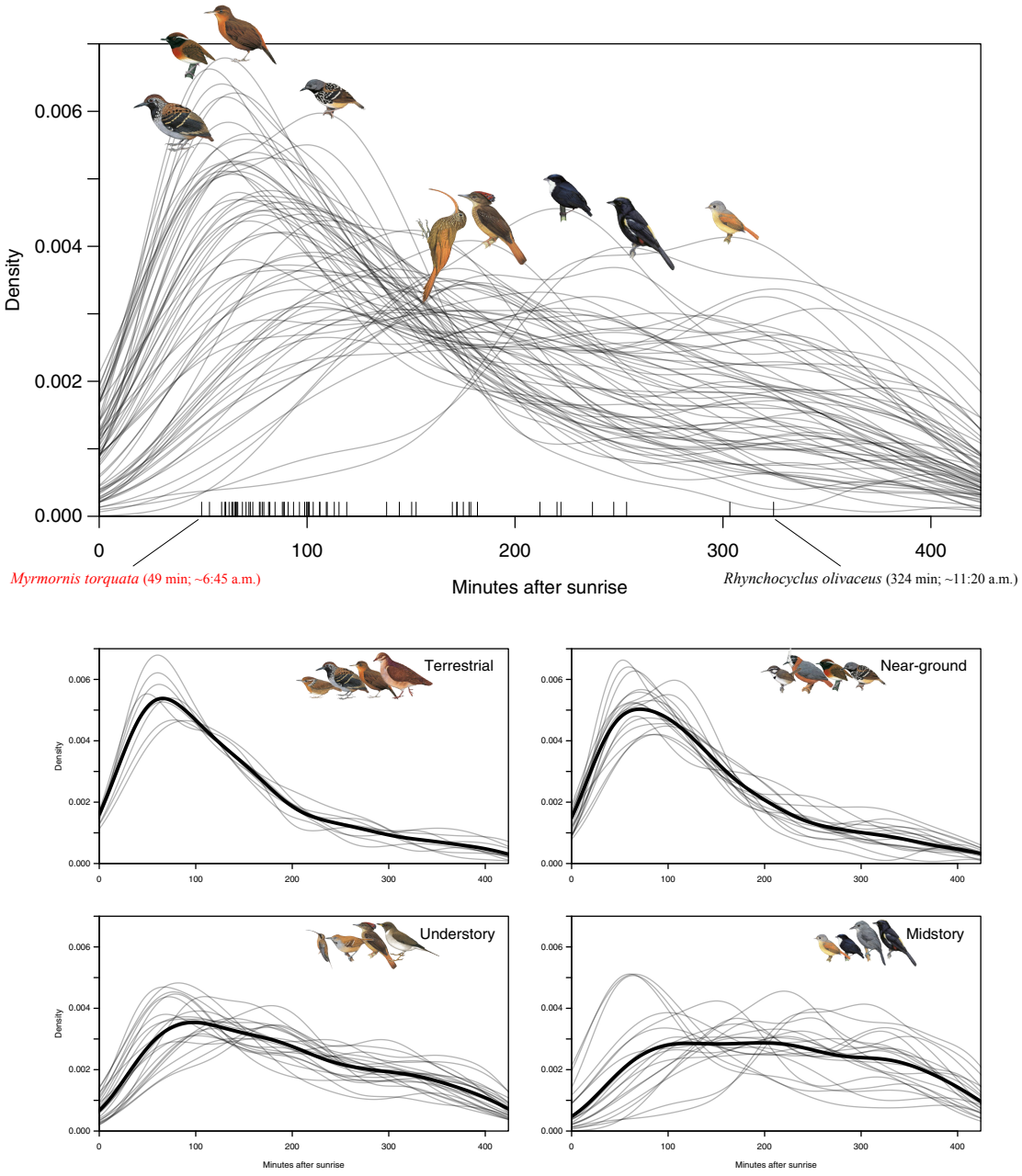

Figure 4. Probability distributions of capture times for 65 species of birds in the lower understory. The rug plot along the lower border of the top panel highlights peak capture times for each species, indicating that activity for most species peaked within the first two hours after sunrise. For reference, the deviation since the time of the average sunrise (05:56 h) is denoted for the earliest and latest species. This diversity of species-specific responses was united by preferred vertical foraging strata (bottom panels), with the exception of midstory birds, which showed variable responses. Bold lines indicate the average probability distribution for each stratum. Bird illustrations from ©Lynx Edicions.

in activity height (> 2.5 m; Remsen and Good 1996). For terrestrial and near-ground birds, which rarely ascend above the height of mist nets (Fig. 2), the apparent reduction in 'activity' during the mid- to late morning (Fig. 4) is not likely to emerge from vertical shifts. For example, we know that ant-following birds largely switch from long-distance commutes in the early morning to more deliberate, area-restricted searches later in the day (Willis 1972, Chaves-Campos 2011), collectively serving to reduce the probability of midday capture (via behavioral adjustments and, potentially, net avoidance). In contrast, however, the more arboreal, flight-dominated lifestyles of understory and midstory birds, which must fly to move between foraging substrates, presumably helps to explain their prolonged period of mid- to late morning captures (Fig. 4, 5).

Despite the fact that biologists have long appreciated strong microclimate gradients and vertical stratification in tropical wet forests, it has proven difficult to associate bird

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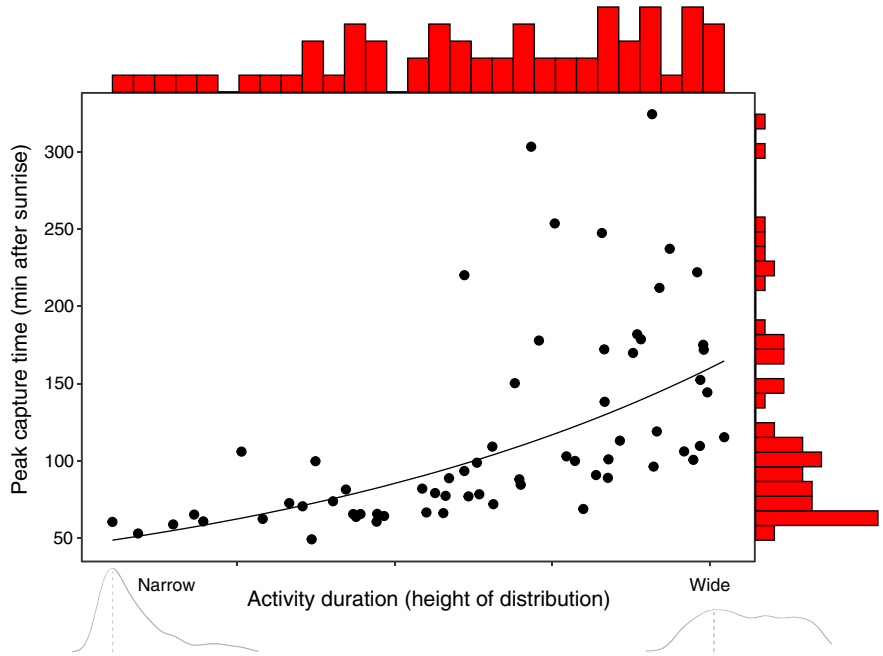

Figure 5. Timing of activity is related to the duration of mist-net activity in the lower understory. Early morning species tend to have restricted bouts of peak activity (left), whereas those that peak later remain active for longer (right). Note that activity duration is derived from peak capture densities, arranged from largest to smallest (left to right). Bar plots portray histograms for the corresponding axes.

locations with local microclimatic conditions (Karr and Freemark 1983, Sekercioglu et al. 2007, Patten and Smith-Patten 2012, Pollock et al. 2015). Temporal gradients, however, offer a promising alternative because they allow one to make inferences about what may limit or inhibit activity within a known-to-be-used microhabitat. Our results indicate that many arboreal species from higher strata delay their arrival into the lower understory. The average peak capture time for understory species was 35–45 min behind that of near-ground and terrestrial birds, respectively, while midstory species were delayed even further (01:35–01:45 h). In fact, the last 25 species to peak in ground-level mist nets were exclusively understory and midstory birds (Supporting information). Forest birds throughout the tropics have been

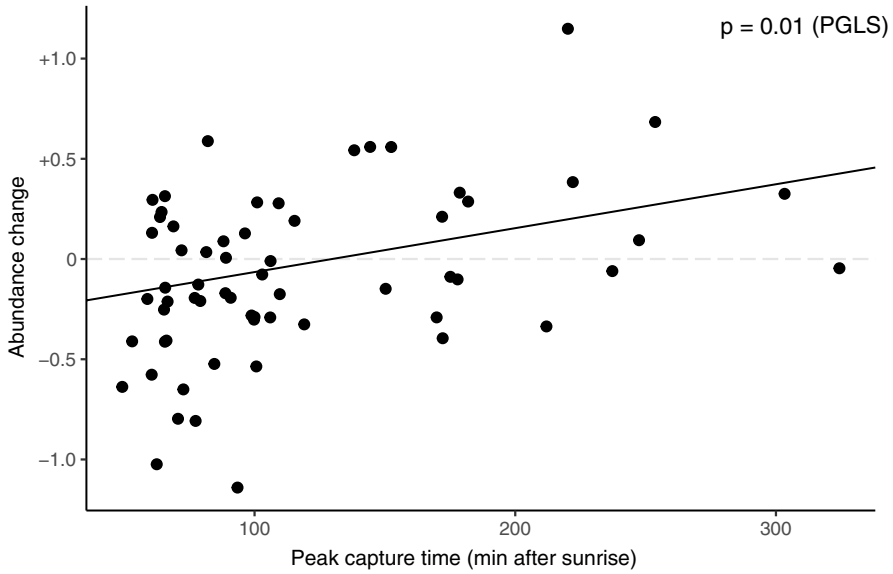

Figure 6. Only species with the earliest capture times showed the strongest declines in local rainforest over the past ~30 years. This suggests that associations with early morning microclimates may contribute to a species' vulnerability. The significant, positive relationship is the result of a phylogenetic generalized least-squares (PGLS) model. Note that two species lacked long-term abundance trends and were thus excluded from this analysis.

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documented shifting to lower levels, but these shifts have been centered on the middle of the day, attributed to the effects of midday heat and bright sunlight (Pearson 1971, 1977, Bell 1982, Walther 2002, Rajaonarivelo et al. 2020). We found similar results, but at the beginning of the diurnal spectrum, implicating low light levels as the most likely causal factor, whether directly or indirectly. Light intensity accelerates rapidly at sunrise, multiplying by an average of 10–15× within the first 30 min alone (CLR unpubl.), whereas, for instance, understory temperatures rise less than 10% across the next three hours (Fig. 1): 06:00 h (23.5°C), 07:00 h (+ 0.1°C), 08:00 h (+ 0.9°C), and 09:00 h (+ 2.1°C). Further, we know that decreased light intensity on overcast mornings delays other circadian rhythms in birds, such as the onset of dawn song (Leopold and Eynon 1961). Therefore, we speculate that arboreal birds from higher forest strata may be visually constrained by the dim, early morning light of the lowest stratum and thus lack the visual capacity to either forage efficiently and/or evade predators until the understory brightens.

Daily vertical movements are most widely documented in marine and freshwater environments, where migrations of both predator (fish) and prey (zooplankton) are regulated by changing light intensity (Lampert 1989, Hays 2003). Due to pressure from visual predators, zooplankton ascend to surface waters at night, retreating to dark refugia during the daytime, while predators track these vertically migrating prey (Hays 2003, Sims et al. 2005, Hrabik et al. 2006). Thus, the ultimate reason for this phenomenon differs between trophic levels, with broad support for both predator evasion (prey) and food availability (predators; Lampert 1989, Hays 2003). As both visual predators and prey, it is conceivable that insectivorous birds could be influenced by one or both of these constraints. Similarly, for nectivorous birds (e.g. hummingbirds), daily activity patterns could be driven by the vertical distribution of flowers and the daily rhythm of flower opening, closure (or destruction), and nectar expression (Stiles 1975, van Doorn and van Meeteren 2003, Gottlieb et al. 2005). Although tropical rainforests might exhibit something analogous to daily vertical movements in marine environments, we currently lack the details necessary to explore these predator–prey dynamics and the timing and distribution of food resources. Nonetheless, because some insectivorous birds were already moving and, presumably, foraging in the lower understory before more arboreal birds, the degree of adaptation to low levels of ambient light could also represent a more direct physical limitation.

Although time of capture has often been overlooked in capture–recapture datasets, we predict that subtle, but important, shifts in daily activity patterns would materialize if other biodiversity-monitoring programs could analyze similar, rigorously standardized temporal data. Such studies would not only unearth novel insights about ecological processes but could also elucidate seasonal (Pearson 1971, Fitzgerald et al. 1989) or decadal changes in activity patterns, which might otherwise go unnoticed. This would be especially valuable for predicting short-term, species-specific responses to global climate change. In the central Amazon, we know that recent decades have brought warmer temperatures and shifting rainfall regimes (Feng et al. 2013, Almeida et al. 2017). These changes almost certainly accompany simultaneous shifts in humidity and light levels, two microclimate variables that vary seasonally in accordance with precipitation and cloud cover (Windsor 1990, Wright and van Schaik 1994, Graham et al. 2003). However, to uncover shifts related to climate, we need to compare the daily activity patterns of individual organisms with daily weather conditions (e.g. are delays in arrival times especially pronounced on dark, overcast mornings?), not merely correlations between net effects and long-term climate trends. To circumvent this, we recommend recording fine-scale microclimate conditions at time-stamped animal locations, which would accelerate our understanding of how animals respond to natural climatic variation: hot, sunny days; heat waves; and El Niño/La Niña events. Alongside advances in avian ecophysiology, innovative use of biologging technology (Wilmers et al. 2015) will continue to revolutionize this work by explicitly linking environmental conditions to individuals (e.g. light sensors on wild birds; Ausprey et al. 2021), but creative thinking will be necessary to tease apart environmental conditions in used versus available habitat (Jones 2001; e.g. deploying a network of microclimate sensors to simultaneously record conditions at previously used locations).

Finally, our results stress the importance of strictly maintaining standardized capture effort, and we encourage cautious interpretation of any abundance trends where biologically meaningful start and end times have also shifted. For example, apparent trends in animal abundance could simply be an artifact of systematic changes in effort if one time period is disproportionately biased for or against early/late species. Our results empirically demonstrate that shifts in movement patterns strongly affect species' capture probabilities, validating the simulations of Remsen and Good (1996) and proving that not all effort is comparable (i.e. early versus late morning hours; Fig. 4, Supporting information). Therefore, for studies asserting long-term trends in animal populations, it is especially critical to standardize start/end times and duration of sampling effort. However, some studies are vague about variation in start or end times, while others omit these crucial details altogether (Whitfield et al. 2007, Lister and Garcia 2018, Willig et al. 2019). Instead of arbitrary human clocks, we also advocate using biologically relevant clocks to set meaningful start and end times – such as sunrise or sunset (Supporting information, Sauer et al. 2013, Blake and Loiselle 2016) – which becomes increasingly important at higher latitudes. Regardless, to ensure that peaks of activity are not stranded near sampling boundaries, all long-term capture studies should first explore temporal activity patterns.

Overall, our findings suggest that the environmental conditions of a bird's preferred stratum may shape both its activity patterns and its degree of specialization. By combining rigorously collected field observations with a large-scale, long-term capture dataset, we established that 1) species from different strata differ predictably in activity patterns and 2)

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that many arboreal species largely avoid the lower understory in the early morning. With their broader vertical niches (i.e. greater behavioral plasticity) and reliance on brighter microhabitats (Fig. 2), we suggest that an arboreal lifestyle diminishes specialization and may increase the capacity to cope with climatic variability (Fig. 6, Scheffers et al. 2017). We expect that our results for birds likely extend to other mobile, arboreal taxa within vertically stratified rainforest. In the lowland tropics, realized microclimate conditions may have important implications and unexpected consequences for how species fare in the altered microclimates of human-modified forests (Ausprey 2021) or will fare in the future microclimates of climate-changed forests. Therefore, studying the activity patterns and experienced microclimates of organisms, in both space and time, will be a ripe arena for future investigations.

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Author contributions

Cameron L. Rutt: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead). **Philip C Stouffer**: Funding acquisition (equal); Investigation-Supporting, Project administration (equal); Writing – review and editing (equal). **Bruna R. Amaral**: Data curation-Supporting, Writing – review and editing-Supporting. **David A. Luther**: Funding acquisition (equal); Investigation-Supporting, Project administration (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rr4xgxdd8 (Rutt et al. 2023).

Supporting information

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

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