

TITLE

Severe seasonal shifts in tropical insect ephemerality drive bat foraging effort

AUTHORS AND AFFILIATIONS

Jenna E. Kohles^{1,2,3,4,5*}, Rachel A. Page^{4,6}, Martin Wikelski^{1,2,3,7}, Dina K. N. Dechmann^{1,2,3,4,8}

¹Department of Migration, Max Planck Institute of Animal Behavior, Radolfzell, Germany, ²Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany, ³Department of Biology, University of Konstanz, Konstanz, Germany, ⁴Smithsonian Tropical Research Institute, Balboa, Ancón, República de Panamá, ⁵jkohles@ab.mpg.de, ⁶pager@si.edu, ⁷wikelski@ab.mpg.de, ⁸ddechmann@ab.mpg.de

* Corresponding author

Max Planck Institute of Animal Behavior
Am Obstberg 1, 78315 Radolfzell, Germany
jkohles@ab.mpg.de

STATEMENT OF AUTHORSHIP

J.E.K. and D.K.N.D conceived the study, J.E.K collected the data, J.E.K. performed the analyses, J.E.K. wrote the first draft of the manuscript and all authors contributed to the final manuscript.

DATA ACCESSIBILITY STATEMENT

All data and code required to replicate the present study are publicly available in the Movebank Data Repository, <https://doi.org/10.5441/001/1.297> (Kohles et al., 2023) and the Figshare repositories, data: 10.6084/m9.figshare.24543688 [available with this link for editors/reviewers:

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ABSTRACT

Food distribution and availability fundamentally shape foraging. Yet spatiotemporal distribution of mobile prey and its proximate effects on animals have rarely been assessed. The neotropical bat, *Noctilio albiventris*, forages on aquatic swarming insects which peak just one to two hours after dusk. We matched seasonal insect distribution at high spatiotemporal resolution to the foraging behavior of adult female bats. Surprisingly, insect abundance was lower in the wet season, and insect patches dispersed more rapidly. Correspondingly, bats emerged 45% earlier, foraged over 40% longer, and flew almost twice as far compared to the dry season. Wet season bats also spent less time at each patch, suggesting that patches, though the same size, were less dense and depleted more rapidly. Our results highlight the tight link between foraging and sharp seasonal shifts in the spatial unpredictability and temporal ephemerality of resources, shedding light on behavioral adaptations and plasticity in response to resource fluctuation.

INTRODUCTION

The timing and movement of animal foraging is fundamentally shaped by food availability in time and space. This relationship is evident across scales, from migrating animals tracking green waves across large landscapes (Aikens *et al.* 2017; Hurme *et al.* 2022), to central-place foragers who match foraging to locally varying resources (Bell 1990). The relationship is particularly strong for unpredictable and ephemeral resources, i.e. food sources that become available in space or time without strong patterns and, or persist in single locations for short periods of time. Such resources often require increased effort to find and must be exploited rapidly, resulting in variable foraging success (Real & Caraco 1986). However, these food sources are also often abundant, enabling rapid intake of energy (Wiens 1976). Extreme examples include seabirds searching for large schools of fish (Ashmole 1971) or birds, bats, and fish, exploiting brief mass emergences of mayflies (Sweeney & Vannote 1982).

We only vaguely understand true distribution of food in space and time for the majority of species, despite its importance for understanding species ecology (Weimerskirch 2007), and predicting animal decisions of when and where to forage (Bell 1990; Fagan *et al.* 2017; Kohles *et al.* 2022). The ephemerality of resources can also differ depending on the spatial or temporal scale (Kotliar & Wiens 1990). For example, figs fruit irregularly but then provide abundant food for days, while insects form exploitable swarms locally for just minutes to hours. At broad spatial scales both can be predictable, like the location of fig trees in a home range or insect swarms commonly occurring over water bodies (Kohles *et al.* 2022). Both scales have fundamental implications for animal foraging behavior.

In theoretical research on foraging behavior food distribution has long been fundamental. Yet in empirical studies variation in food distribution is often investigated only qualitatively, i.e., predictable versus ephemeral, or homogeneous versus patchy or clumped, even though such discrete categories do not occur in the real world (Wiens 1976; Kotliar & Wiens 1990; Weimerskirch 2007). Generalized food distributions have revealed important patterns of behavior, especially related to sociality (Egert-Berg *et al.* 2018; Jones *et al.* 2020; Roeleke *et al.* 2020), but are limited in explaining differences or shifts in foraging strategies between species, populations, or within individuals. This prevents us from understanding additional influences, such as energetic or nutritional needs, predation pressure, or social constraints.

Animal movement data has helped to bridge these gaps, for example, letting us consider “patchiness” from the perception of the animals themselves (Wiens 1976; Weimerskirch 2007). Bluefin tuna (*Thunnus thynnus*) encounter food patches every two hours when only 5-9 patches with an average radius of 1km occur per 100km² (Gutenkunst *et al.* 2007). Tracking Antarctic petrels (*Thalassoica antarctica*) revealed that krill (*Euphausia superba*) are concentrated for weeks at the largest spatial scale, but for only days at smaller scales (Fauchald & Tveraa 2006). These data are essential for predictive models of habitat use and behavior, but false conclusions can be easily drawn without actual resource data, e.g., that concentrated foraging in an area always increases with prey density (Florko *et al.* 2023). Furthermore, this research is heavily biased towards marine predator systems (birds, mammals, and fish). Exploration into wild non-marine systems, especially at smaller spatial scales are needed.

Bats are exceptionally energetically constrained while foraging (Schmidt-Nielsen 1972). Those that specialize on flying insects, in particular, must fly continuously, and maintain extremely high

heart rates for entire foraging bouts, balancing this with adequate food intake (Dechmann *et al.* 2011; Keicher *et al.* 2023). Many bat species specialize on swarming insects, which are ephemeral and unpredictable, but permit rapid food intake when found (Safi & Kerth 2007), and may be easier to detect with echolocation than individual insects (Boonman *et al.* 2019). However, we do not understand the spatiotemporal distribution of “swarms” across the landscape. They are often associated with bodies of water and emerge around dusk (Ruczyński *et al.* 2020), but where they emerge each night and how quickly they disperse due to their own mobility, wind, or disturbance by predators has only received speculation. Few studies consider such critical temporal and spatial dynamics of prey and their effect on bat foraging behavior (e.g., Fukui *et al.* 2006; Gonsalves *et al.* 2013; Moretto & Francis 2017, but see Wilkinson 1992). Quantifying seasonal shifts in food availability allows us to directly test the effect of food distribution on individual foraging effort, as seasonal increases in abundance may make unpredictable and ephemeral resources like insect swarms easier to find. Thus, empirical quantification of spatiotemporal variation in seasonal food landscapes can provide insights into species' adaptation to ecological niches and behavioral plasticity. Without such specific quantifications it is difficult to predict the energetic requirements needed to find food efficiently enough to achieve foraging success (Norberg 1977).

The lesser bulldog bat (*Noctilio albiventris*), a neotropical insectivore, primarily forages low over water for a wide range of primarily small flying insects in a single short bout after dusk (Hooper & Brown 1968; Brown *et al.* 1983; Aguirre *et al.* 2003; Dechmann *et al.* 2009). At our study site in central Panama the long wet season is interrupted by a dry season from January through April, likely providing a dynamic resource landscape. To investigate the relationship between food distribution and foraging effort, we asked: Does insect availability in space and time differ within

a foraging bout between seasons? We hypothesized that patches of flying insects would less abundant and more ephemeral during the dry season. Correspondingly, during the dry season *N. albiventris* should spend more time searching larger areas to find sufficient food patches, visiting more, smaller insect patches. We GPS-tracked foraging *N. albiventris*, and quantified nocturnal insect distribution at high spatiotemporal resolution using floating camera traps, across seasons. Understanding the relationships between dynamic resource landscapes and the strategies animals use to efficiently exploit them is essential for predicting how animals will adapt to our rapidly changing world.

METHODS

We conducted this study in Gamboa, Panama (9.117°N, -79.691°W), from January 2019 to April 2020. All methods conformed to the ASAB/ABS Guidelines for the Use of Animals in Research and were approved by the Ministerio del Ambiente (SE/A-29-18, SE/A-96-18, SE/A-38-2020), and the IACUC of the Smithsonian Tropical Research Institute (2017-0815-2020).

Insect monitoring

We placed waterproof digital cameras (Ricoh WG-5) on floating platforms in the river delta where *Noctilio albiventris* forages (Figure 1; (Ruczyński *et al.* 2020). Starting at 18:30, before dusk in both seasons, cameras took a photo with flash every 1-5 min, on which insects appear as white dots of irregular shape, occasionally with visible wings and appendages (Figure S1).

We anchored floating platforms with cinder blocks in transects 25-50m from shore, approximately 250m apart. We changed some monitoring locations between our three field seasons to avoid strong river currents and moving vegetation which displaced or destroyed

platforms, and after learning that our bats foraged primarily on the west side of the river delta. This resulted in four locations that overlapped exactly between the wet and dry seasons (Figure 1). Cameras detect insects of *N. albiventris*' typical prey size (5-15mm length; Aguirre *et al.* 2003) up to a height of ca. 8m (volume 125m³; Ruczyński *et al.* 2020), thus encompassing prey available to our bats which forage 20cm up to 5m above the water surface (Kalko *et al.* 1998).

Bat tracking

We caught entire colonies of *N. albiventris* as they emerged from their roosts using modified funnel traps and mist-nets (range: 17-37 bats per roost). We recorded mass (g), forearm length (mm), age class, and reproductive status. We took a 3mm wing skin sample and marked each individual with a subcutaneous PIT-tag (Trovan ID-100, Euro ID, Weilerswist, Germany). We tagged adult females with Pathtrack nanofix® Geo mini-GPS loggers (1.6-1.8g). We attached loggers using detachable shoestring collars closed with suture thread (Teague O'Mara *et al.* 2014). In our first and second field season we additionally attached radio transmitters (Holohil Systems Ltd model LB-2X weighing 0.27g), so tags weighed approximately 8% of bat body mass (Table S11). Tags turned on from 18:45-20:45 (foraging period confirmed by observing roost emergences and returns), and collected a GPS fix every 30s. Tags began collecting data two days after capture in the first and second field seasons, but 4-5 days after capture in the third, to allow tags on bats captured on different nights from different roosts to begin collecting data on the same night. We released bats at the capture site the same night they were captured. We recovered loggers by recapturing bats at roosts or once they had fallen off.

Insect distribution in space and time

We counted the number of insects per photo via a machine learning algorithm (Choinski *et al.* 2023). We compared the algorithm's insect counts with manual counts by JEK for a subset of 1,177 photos that spanned a range of conditions and insect numbers (Spearman Rank Correlation 0.80; Choinski *et al.* 2023). We excluded nights with rain, or manually counted photos where rain occurred for 10-15min.

To assess differences in spatiotemporal insect availability during the dry and wet seasons within a bat foraging bout, and break the temporal autocorrelation of insect counts, we calculated mean and maximum insects per photo and counted the number of photos without insects during the first 2.5h of photos for each location and each monitoring night. These metrics estimate average abundance, the largest peak, and instances of no insect availability, respectively, for single locations.

We estimated the number of "swarms" per monitoring night across all locations by counting the number of times that consecutive photos from a single location contained ≥ 10 insects each, separated by at least one photo with < 10 insects. We selected 10 insects in accordance with Ruczyński *et al.* (2020), but assessed whether this biased our results using a sensitivity analysis: We compared dense insect patch counts between the wet and dry season at increasing thresholds from 3-16 insects (no wet season data contained more than two consecutive photos with ≥ 16 insects) to determine whether differences were driven by the threshold or were a property of the insect distribution (Figure S2, Table S1). We then took the largest insect patch of each location and night and multiplied the number of consecutive photos with ≥ 10 insects by 5min to determine the duration of that patch. We compared durations between seasons. This estimate is conservative

because it could overestimate duration by up to 5min if the insect patch dispersed or was depleted soon after the last photo. We also tested whether differences in persistence durations were driven by the selected threshold (Figure S3, Table S2).

Bat foraging effort in time and space

We calculated foraging durations from the difference in minutes between the first and last GPS fix on each tracking night (GPS did not function inside the roost, and outside the roost bats fly continuously). We calculated emergence time as minutes after sunset with the R package “photobiology”.

We analyzed only GPS positions calculated with ≥ 5 satellites from the first three nights of tracking for behavioral segmentation. Afterwards, low batteries caused sporadic fixes. We then interpolated GPS positions at 30s intervals, to account for the slight variation in GPS time-to-fix (range: 1-18s; 23% of fixes required interpolation). We interpolated positions of missing fixes for gaps ≤ 4 fixes (< 120 s; 3% of fixes). For slightly larger gaps (180-270s), we split the tracks and ran segmentation separately (n=3 of 71 tracks). We calculated turning angle and speed using the R package “move”, then ran EMbC clustering on each track separately to account for variation between individuals and nights (“EMbC” R package). The algorithm clusters GPS segments into “high turning angle-high speed”, “low turning angle-high speed”, “high turning angle-low speed”, and “low turning angle-low speed”. We did posterior smoothing on single instances of a class nested within multiple instances of another class with the function `smth(delta=1)`. We then assigned behavioral states on tracks visualized in space. We assigned “low turning angle-high speed” as “commuting-searching” and all three other clusters as “ARS (area restricted search)-

feeding". For final smoothing of remaining single instances of a behavioral state nested within multiple instances of another state, we assigned the mode of the two states before and after.

We used transitions between behavioral states to investigate fine-scale foraging behavior, defining commuting-searching and ARS-feeding segments conservatively as stretches of ≥ 2 consecutive fixes (1min) of the same behavior. We calculated durations of segments at a resolution of 30s (GPS inter-fix interval), and counted the number of ARS-feeding segments to calculate 'number of insect patches visited' per bat foraging bout (one tracking night). We summarized the total duration of each behavior, and calculated the proportion of ARS-feeding relative to commuting-searching behavior for each bout.

We calculated maximum distance from the roost and the total flight distance each night using the `as.ltraj()` function (R package "adehabitatLT"). To estimate the area of concentrated feeding activity, as a metric for estimating insect patch size, we calculated the minimum convex polygon (MCP) around the GPS positions for each feeding segment > 4 fixes (function requires min 5 locations) of each track (R packages "SpatialPoints", "Move", and "adehabitatHR"). We took the square root of MCP values to report them in meters.

Statistical analyses

We performed non-metric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity measure (R package "vegan") with both insect and bat data. We assessed ordinations with the stress metric, which indicates how easily the multidimensional data could be condensed into 2-dimensional space (0.05-0.1 indicates very good representation in 2-D space). We fit numerical

and categorical variables to the ordinations and assessed the significance of the fitted vectors and factors using permutation tests (999 iterations).

Insects: ordinations included the intrinsic variables (vectors) mean/maximum insects per photo, location, and monitoring night; number of photos without insects per location and monitoring night; number of insect patches per monitoring night across all locations; and persistence of insect patches at locations. We then visualized how the extrinsic variables (factors) season, location (1-4), and monitoring date contributed to the ordination's structure.

Bats: ordinations included the intrinsic variables per foraging bout: emergence time after sunset, bout duration, duration of commuting-searching segments, duration of ARS-feeding segments, total commuting-searching duration, total ARS-feeding duration, proportion spent in ARS-feeding, maximum distance traveled from roost, total distance flown, number of insect patches visited, and MCP around GPS points in ARS-feeding segments. We visualized patterns in ordination space according to the extrinsic variables season, season-year (dry 2019, wet 2019, and dry 2020), bat ID, and tracking night (1-3).

We assessed the effects of season, camera location, and monitoring night for insect data, and of season, season-year, and bat ID for bat data with a permutation multivariate analysis of variance (PERMANOVA) on dissimilarity matrices of insect and bat data. We calculated dissimilarity matrices using Gower's distance, with numerical and categorical variables. We showed which individuals diverged significantly within each season with a Multi Response Permutation Procedure (MRPP) on bat data per season, grouped by individual.

We calculated 95% confidence intervals (CIs) around each metric's mean per season with nonparametric bootstrapping (R package “boot”, 5000 iterations). We compared the effect of season on these metrics, with permutation t-tests (two-tailed t-statistic, 9999 permutations). We adjusted P-values with sequential Bonferroni correction to control for multiple comparisons. We calculated Hedge’s *g* to estimate strength of effect sizes (small: 0.20, medium: 0.50, large: 0.80).

We conducted all statistical analyses in R (version 4.2.2).

RESULTS

Insect distribution in time and space

We analyzed the first 2.5h from seven nights in the dry season and ten in the wet season. Photos from some locations for some monitoring nights were excluded due to rare camera malfunctions or aquatic vegetation obscuring the lens, resulting in 22 and 31 location-monitoring nights for the dry and wet seasons, respectively.

Insect data clustered and diverged significantly in NMDS ordination space by season across all numerical variables (stress level: 0.06; Figure S4; Table S3). Camera location had no significant effect on ordinations (Figure S4, Figure S5, Table S4), supporting the hypothesis that insects were spatially unpredictable. Season and monitoring night had significant effects on ordinations (Figure S5, Table S4); however, PERMANOVA results revealed that season explained more variation (R^2) and had a stronger relationship with the dissimilarity matrix of numerical variables (F statistic) than monitoring date, indicating that insect distribution differed more strongly between seasons than between nights within a season (Table S7). However, clustering of

individual monitoring nights was weaker during the wet season and likely reflects lower overall predictability of the prey landscape, as nights were less similar across many metrics (Figure S5).

The mean and maximum number of insects per photo strongly decreased from the dry to the wet season and the mean number of photos without insects strongly increased (Figure 2; Table 1).

The mean number of insect patches per monitoring night was also lower in the wet than in the dry season and they persisted for less time (Figure 2; Table 1). The mean insect count was greater and persistence longer in the dry season for all insect count threshold values. For most thresholds the differences were significant, but less so with decreasing patch counts or sample sizes at higher thresholds (Figure S2, Figure S3; Table S1, Table S2).

Bat foraging effort in time and space

We GPS tracked bats in one wet season (Jun 2019) and two dry seasons (Feb 2019 and Feb 2020). We obtained 48 tracks from 16 individuals in the wet season, and 23 tracks from 9 individuals in the dry seasons. From each bat we obtained 1-3 nights of tracking data.

Bat data clustered and diverged significantly in NMDS ordination space according to season across all numerical variables (stress level: 0.08; Figure S6a, S6b; Table S5). Tracking night had no significant effect on ordinations, suggesting that capture did not have a strong effect on foraging behavior (Figure S6a, S6b; Table S6). Season, season-year, and bat ID all had significant effects on ordinations (Figure S6a, S6b, S7; Table S6); however, PERMANOVA results revealed that the relationship of season with the dissimilarity matrix of numerical variables (F statistic) was stronger than bat ID and the relationship of season-year was not significant. This indicates that bat foraging behavior differed more strongly between seasons than

years or individuals. Season and bat ID had similar R^2 values, which may be driven by weaker clustering overall between dry season individuals. The stronger clustering of individuals in the wet season (Figure S7), indicating more similarity across many metrics, may reflect constraints on foraging behavior caused by the less predictable prey landscape (and weak clustering between insect monitoring nights, Figure S5). MRPP results revealed that in the dry season one individual (BatG5b) diverged strongly from all others ($\delta > 0.2$; A: 0.191) and two individuals in the wet season (Bat02 and Bat04; $\delta > 0.2$; A: 0.276), although the effects here were weak.

In the wet season when insects were less predictable and more ephemeral, mean bat emergence was 45% earlier relative to sunset (Figure 2; Table 2). Mean foraging bout duration was 44% longer (Figure 2; Table 2). Bats spent less time in ARS-feeding per patch, and commuted-searched longer for their next patch (Figure 2; Table 2). ARS-feeding time per foraging bout was the same between seasons, but wet season commuting-searching lasted nearly three times longer (Figure 2; Table 2). Because foraging bouts in the wet season were longer, the proportion of ARS-feeding was 23% less (Figure 2; Table 2).

In the wet season, bats flew nearly twice as far from the roost (0.9km) and in total distance (5.1km; Figure 3; Table 3). They visited a mean of 1.7 more insect patches during the wet season (Figure 3; Table 3). Area used for ARS-feeding was similar, suggesting similar patch sizes between seasons (Figure 3; Table 3). In contrast, ARS-feeding time per insect patch was shorter in the wet season, suggesting that patches were less dense and depleted more rapidly (Figure 2; Table 2). Three wet season individuals on one night each, were still active when the GPS loggers turned off. This means wet season summary metrics may be underestimated, and differences between seasons could be even larger.

DISCUSSION

Our results exemplify the importance of detailed mapping of the resource landscape for understanding animal foraging behavior. Our insectivorous bats, specialized on patchy ephemeral insect swarms, experienced substantial shifts in prey availability between seasons which strongly affected their foraging behavior. Against our expectations, insect availability was significantly lower and less predictable in the wet season. As wet season insect patches were apparently more difficult to find, bats emerged 45% earlier, foraged 44% longer and increased distance and duration of commuting and searching, likely also increasing energy expenditure. Feeding behavior made up nearly 25% less time of each foraging bout in the wet season. Bats left patches more quickly, matching that insect patches were more ephemeral, and searched longer for subsequent patches. This overall pattern is corroborated by non-metric dimensional scaling (NMDS), where insect monitoring nights were less clustered in the wet season, reflecting a less predictable prey landscape. Correspondingly, individual bat data were more clustered in ordination space in the wet season. This clustering may indicate bats were more constrained to match the limited peaks of prey availability across many aspects of foraging behavior, whereas in the dry season a more predictable prey landscape permitted greater liberty and flexibility without jeopardizing foraging success.

We predicted that insect abundance would be lower and patches less predictable and more ephemeral in the dry season, as tropical insect abundance usually peaks during the transition to, or in the wet season, including for nocturnal flying insects in Panama (Ricklefs 1975; Tanaka & Tanaka 1982; Rautenbach *et al.* 1988; Kishimoto-Yamada & Itioka 2015). In contrast, we detected much fewer nocturnal flying insects over water during the wet season, and this was

reflected in the bats' foraging behavior. The difference may be related to the specific insects exploited by *Noctilio albiventris*. In temperate zones, aquatic emerging insects synchronize mass emergences during early summer months, but tropical insects may maintain less obvious seasonal reproductive cycles (Brittain 1982; Sweeney & Vannote 1982). Our study site, the Chagres River delta, experiences higher water levels, faster currents, and far more floating aquatic vegetation in the wet season. These environmental conditions may limit the abundance of nymphs (Righi-Cavallaro *et al.* 2010) and may not be ideal for adult emergence and swarming, driving the majority of species or populations to mate in the dry season (Corbet 1964; Brittain 1982).

Another reason we expected higher insect abundance during the wet season was because both reproductive peaks of *N. albiventris* occur during this period of the year. During peak lactation, when bat pups are close to fledging, energy demands for mothers can almost double compared to just after parturition (Kurta *et al.* 1989; Kunz *et al.* 1995). Female *N. albiventris* synchronize their primary birthing peak at the end of April and beginning of May, and lactate for up to three months (Rasweiler 1977; Brown *et al.* 1983). Juveniles fledge after seven weeks of age, and wean after three months, representing one of the longest periods of maternal care known for bats (Brown *et al.* 1983). Due to extended lactation, females may be both pregnant and lactating in August. Most bat species appear to time lactation (Racey 1982) or fledging (Fleming *et al.* 1972) with high food abundance. For insectivorous bats, this is typically the onset of the rains and lactation overlaps with the peak of the rainy season (Racey 1982; Racey & Entwistle 2000). Thus, it was surprising that emerging aquatic insect availability was low during the reproductive period for *N. albiventris* in the wet season. Emerging aquatic insects supply essential nutrients for bats and other riparian predators (Baxter *et al.* 2005), namely long-chain omega-3 polyunsaturated fatty acids (LCPUFAs). In birds, LCPUFA content is more important for

offspring performance than food quantity (Twining *et al.* 2016, 2019), and the levels of LCPUFAs available to predators from aquatic prey can vary by insect taxonomy (Mathieu-Resuge *et al.* 2021). *Noctilio albiventris* may time reproduction with a period of exceptional nutritional gain if the wet season supports prey species with higher LCPUFA content, despite lower prey abundance. Future studies should sample insects to elucidate the way resource distribution interacts with both energetic and nutritional requirements for reproductive output in *N. albiventris* and other species specialized on aquatic emerging insects.

That bats flew further and longer in the wet season, likely expending more energy, while spending proportionally less time feeding, suggests multiple non-mutually exclusive hypotheses that warrant further investigation. First, foraging behavior in the dry season may represent periods of energetic surplus because insects appear abundant and relatively easy to find. Only the wet season may push bats close to their energetic edge. This is supported by the fact that in the dry season bats ended foraging bouts and returned to the roost when insect abundance was still relatively high. In contrast, New Zealand long-tailed bats (*Chalinolobus tuberculatus*) and parti-coloured bats (*Vespertilio murinus*) forage longer during nights of higher insect abundance (O'Donnell 2000; Hałat *et al.* 2018), presumably investing more energy into foraging, to achieve proportionally higher energy gain (Norberg 1977). Lactating female parti-coloured bats and Leisler's bats (*Nyctalus leisleri*) also often forage longer, presumably to balance higher energetic demands with greater prey intake (Shiel *et al.* 1999; Hałat *et al.* 2018). However, theory states that animals should forage longer during less profitable periods, when food is limited and when energetic requirements are higher (Schoener 1971). Only our high-resolution assessment of both insect availability and bat foraging behavior allowed us to differentiate between these predictions. A second potential explanation is that in the wet season bats fed on fewer but larger or more

energy-rich insects, as they spent less time performing ARS-feeding in each patch. This could compensate for the energy expenditure of increased searching behavior. Thirdly, flight and or echolocation may be less costly under shifting environmental conditions like lower wind speeds and higher relative humidity in the wet season (Sapir *et al.* 2014; Chaverri & Quirós 2017; O'Mara *et al.* 2019), and, finally, bats may compensate by using additional energy-saving strategies in the wet season like torpor at high body temperature (Dechmann *et al.* 2011).

Noctilio albiventris may also use social foraging to overcome potentially higher energetic costs in the less predictable and more ephemeral prey distribution in the wet season. In the wet season subgroups of females from a roosting colony were consistently co-located for the majority of their foraging bouts, and subgroups rarely overlapped in space and time (Dechmann *et al.* 2009). Bats were also attracted to playbacks of conspecific feeding buzzes. By eavesdropping on group members' feeding buzzes, *N. albiventris* can increase insect detection range tenfold (Dechmann *et al.* 2009). According to our new understanding of how shifting prey distribution makes food much more challenging to exploit, reproduction may only add to this challenge, rather than fully drive it. Insect patches persist far less than the duration of a foraging bout of *N. albiventris*, only 8 min in the wet season, meaning social information about their presence has to be transferred in situ (as opposed to in the roost). *Noctilio albiventris* may use social information flexibly, increasing coordination when food is rare, difficult to find and energetic demands higher, in line with predictions of the framework of Kohles et al. (2022). Interestingly, some wet season individuals foraged for durations comparable to the dry season and non-metric multidimensional scaling revealed some individuals diverging significantly in ordination space from others within the same season, which could reflect more efficient foraging due to the use of social information

strategies. Alternatively, these bats may simply be more experienced, skilled, or competitive foragers, enabling them to exploit food patches more rapidly and or closer to the roost.

While studies assessing shifting food landscapes are rare, they have revealed novel insights into the relationship of foraging behavior with energetic or nutritional needs, social constraints, and predation pressure. Thick-billed murres (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*) increase foraging trip time and distance from colonies to compensate for lower fish abundance, but only in kittiwakes this translated to decreased reproductive output. Even though both birds experience the same prey landscape shift, only kittiwakes are pushed to their energetic edge (Kitaysky *et al.* 2000; Piatt *et al.* 2007). When fluctuations in prey availability occur in non-seasonal patterns, such as larger scale climatic effects, species may not have strategies to compensate, and suffer from reduced foraging success. Little penguins (*Eudyptula minor*) increase foraging effort and lower prey encounter rates when fish are more challenging to find and access (lower density and located lower in the water column), resulting in lower female mass (Phillips *et al.* 2022). Even mapping prey distributions in conjunction with foraging effort for animals exploiting somewhat predictable resources, and over smaller spatial scales, reveals important insights. Bumblebees (*Bombus terrestris*) tracked over their entire foraging landscape, often forage beyond closest available resources, which may indicate preference for quality over quantity (Osborne *et al.* 1999). Indeed, bumblebees respond more to floral diversity than density, indicating the complexity of understanding foraging decisions and how incorporating both food distribution and abundance alters conclusions (Jha & Kremen 2013). Opposing spatial and temporal resource distributions between simple and complex plant landscapes can even influence the effort honeybees (*Apis mellifera carnica*) invest into their complex information sharing strategy, the waggle dance (Steffan-Dewenter & Kuhn 2003). In the dry season of Costa Rica

when many trees are leafless, foraging Seba's short-tailed bats (*Carollia perspicillata*) often invest into commuting back to their day roost between foraging bouts, rather than use nearby night roosts on trees that without leaves probably do not provide enough protection from predators. However, fruit is also less abundant and dispersed during the dry season, which likely contributes to greater foraging commutes in addition to increased predation pressure (Fleming & Heithaus 1986).

It is clear that foraging ecology is complex and crucial for survival and reproduction. Especially in seasonal environments, timing periods of increased energy demand with food availability should be under strong selective pressure. Without quantifying prey distribution at scales relevant for the foragers in question, we cannot disentangle how foraging effort is influenced by factors beyond food distribution, such as behavioral or physiological states. Understanding the relationships between dynamic resource landscapes and the foraging strategies animals use to efficiently exploit them helps predict energetic and social requirements, behavioral plasticity, and potential for adaptation to rapidly changing environments.

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FIGURE CAPTIONS

Figure 1. Study site in Gamboa, Panama, where the Chagres River meets the Panama Canal. Blue balloons indicate the three colonies where we captured, tagged, or recaptured bats. Purple cameras indicate locations of floating platforms with camera traps.

Figure 2. **Insects are less predictable and more ephemeral in the wet season, and bats scale-up temporal foraging effort accordingly.** Overview and summary metrics of temporal and spatial insect distribution and bat foraging effort. In the wet season on average, (A) insect abundance is almost 75% lower, (B) largest insect peaks are nearly 50% lower, (C) instances of no insect availability are over 5x more common, (D) insect patches (≥ 10 insects per photo) are over 2x rarer, and (E) insect patches are more ephemeral, persist for almost 15 min less. Bats in the wet season on average, (A) forage almost 45% longer, (B) emerge 12 mins earlier relative to sunset (45%), (C) feed 30% shorter in each insect patch and search nearly 70% longer for the next insect patch, (D) spend the same total amount of time in ARS-feeding, but (E) spend more time commuting-searching in total, (F) decreasing the proportion of ARS-feeding by nearly 25%. Overview plot: lines represent insects detected in photos (every 5 min) over the night per

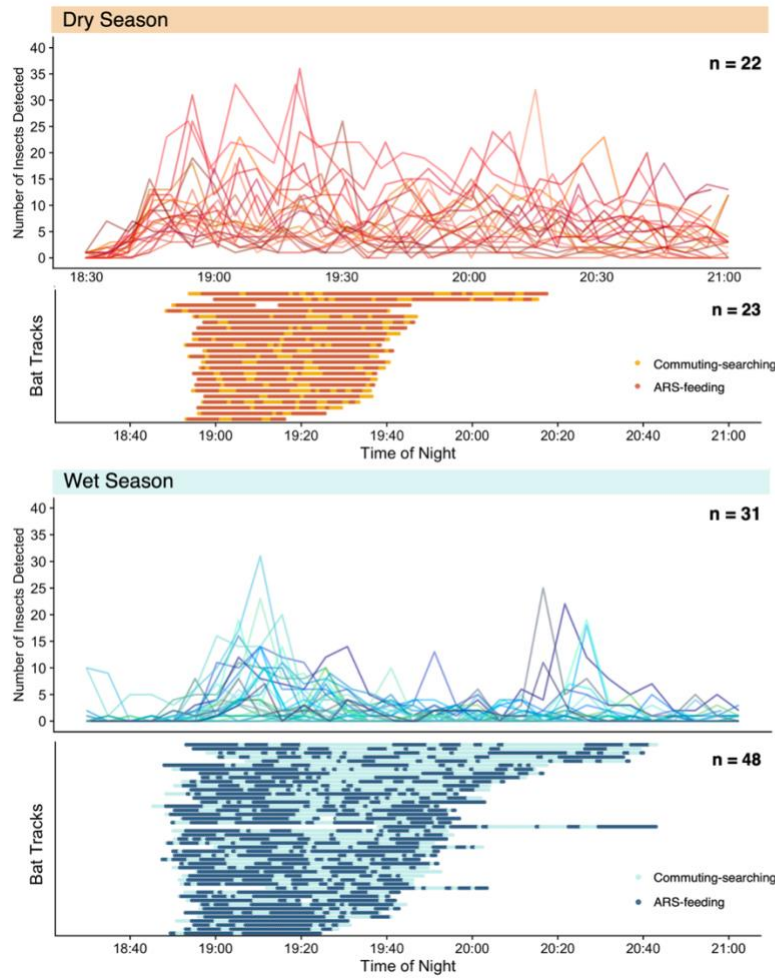
platform for single nights of monitoring at identical locations during the wet (N=31) and dry seasons (N=22). Horizontal bars represent foraging bouts of individual bats, for each date they were tracked, colored by behavioral state: light colors represent commuting-searching and dark colors, ARS-feeding. N=23 foraging bouts in the dry season and N=48 foraging bouts in the wet season. For insect summary metric plots, each point represents a calculation (A-C, E) per photo for one of the same four locations between seasons or (D) for photos across all locations, on each monitoring night. For bat summary metric plots, points represent (A-B, D-F) each night of tracking for every bat, or (C) a segment of a behavioral state within a bat's track. Diamonds represent bootstrapped means and bars represent bootstrapped 95% confidence intervals around means.

Figure 3. Bats scale-up spatial foraging effort in the wet season. Overview of bat foraging tracks in space per season, along with summary metrics quantifying spatial foraging effort. In the wet season on average, bats flew nearly twice as far in (A) maximum distance from roost and (B) total distance, (C) visited close to 2 more insect patches, but (D) but performed ARS-feeding in same-sized areas. Overview plots: tracks are individual foraging bouts of bats, colored by behavioral state: light colors represent commuting-searching and dark colors represent ARS-feeding. N=23 tracks in the dry season and N=48 tracks in the wet season. For summary metric plots, points are (A-C) each track for each bat, or (D) each segment of ARS-feeding within each track of each bat. Diamonds are bootstrapped means and bars bootstrapped 95% confidence intervals.

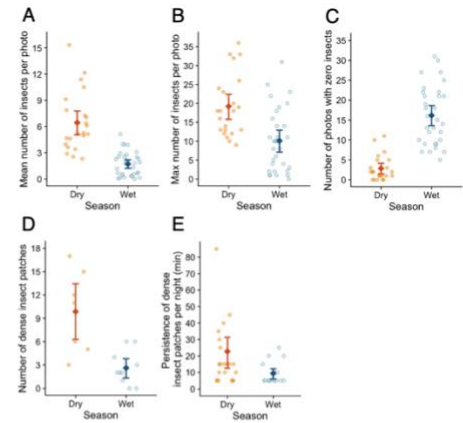
695 **FIGURES**



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Insects in TIME and SPACE



Bats in TIME

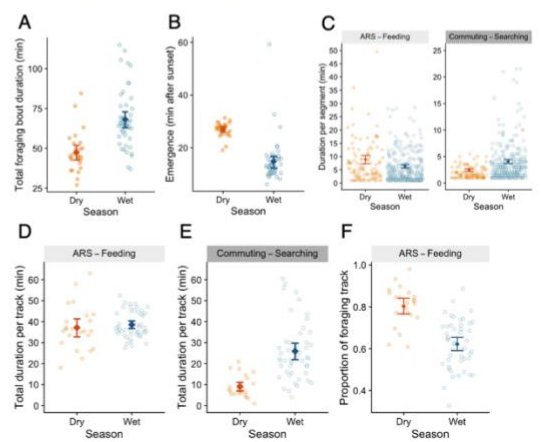


Figure 2.

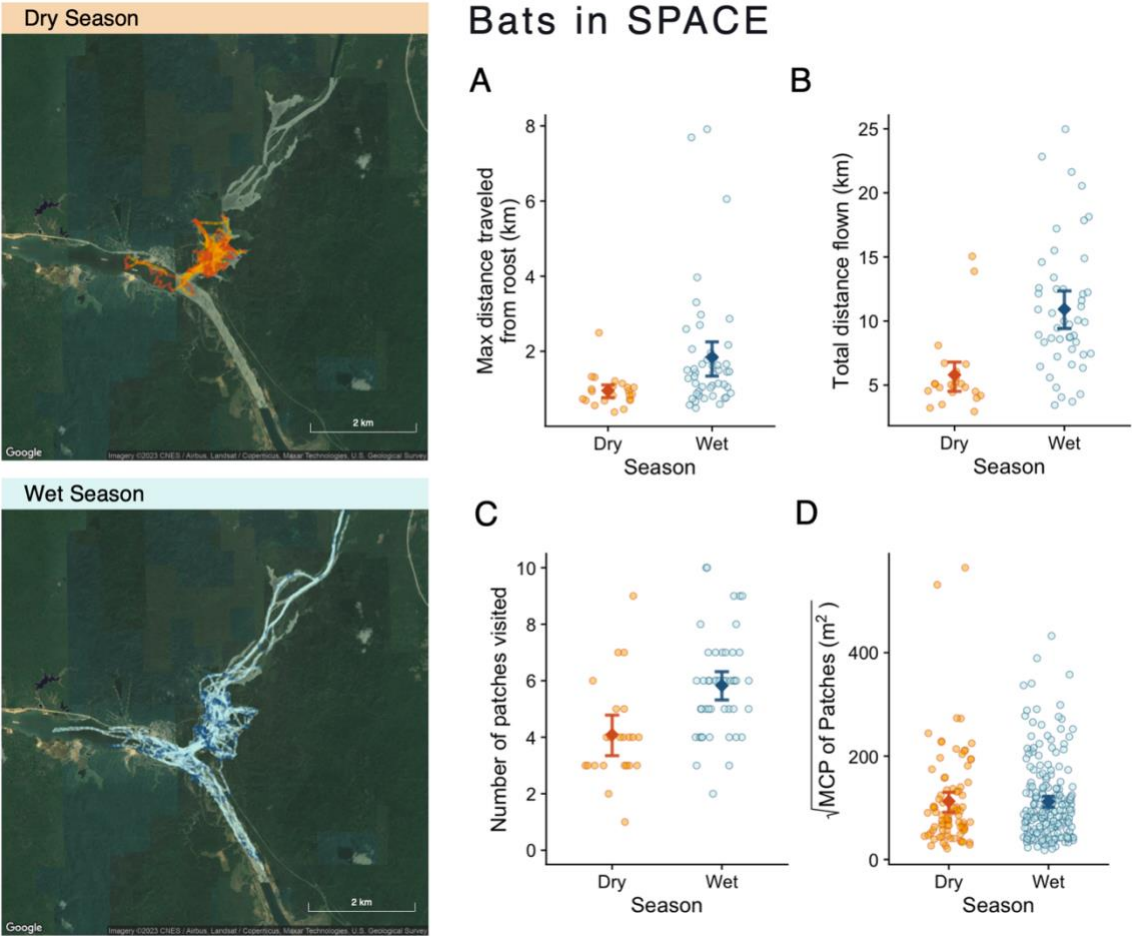


Figure 3.

TABLES

Table 1. Means and their bootstrapped 95% confidence intervals, and sample sizes of insect count summary metrics by season and permutation test results for insect count summary metrics by season.

Metric	Season	Lower	Mean	Upper	N	Mean Change	p	adj. p	Hedge's g
Mean	Dry	5.1	6.4	7.8	22	-4.74	<0.0002	<0.0002	-1.913
	Wet	1.2	1.7	2.2	31				
Maximum	Dry	15.8	19.2	22.4	22	-9.16	<0.0002	0.0005	-1.085
	Wet	7.1	10.1	12.9	31				
Zero Count	Dry	1.5	2.9	4.1	22	13.31	<0.0002	<0.0002	2.162
	Wet	13.6	16.2	18.6	31				
Patch Count	Dry	6.3	9.9	13.4	7	-7.28	0.002	0.012	-1.835
	Wet	1.3	2.6	3.8	10				
Patch Duration (min)	Dry	12.5	22.7	31.4	22	-13.25	0.010	0.048	-0.692
	Wet	5.9	9.4	12.2	16				

Table 2. Means and their bootstrapped 95% confidence intervals, and sample sizes for bat foraging effort summary metrics in time by season.

Metric	Season	Lower	Mean	Upper	n	Mean change	P	adj. P	Hedge's g
Emergence (min after sunset)	Dry	26.0	26.9	28.0	27	-12.11	<0.0002	<0.0002	-1.796
	Wet	12.2	14.8	16.7	48				
Foraging bout duration (min)	Dry	42.5	47.5	51.8	27	20.70	<0.0002	<0.0002	1.256
	Wet	62.9	68.2	72.9	48				
Duration commuting-searching segments (min)	Dry	2.2	2.5	2.7	69	1.62	<0.0002	<0.0002	0.524
	Wet	3.7	4.1	4.5	282				
Duration ARS-feeding segments (min)	Dry	7.3	8.9	10.4	94	-2.60	0.004	0.033	-0.418
	Wet	5.7	6.3	7.0	274				
Total time commuting-searching (min)	Dry	7.0	9.1	11.1	23	16.8	<0.0002	<0.0002	1.402
	Wet	21.9	26.0	29.8	47				
Total time ARS-feeding (min)	Dry	32.8	37.2	41.3	23	1.39	0.571	1.000	0.173
	Wet	36.8	38.6	40.3	47				
Proportion of time ARS-feeding	Dry	0.8	0.8	0.8	23	-0.18	<0.0002	<0.0002	-1.637
	Wet	0.6	0.6	0.7	47				

Table 3. Means and their bootstrapped 95% confidence intervals, and sample sizes for bat foraging effort summary metrics in space by season.

Metric	Season	Lower	Mean	Upper	n	Mean change	P	adj. P	Hedge's g
Maximum distance travelled from roost (km)	Dry	0.8	1.0	1.1	23	0.89	0.0004	0.0008	0.650
	Wet	1.3	1.8	2.3	47				
Total distance flown (km)	Dry	4.5	5.8	6.8	23	5.11	<0.0002	<0.0002	1.129
	Wet	9.4	10.9	12.3	47				
N feeding patches visited	Dry	3.3	4.1	4.8	23	1.73	0.0003	0.002	0.966
	Wet	5.3	5.8	6.3	47				
MCP of feeding patches (m)	Dry	91.2	112.5	129.9	85	-0.18	0.976	-	-0.004
	Wet	101.3	112.2	122.2	204				