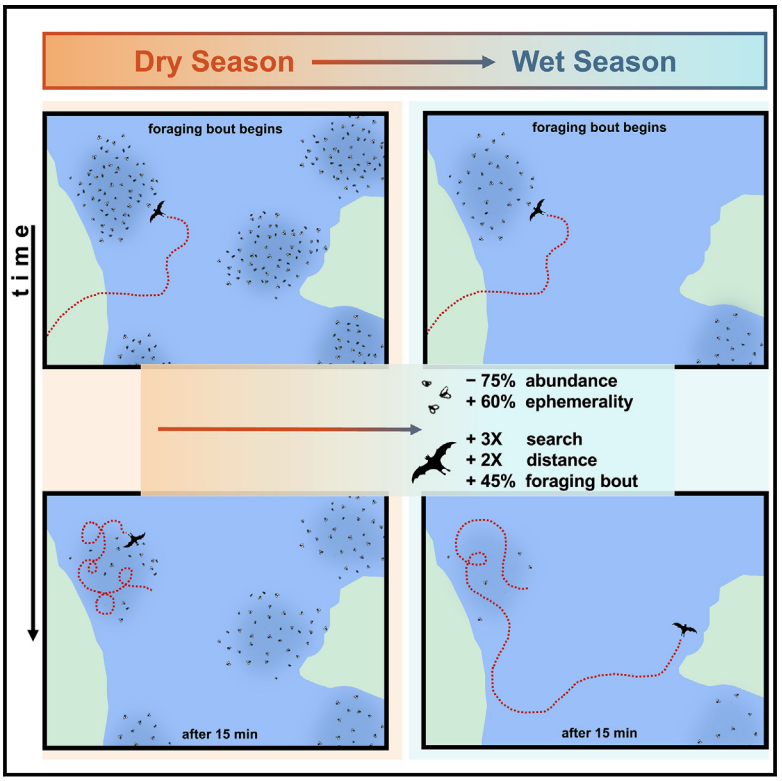
Report

Current Biology

Seasonal shifts in insect ephemerality drive bat foraging effort

Graphical abstract



Highlights

- Quantifying food distribution in nature is vital to understanding foraging behavior
- We quantified coinciding shifts in insect ephemerality and bat foraging effort
- Wet season insects were 75% less abundant and swarms 60% shorter lived
- Wet season bats flew twice as far, searched 3× more, and foraged 45% longer per night

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In brief

Kohles et al. show that bats increase their foraging effort when swarms of tropical aquatic flying insects are less predictable and more ephemeral during the wet season. Food availability and bat foraging effort are tightly linked and driven by seasonal changes.

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Report

Seasonal shifts in insect ephemerality drive bat foraging effort

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SUMMARY

Animal foraging is fundamentally shaped by food distribution and availability.[1] However, the quantification of spatiotemporal food distribution is rare[2] but crucial to explain variation in foraging behavior among species, populations, or individuals. Clumped but ephemeral food sources enable rapid energy intake but require increased effort to find,[3] can generate variable foraging success,[4] and force animals to forage more efficiently. We quantified seasonal shifts in the availability of such resources to test the proximate effects of food distribution on changes in movement patterns. The neotropical lesser bulldog bat (*Noctilio albiventris*) forages in a seasonal environment on emerging aquatic insects, whose numbers peak shortly after dusk.[5,6] We GPS-tracked bats and quantified nocturnal insect distribution in their foraging area using floating camera traps across wet and dry seasons. Surprisingly, insects were 75% less abundant and swarms were 60% shorter lived (more ephemeral) in the wet season. As a result, wet season bats had to fly twice as far (total and maximum distance fromroost distances) and 45% longer (duration) per night. Within foraging bouts, wet season bats spent less time in each insect patch and searched longer for subsequent patches, reflecting increased temporal ephemerality and decreased spatial predictability of insects. Our results highlight the tight link between foraging effort and spatiotemporal distribution of food and the influence of constraints imposed by reproduction on behavioral flexibility and adaptations to the highly dynamic resource landscapes of mobile prey.[7,8] Examining foraging behavior in light of spatiotemporal dynamics of resources can help predict how animals respond to shifts in food availability caused by escalating environmental changes.

RESULTS

Insects were less spatially predictable and more ephemeral in the wet season

We quantified the distribution of nocturnal flying insects in the primary foraging area of lesser bulldog bats (approximately 2.5 km^2) using a transect of five floating camera traps in the wet (2019) and dry (2020) season (Figure 1). Every 5 min, cameras took a flash photo in which insects could be counted as white reflections (Figure S1).[9,10] We analyzed 2.5 h after dusk (encompassing entire bat foraging bouts) from seven dry season and ten wet season nights. Some sets of photos were excluded due to rare camera malfunctions or aquatic vegetation obscuring the lens, resulting in 26 and 37 location-monitoring nights for the dry and wet season, respectively (13 ± 2 nights per location).

We calculated mean and maximum insects per photo (including photos without insects) and counted the number of photos without insects for each location on each monitoring night (first 2.5 h after dusk) during both seasons. These metrics estimate average abundance, the largest peak, and instances of no insect availability, for each location-monitoring night. We estimated the number of "swarms" per monitoring night across locations by counting the number of consecutive photos from a single location with $\geq$10 insects each, separated by at least one photo with <10 insects. We implemented a sensitivity analysis to assess the influence of this threshold (Figure S2; Table S1; STAR Methods). We estimated swarm persistence by multiplying the number of consecutive photos with $\geq$10 insects by five (photos taken every 5 min) for the largest swarm per location-monitoring night.

We performed non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA) to assess the influence of season on quantitative metrics while accounting for repeated measures across locations and monitoring nights. Insect data clustered and diverged significantly in NMDS ordination space by season across all numerical variables (per location-monitoring night: mean/max insects per photo, number of photos without insects, persistence of longest-lasting patch; per monitoring night: number of insect patches; stress level: 0.05; Figure S3; Table S2). Monitoring

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Figure 1. Study site in Gamboa, Panama, where the Chagres River meets the Panama Canal

White circles: the three captured colonies. Green balloons: locations of floating platforms with camera traps. Note scale bar in bottom right corner.

See also Figure S1 and Table S5.

location had no significant effect on ordinations (Figure S3; Table S2), supporting the hypothesis that insects were spatially unpredictable. Although during periods of highest insect availability, shortly after dusk, this could also reflect a more even distribution of insects across locations. Season and monitoring night had significant effects on ordinations (Figure S3; Table S2). However, variation of location-monitoring nights was much greater between than within seasons (PERMANOVA, $F = 91.45$), and season explained more variation ($R^2 = 0.53$) than monitoring night ($R^2 = 0.17$; $F = 3.25$; Table S3). Monitoring nights clustered less during the wet season, which likely reflects lower overall predictability of the prey landscape, as nights were less similar across many metrics (Figure S3B).

The mean and maximum number of insects per photo decreased by 78% and 59%, respectively, from the dry to the wet season, and photos without insects were an astounding six times more common (Figures 2A–2E; Table 1). The mean number of insect patches per monitoring night was 81% lower in the wet than in the dry season and they persisted for 60% less time (Figures 2A, 2B, 2F, and 2G; Table 1). For most wet season nights, and even some dry season nights, some locations did not have a single swarm, again confirming the spatial unpredictability of this food source (Figure 2G). Our 10-insect count threshold did not bias results, as the mean insect count was greater and persistence longer in the dry season for all tested insect count threshold values (Figure S2; Table S1).

Bats scale up temporal and spatial foraging effort in the wet season

We GPS-tracked bats with 30-s resolution in one wet season (June 2019), when most females were lactating, and two dry seasons (February 2019 and 2020), when all females were non-reproductive. We obtained 48 tracks from 16 individuals in the wet season and 23 tracks from nine individuals in the dry seasons. From each bat we obtained 1–3 nights of tracking data.

To quantify temporal foraging effort, we calculated emergence time relative to sunset and duration for each track (foraging bout). We then segmented tracks into ''commuting-searching'' and ''ARS (area restricted search)-feeding'' to investigate fine-scale foraging behavior, including the number of patches visited per track, i.e., independent segments of ARS-feeding (Figure S4; STAR Methods). We quantified spatial foraging effort per track by calculating maximum distance from the roost and total flight distance, and the area of concentrated feeding activity (ARS-feeding segments) to estimate insect patch size. We performed NMDS, PERMANOVA, and multiple response permutation procedure (MRPP) to assess the influence of season on quantitative metrics, while accounting for repeated measures across bats, nights-since-capture, and years.

Bat data clustered and diverged significantly in NMDS ordination space according to season across all numerical variables (emergence time, bout duration, duration of commuting-searching and ARS-feeding segments, total duration of commuting-searching and ARS-feeding, maximum distance traveled from roost, total distance flown, number of insect patches visited, and minimum convex polygon [MCP] area around GPS points in ARS-feeding segments; stress level: 0.08; Figure S3; Table S2). Nights-since-capture did not have a significant effect on ordinations (Figure S3; Table S2). Season, season-year, and bat ID all had significant effects on ordinations (Figure S3; Table S2); the variation of tracks was greater between seasons versus within seasons (PERMANOVA; $F = 41.48$), and this ratio was stronger than the variation between versus within bats ($F = 3.34$) or between versus within season-year ($F = 3.56$; Table S3). Bat ID did, however, explain a large portion of variation between tracks within season (SofSq = 0.99, $R^2 = 0.437$; Table S3). The average delta value (within and out-of-group disagreement) among individuals was lower in the wet season (MRPP; delta = 0.118) than in the dry season (delta = 0.154) (Table S4). This stronger clustering of individuals in the wet season, indicating more similarity across many foraging metrics, may reflect constraints on foraging behavior caused by the less-predictable prey landscape in the wet season (and weaker clustering between insect monitoring nights; Figure S3).

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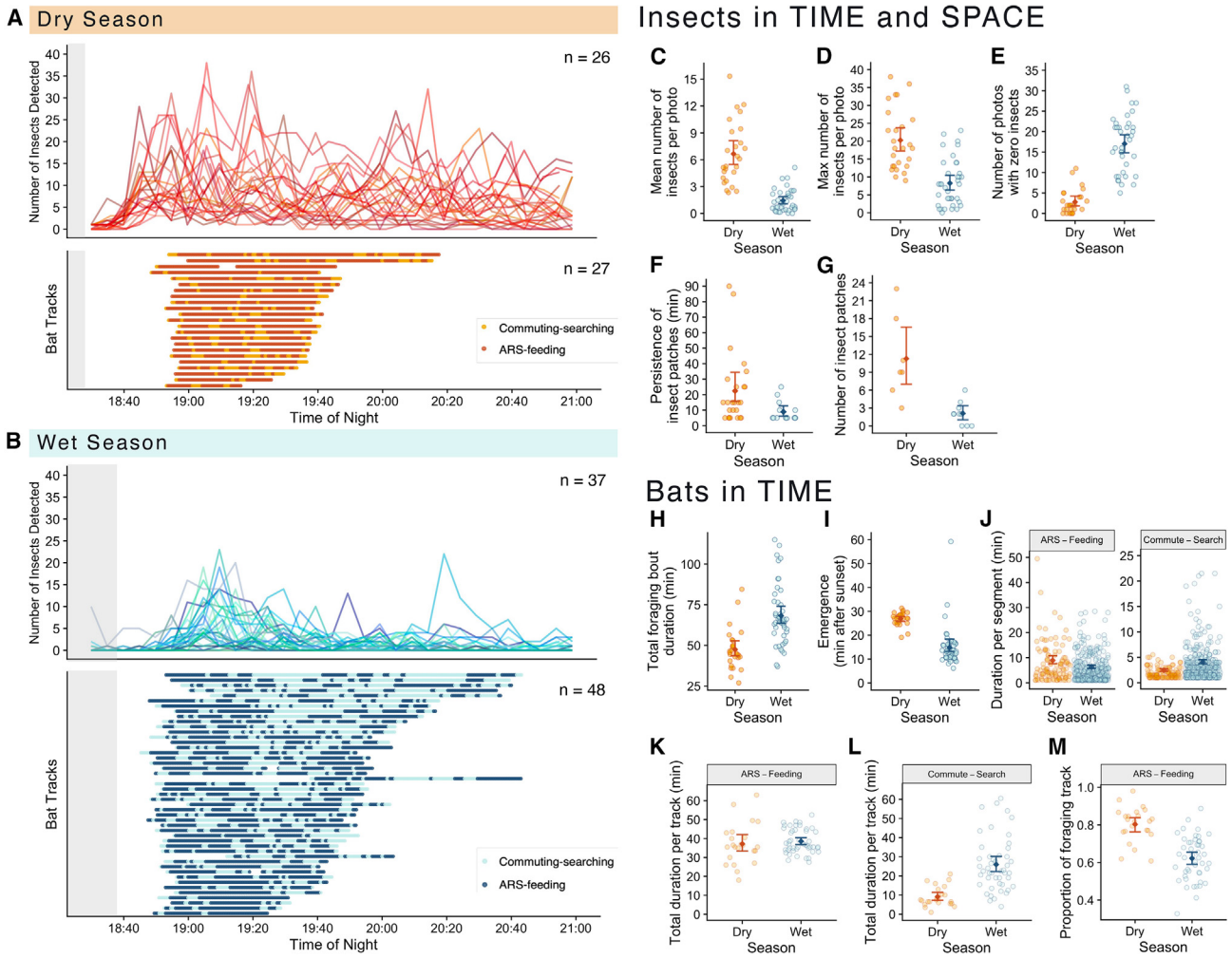

Figure 2. Insects are less predictable and more ephemeral in the wet season, and bats scale up temporal foraging effort accordingly

(A and B) Top: overview of insect data per season, each line represents a single monitoring night at one of five locations (identical between seasons), showing insects detected per photo (every 5 min) across the 2.5 h monitoring period (gray box represents pre-sunset). Bottom: temporal overview of bat data per season. Horizontal bars represent individual foraging bouts for each tracking night, colored by behavioral segmentation. Light colors, commuting-searching; dark colors, ARS-feeding.

(C–F) Each point represents a line from insect overview plots—metrics are calculated on photos for a single location-monitoring night.

(G) Each point represents a monitoring night—the total number of insect patches detected across all five locations.

(H–M) Each point represents a single night of tracking for each bat (H, I, and K–M) or a segment of a behavioral state within a bat's track (J). Diamonds represent bootstrapped means and bars represent bootstrapped 95% confidence intervals around means.

See also Figures S1–S4 and Tables S1–S4.

In the wet season, when insects were less predictable and more ephemeral, bats emerged 45% earlier relative to sunset (Figures 2A, 2B, and 2I; Table 1). Mean foraging bout duration was 44% longer (Figures 2A, 2B, and 2H; Table 1). Bats spent less time in ARS-feeding per patch and commuted-searched longer for their next patch (Figure 2J; Table 1). ARS-feeding time per foraging bout was the same between seasons, but wet season commuting-searching lasted nearly three times longer (Figures 2K and 2L; Table 1). Because foraging bouts in the wet season were longer, the proportion of ARS-feeding was 23% less on average (Figure 2M; Table 1).

In the wet season, bats flew nearly twice as far from the roost (0.9 ± 0.35 km; ±SE) and in total distance (5.1 ± 1.29 km; Figures 3A–3D; Table 1). The size of area (m^2) used for ARS-feeding was similar, suggesting similar patch sizes between seasons (Figure 3F; Table 1). 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 2J; Table 1). Correspondingly, bats visited a mean of 1.7 ± 0.50 more insect patches during the wet season (Figure 3E; Table 1).

DISCUSSION

Mapping the spatiotemporal distribution of resources is critical to understand the drivers of variation in animal foraging behavior. Our insectivorous bats, specialized on patchy ephemeral insect

Table 1. Insects are less predictable and more ephemeral in the wet season, and bats scale up temporal and spatial foraging effort accordingly

Metric	Season	Lower	Mean	Upper	*n*	Mean change	*p*	adj. *p*	Hedge's g
Insect distribution									
Mean	dry	5.5	6.7	8.1	26	−5.22	<0.0002	<0.0002	−2.134
	wet	1.1	1.4	1.9	37				
Maximum	dry	17.3	20.3	23.7	26	−12.00	<0.0002	<0.0002	−1.586
	wet	6.3	8.3	10.5	37				
Zero count	dry	1.8	2.8	4.2	26	14.2	<0.0002	<0.0002	2.474
	wet	14.8	17.0	19.2	37				
Patch count	dry	7.0	11.3	16.6	7	−9.19	0.0008	0.004	−1.881
	wet	1.0	2.1	3.4	10				
Patch duration (min)	dry	15.6	22.4	34.4	25	−13.47	0.008	0.042	−0.700
	wet	6.1	8.9	12.9	14				
Bat foraging effort in time									
Emergence (min after sunset)	dry	25.7	26.9	27.8	27	−12.14	<0.0002	<0.0002	−1.796
	wet	12.2	14.8	16.7	48				
Foraging bout duration (min)	dry	43.6	47.5	52.9	27	20.74	<0.0002	<0.0002	1.256
	wet	63.6	68.2	74.1	48				
Duration commuting-searching segments (min)	dry	2.2	2.5	2.7	69	1.63	<0.0002	<0.0002	0.524
	wet	3.7	4.1	4.5	282				
Duration ARS-feeding segments (min)	dry	7.6	8.9	10.8	94	−2.60	0.004	0.033	−0.418
	wet	5.7	6.3	7.0	274				
Total time commuting-searching (min)	dry	7.2	9.1	11.4	23	16.8	<0.0002	<0.0002	1.402
	wet	22.3	26.0	30.2	47				
Total time ARS-feeding (min)	dry	33.3	37.2	42.0	23	1.39	0.574	1.000	0.172
	wet	36.9	38.5	40.4	47				
Proportion of time ARS-feeding	dry	0.8	0.8	0.8	23	−0.18	<0.0002	<0.0002	−1.638
	wet	0.6	0.6	0.7	47				
Bat foraging effort in space									
Maximum distance traveled from roost (km)	dry	0.8	1.0	1.2	23	0.89	0.0004	0.0008	0.650
	wet	1.5	1.8	2.4	47				
Total distance flown (km)	dry	4.9	5.8	7.6	23	5.12	<0.0002	<0.0002	1.129
	wet	9.6	10.9	12.4	47				
No. feeding patches visited	dry	3.4	4.1	4.8	23	1.74	0.0003	0.002	0.966
	wet	5.3	5.8	6.3	47				
MCP of feeding patches (m)	dry	96.5	112.5	136.7	85	−0.18	0.999	N/A	−0.000
	wet	102.8	112.5	124.4	203				

Means and their bootstrapped 95% confidence intervals, sample sizes, and permutation test results of insect count summary metrics and bat foraging effort in time and space summary metrics by season.
See also Figures S1–S4 and Tables S1–S4.

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 and likely energy expenditure as well. Bats spent nearly 25% less time of each foraging bout feeding in the wet season. Bats left patches more quickly, matching the fact that insect patches were more ephemeral, and searched longer for subsequent patches. This overall pattern is corroborated by NMDS, where insect distribution differed more strongly between monitoring nights in the wet season, reflecting a less-predictable prey landscape. Correspondingly, movement patterns of bats were more similar between individuals in the wet season. This may indicate that bats were more constrained to match the limited peaks of prey availability, whereas in the dry season a more predictable prey landscape permitted greater behavioral flexibility without jeopardizing foraging success.

We predicted that insect abundance would be lower and patches less predictable and more ephemeral in the dry season,

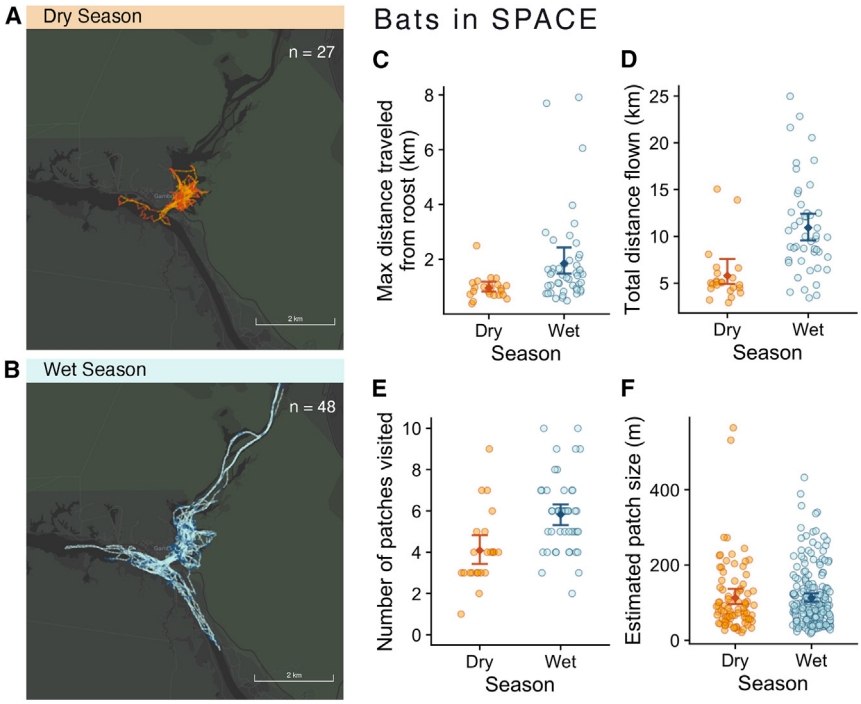

Figure 3. Bats scale up spatial foraging effort in the wet season

(A and B) Spatial overview of bat GPS data by season; tracks colored by behavioral segmentation (horizontal bars in Figures 2A and 2B). Light colors, commuting-searching; dark colors, ARS-feeding. Note scale bars in bottom right corners.

(C–E) Each point represents the metric calculated for a single track (night of foraging) of a bat.

(F) Each point represents a segment of ARS-feeding within each bat's track. Diamonds are bootstrapped means and bars bootstrapped 95% confidence intervals.

See also Figures S2–S4 and Tables S1–S4.

as tropical insect abundance usually peaks during the transition to, or in, the wet season. This includes nocturnal flying insects in Panama.[11–14] By 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 lesser bulldog bats. In temperate zones, aquatic emerging insects synchronize mass emergences during early summer months, but tropical insects may maintain less clear-cut seasonal reproductive cycles.[15,16] There are higher water levels, faster currents, and far more floating aquatic vegetation at our study site in the wet season. These environmental conditions may limit the abundance of nymphs[17] and/or adult emergence and swarming, driving the majority of species to mate in the dry season.[16,18] Importantly, even though tropical environments are generally less seasonal than their temperate counterparts, they clearly generate enough variation to shift food availability and predator behavior.[14,19]

Another reason we expected higher insect abundance during the wet season was because both reproductive peaks of lesser bulldog bats occur during this season. During peak lactation, when bat pups are close to fledging, energy demands for mothers can almost double compared with just after parturition.[20,21] Lesser bulldog bats synchronize their primary birthing peak at the end of April and beginning of May.[22,23] Juveniles fledge 7 weeks after birth but wean after 3 months, one of the longest periods of maternal care known for bats.[23] Due to extended lactation, females may be both pregnant and lactating in August. Most bat species appear to time lactation[24] or fledging[25] 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.[24,26] Thus, it was surprising that insect availability was low during reproduction. Emerging aquatic insects supply essential nutrients for bats and other riparian predators,[27] namely long-chain omega-3 polyunsaturated fatty acids (LCPUFAs). In some birds, LCPUFA content is more important for offspring performance than food quantity,[28,29] and the levels of LCPUFAs available to predators from aquatic prey can vary by insect taxonomy.[30] Lesser bulldog bats 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 in which resource distribution interacts with both energetic and nutritional requirements for reproductive output in bulldog bats and other species specialized on aquatic emerging insects.

That bats flew further and longer in the wet season, expending more energy while spending less time feeding, suggests multiple non-mutually exclusive hypotheses that warrant further investigation. First, the dry season may offer energetic surpluses because insects appear abundant and relatively easy to find. Indeed, dry season bats ended foraging bouts and returned to the roost when insect abundance was still relatively high. Bats may only be pushed close to their energetic edge in the wet season, although body condition (forearm-mass index) at capture did not differ between seasons (permuted difference of means ± SE: −0.03 ± 0.06; $p = 0.66$). The most important part of the foraging period may, in fact, be the beginning of the night. These bats emerge in the evening after roughly 23 h of fasting, fueling flight with body fat and leading to high body fat turnover. They then switch to fueling flight with ingested insects within as little as 20 min.[31] Returning to the roost when satiated allows them to turn most of the ingested insects into body fat and restart this cycle.

New Zealand long-tailed bats (*Chalinolobus tuberculatus*) and parti-colored bats (*Vespertilio murinus*), in contrast, forage longer during nights of higher insect abundance,[32,33] presumably investing more energy into foraging to achieve proportionally higher energy gain.[7] Lactating female parti-colored bats and Leisler's bats (*Nyctalus leisleri*) also often forage longer, presumably to balance higher energetic demands with greater prey intake.[33,34] However, animals should forage longer during less profitable periods, when food is limited and energetic requirements higher.[35] Only our high-resolution assessment of both

insect availability and bat foraging behavior allowed us to differentiate between the hypotheses that bats forage longer to take advantage of higher food abundance or because food is harder to find. A second potential explanation is that 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,[36–39] or bats may compensate by using additional energy-saving strategies in the wet season, like torpor at high body temperature.[40] Reproduction may constrain this ability, however, as a high metabolism is needed for lactation.[41]

Quantifying shifts in food distribution is crucial for understanding immediate impacts on animal foraging and broader effects on species' ecology and life history, particularly in the context of energetic or nutritional pressures. When fish are less abundant, little penguins (*Eudyptula minor*) increase diving time and depth to maximize chances for prey encounter.[42] Yet when fish are also lower in the water column (information available only through detailed spatial mapping of the prey landscape), beyond their typical dive reach, penguins cannot compensate without compromising reproductive fitness.[42,43] Wildebeests, which exploit ephemeral grasses in heterogeneous landscapes, increase their commuting-to-feeding ratio (foraging effort), to prioritize exploiting grass that is less concentrated but higher quality, especially in the dry season when grass production slows and grass patches are depleted more quickly.[44] However, in the wet season when wildebeests reduce this ratio, feeding longer in the same area, mothers have calves. Thus, this shift could additionally be driven by higher nutritional needs for lactation or even increased predation risk with calves, revealing the complexity of drivers of foraging movements.[44] Similar to our insectivorous bats, these studies emphasize the way in which detailing food distribution beyond abundance can elucidate the interactions between foraging movements and spatiotemporal food distribution with energetic or nutritional constraints.

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 selective pressure. Quantifying detailed food distribution at scales relevant for the foragers in question allows us to consider alternative hypotheses when this assumption is not supported, as in the case of bulldog bats. Animal movement data have also helped to bridge gaps in our understanding of prey landscapes, letting us consider "patchiness" from the animals' perception.[3,45] These data are essential for predictive models of habitat use and behavior, but false conclusions can be made without actual food resource data, e.g., that concentrated foraging in an area always increases with prey density.[46] Furthermore, this research is heavily biased toward marine predator systems (birds, mammals, and fish). Combining fine-scale predator movement with high-resolution spatiotemporal food distribution, especially with wild non-marine systems and at smaller spatial scales, is a promising avenue for future research. As insect abundance declines worldwide,[47] animals that exploit aquatic emerging insects, including many insectivorous bats, will likely experience greater unpredictability and ephemerality of this resource, a pattern corroborated by our study. Without behavioral plasticity or alternative foraging strategies, these predators may be pushed beyond their energetic edge. More generally, as the dynamics of ephemeral resources and unpredictable environments become more severe under rapid human alteration of landscapes and the changing climate, foraging adaptations for their efficient exploitation will likely be critical for population and species survival, rendering our understanding of these processes urgent and essential.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- QUANTIFICATION AND STATISTICAL ANALYSIS
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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2024.05.074.

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AUTHOR CONTRIBUTIONS

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

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw data	Figshare[48]	https://doi.org/10.6084/m9.figshare.24543688.v1
Statistical analyses and figures	Figshare[49]	https://doi.org/10.6084/m9.figshare.24543550.v1
GPS tracks	Movebank Data Repository[50]	https://doi.org/10.5441/001/1.297
Experimental models: Organisms/strains		
Lesser bulldog bat, *Noctilio albiventris*	Wild	N/A
Software and algorithms		
R version 4.2.2.	R	https://www.r-project.org/
Insect detection on high-resolution images using Deep Learning	Choiński et al.[10]	https://doi.org/10.1007/978-3-031-42823-4_17

RESOURCE AVAILABILITY

Lead contact

Further information and requests should be directed to and will be fulfilled by the lead contact, Jenna E. Kohles (jkohles@ab.mpg.de).

Materials availability

This study did not generate new unique materials.

Data and code availability

All data and code required to replicate the present study are available in the Movebank Data Repository: tracking data[50] and the Figshare repositories: datasets,[48] code.[49]

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

For our study, we GPS tracked 16 individual female lesser bulldog bats (*Noctilio albiventris*) in one wet season (June 2019) when most females are reproductive, i.e., lactating, and 9 female individuals across two dry seasons (February 2019 and February 2020), when all females are non-reproductive.[48,50] The lesser bulldog bat is a common neotropical insectivorous bat that primarily forages over water,[23,51,52] and eats a wide range of flying insects, with a bias towards smaller aquatic insects.[5,53,54] They are most commonly seen foraging within a few meters above water surfaces[23,55] during a short time after dusk,[6,23,56] likely constrained by insect prey availability.[57]

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 3 mm wing skin sample and marked each individual with a subcutaneous PIT-tag (Trovan ID-100, Euro ID, Weilerswist, Germany). Colonies generally contain more adult females than adult males, reflecting a harem mating structure. We restricted our study to data collected from adult females to account for the influence of reproductive state which is synchronized among females but not males.[58] We attached Pathtrack nanofix Geo mini-GPS loggers (1.6-1.8 g) to adult females using detachable shoestring collars closed with suture thread.[59] In our first and second field season we additionally attached radio transmitters for relocating bats that did not return to the roost at which they were captured (Holohil Systems Ltd model LB-2X weighing 0.27 g), so tags weighed approximately 8% of bat body mass (Table S5). We released bats at the capture site the same night they were captured. 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).

METHOD DETAILS

We conducted this study in Gamboa, Panama (9.117°N, -79.691°W), from January 2019 to April 2020 (Figure 1).

Insect monitoring

We placed waterproof digital cameras (Ricoh WG-5) on floating platforms in the river delta where *Noctilio albiventris* forages (Figure 1).[9] 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).[48]

We anchored floating platforms with cinder blocks in transects 25-50 m from shore, approximately 250 m apart, setting precise locations (± a few meters) according to a handheld Garmin GPS device. For our analysis, we used data from five locations monitored in both the 2019 wet season and the 2020 dry season (Figure 1). We attempted to monitor insects from other locations in the 2019 dry season and additional locations in the 2019 wet and 2020 dry seasons, but strong river currents and moving vegetation which displaced or destroyed platforms precluded us from obtaining sufficient data from these locations. Cameras detect insects of *N. albiventris'* typical prey size (5-15 mm length)[54] up to a height of ca. 8 m (volume 125 m^3),[9] thus encompassing prey available to our bats which forage 20 cm up to 5 m above the water surface.[55]

Bat tracking

We tagged adult females with Pathtrack nanofix Geo mini-GPS loggers. Tags turned on from 18:45-20:45 (foraging period confirmed by observing roost emergences and returns), and collected a GPS fix every 30 s.[48,50] 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 recovered loggers by recapturing bats at roosts or once they had fallen off. In the wet season only, three individuals on one night of tracking each, had not returned to a roost by 20:45 when GPS loggers were programmed to turn off. This means wet season summary metrics may be slightly underestimated, and differences between seasons could be even larger.

QUANTIFICATION AND STATISTICAL ANALYSIS

Insect distribution in time and space

We counted the number of insects per photo via a machine learning algorithm.[10] 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).[10] We excluded nights with rain, or manually counted photos where rain occurred for 5-15 min (1-3 photos).

To assess differences in spatiotemporal insect availability during the dry and wet seasons within a bat foraging bout, we calculated mean and maximum insects per photo and counted the number of photos without insects during the first 2.5 h of photos for each location and each monitoring night.[49] 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 $\geq$10 insects each, separated by at least one photo with <10 insects.[49] We selected 10 insects in accordance with Ruczyński et al.,[9] 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 3-17 insects (no wet season data contained more than two consecutive photos with $\geq$17 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 $\geq$10 insects by 5 min to determine the duration of that patch. We compared durations between seasons. We also tested whether differences in persistence were driven by the selected threshold (Figure S2; Table S1).

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).[49] We calculated emergence time as minutes after sunset with the R package "photobiology".

We analyzed only GPS positions calculated with $\geq$5 satellites from the first three nights of tracking for behavioral segmentation. Afterwards, low batteries caused sporadic fixes. We then interpolated GPS positions at 30 s intervals, to account for the slight variation in GPS time-to-fix (range: 1 to ± 9 s; 23% of fixes required interpolation). We interpolated positions of missing fixes for gaps $\leq$4 fixes (<120 s; 3% of fixes). For slightly larger gaps (180-270 s), 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 (Expectation-maximization Binary 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 (Figure S4). We assigned "low turning angle-high speed" as "commuting-searching" and all three other clusters as "ARS (area restricted search)-feeding" (Figure S4). 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 $\geq$3 consecutive fixes (1.5 min) of the same behavior. We calculated durations of segments at a resolution of 30 s (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 $\geq$5 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.[49] 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, R package "vegan").

Insects: ordinations included the numerical variables: mean/maximum insects per photo, per location-monitoring night; number of photos without insects per location-monitoring night; persistence of longest-lasting insect patches per location-monitoring night; and number of insect patches per monitoring night across all locations. We then visualized how the categorical variables season, location (1-5), and monitoring night contributed to the ordination's structure.

Bats: ordinations included the numerical 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, maximum distance traveled from roost, total distance flown, number of insect patches visited, and MCP area (m^2) around GPS points in ARS-feeding segments. We visualized patterns in ordination space according to the categorical variables season, season-year (dry 2019, wet 2019, and dry 2020), bat ID, and nights-since-capture (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, R package "vegan") on dissimilarity matrices of insect and bat data. We calculated dissimilarity matrices using Gower's distance, with numerical and categorical variables. We showed how much individuals diverged within each season with a Multi Response Permutation Procedure (MRPP, R package "vegan") on bat data per season, grouped by individual.

We calculated 95% confidence intervals (CIs) around each metric's mean per season with nonparametric bootstrapping using the adjusted bootstrap percentile (BCa) interval (5000 iterations, R package "boot"). We compared the effect of season on these metrics, with permutation t-tests (two-tailed t-statistic, 9999 permutations, R package "MKinfer"). 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; R package "effsize").

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