Severe seasonal shifts in tropical insect ephemerality drive bat foraging effort

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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.



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.

1 **TITLE**

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47 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.

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71 INTRODUCTION

72 The timing and movement of animal foraging is fundamentally shaped by food availability in 73 time and space. This relationship is evident across scales, from migrating animals tracking green 74 waves across large landscapes (Aikens et al. 2017; Hurme et al. 2022), to central-place foragers 75 who match foraging to locally varying resources (Bell 1990). The relationship is particularly 76 strong for unpredictable and ephemeral resources, i.e. food sources that become available in 77 space or time without strong patterns and, or persist in single locations for short periods of time. 78 Such resources often require increased effort to find and must be exploited rapidly, resulting in 79 variable foraging success (Real & Caraco 1986). However, these food sources are also often 80 abundant, enabling rapid intake of energy (Wiens 1976). Extreme examples include seabirds 81 searching for large schools of fish (Ashmole 1971) or birds, bats, and fish, exploiting brief mass 82 emergences of mayflies (Sweeney & Vannote 1982).

83

84 We only vaguely understand true distribution of food in space and time for the majority of 85 species, despite its importance for understanding species ecology (Weimerskirch 2007), and 86 predicting animal decisions of when and where to forage (Bell 1990; Fagan et al. 2017; Kohles et 87 al. 2022). The ephemerality of resources can also differ depending on the spatial or temporal 88 scale (Kotliar & Wiens 1990). For example, figs fruit irregularly but then provide abundant food 89 for days, while insects form exploitable swarms locally for just minutes to hours. At broad spatial 90 scales both can be predictable, like the location of fig trees in a home range or insect swarms 91 commonly occurring over water bodies (Kohles et al. 2022). Both scales have fundamental 92 implications for animal foraging behavior.

93

94	In theoretical research on foraging behavior food distribution has long been fundamental. Yet in
95	empirical studies variation in food distribution is often investigated only qualitatively, i.e.,
96	predictable versus ephemeral, or homogeneous versus patchy or clumped, even though such
97	discrete categories do not occur in the real world (Wiens 1976; Kotliar & Wiens 1990;
98	Weimerskirch 2007). Generalized food distributions have revealed important patterns of
99	behavior, especially related to sociality (Egert-Berg et al. 2018; Jones et al. 2020; Roeleke et al.
100	2020), but are limited in explaining differences or shifts in foraging strategies between species,
101	populations, or within individuals. This prevents us from understanding additional influences,
102	such as energetic or nutritional needs, predation pressure, or social constraints.
103	
104	Animal movement data has helped to bridge these gaps, for example, letting us consider
105	"patchiness" from the perception of the animals themselves (Wiens 1976; Weimerskirch 2007).
106	Bluefin tuna (Thunnus thynnus) encounter food patches every two hours when only 5-9 patches
107	with an average radius of 1km occur per 100km ² (Gutenkunst et al. 2007). Tracking Antarctic
108	petrels (Thalassoica antarctica) revealed that krill (Euphausia superba) are concentrated for
109	weeks at the largest spatial scale, but for only days at smaller scales (Fauchald & Tveraa 2006).
110	These data are essential for predictive models of habitat use and behavior, but false conclusions
111	can be easily drawn without actual resource data, e.g., that concentrated foraging in an area
112	always increases with prey density (Florko et al. 2023). Furthermore, this research is heavily
113	biased towards marine predator systems (birds, mammals, and fish). Exploration into wild non-
114	marine systems, especially at smaller spatial scales are needed.
115	

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

118 heart rates for entire foraging bouts, balancing this with adequate food intake (Dechmann et al. 119 2011; Keicher *et al.* 2023). Many bat species specialize on swarming insects, which are 120 ephemeral and unpredictable, but permit rapid food intake when found (Safi & Kerth 2007), and 121 may be easier to detect with echolocation than individual insects (Boonman et al. 2019). 122 However, we do not understand the spatiotemporal distribution of "swarms" across the 123 landscape. They are often associated with bodies of water and emerge around dusk (Ruczyński et 124 al. 2020), but where they emerge each night and how quickly they disperse due to their own 125 mobility, wind, or disturbance by predators has only received speculation. Few studies consider 126 such critical temporal and spatial dynamics of prey and their effect on bat foraging behavior (e.g., 127 Fukui et al. 2006; Gonsalves et al. 2013; Moretto & Francis 2017, but see Wilkinson 1992). 128 Quantifying seasonal shifts in food availability allows us to directly test the effect of food 129 distribution on individual foraging effort, as seasonal increases in abundance may make 130 unpredictable and ephemeral resources like insect swarms easier to find. Thus, empirical quantification of spatiotemporal variation in seasonal food landscapes can provide insights into 131 132 species' adaptation to ecological niches and behavioral plasticity. Without such specific 133 quantifications it is difficult to predict the energetic requirements needed to find food efficiently 134 enough to achieve foraging success (Norberg 1977).

135

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

142	a foraging bout between seasons? We hypothesized that patches of flying insects would less
143	abundant and more ephemeral during the dry season. Correspondingly, during the dry season N.
144	albiventris should spend more time searching larger areas to find sufficient food patches, visiting
145	more, smaller insect patches. We GPS-tracked foraging N. albiventris, and quantified nocturnal
146	insect distribution at high spatiotemporal resolution using floating camera traps, across seasons.
147	Understanding the relationships between dynamic resource landscapes and the strategies animals
148	use to efficiently exploit them is essential for predicting how animals will adapt to our rapidly
149	changing world.
150	
151	METHODS
152	We conducted this study in Gamboa, Panama (9.117°N, -79.691°W), from January 2019 to April
153	2020. All methods conformed to the ASAB/ABS Guidelines for the Use of Animals in Research
154	and were approved by the Ministerio del Ambiente (SE/A-29-18, SE/A-96-18, SE/A-38-2020),
155	and the IACUC of the Smithsonian Tropical Research Institute (2017-0815-2020).
156	
157	Insect monitoring
158	We placed waterproof digital cameras (Ricoh WG-5) on floating platforms in the river delta
159	where Noctilio albiventris forages (Figure 1; (Ruczyński et al. 2020). Starting at 18:30, before
160	dusk in both seasons, cameras took a photo with flash every 1-5 min, on which insects appear as
161	white dots of irregular shape, occasionally with visible wings and appendages (Figure S1).
162	
163	We anchored floating platforms with cinder blocks in transects 25-50m from shore,
164	approximately 250m apart. We changed some monitoring locations between our three field
165	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).

171

172 Bat tracking

173 We caught entire colonies of *N. albiventris* as they emerged from their roosts using modified 174 funnel traps and mist-nets (range: 17-37 bats per roost). We recorded mass (g), forearm length 175 (mm), age class, and reproductive status. We took a 3mm wing skin sample and marked each 176 individual with a subcutaneous PIT-tag (Trovan ID-100, Euro ID, Weilerswist, Germany). We 177 tagged adult females with Pathtrack nanofix® Geo mini-GPS loggers (1.6-1.8g). We attached 178 loggers using detachable shoestring collars closed with suture thread (Teague O'Mara et al. 179 2014). In our first and second field season we additionally attached radio transmitters (Holohil 180 Systems Ltd model LB-2X weighing 0.27g), so tags weighed approximately 8% of bat body mass 181 (Table S11). Tags turned on from 18:45-20:45 (foraging period confirmed by observing roost 182 emergences and returns), and collected a GPS fix every 30s. Tags began collecting data two days 183 after capture in the first and second field seasons, but 4-5 days after capture in the third, to allow 184 tags on bats captured on different nights from different roosts to begin collecting data on the 185 same night. We released bats at the capture site the same night they were captured. We recovered 186 loggers by recapturing bats at roosts or once they had fallen off.

187

188 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.

194

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.

201

202 We estimated the number of "swarms" per monitoring night across all locations by counting the 203 number of times that consecutive photos from a single location contained ≥ 10 insects each, 204 separated by at least one photo with <10 insects. We selected 10 insects in accordance with 205 Ruczyński et al. (2020), but assessed whether this biased our results using a sensitivity analysis: 206 We compared dense insect patch counts between the wet and dry season at increasing thresholds 207 from 3-16 insects (no wet season data contained more than two consecutive photos with ≥ 16 208 insects) to determine whether differences were driven by the threshold or were a property of the 209 insect distribution (Figure S2, Table S1). We then took the largest insect patch of each location 210 and night and multiplied the number of consecutive photos with ≥ 10 insects by 5min to determine 211 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).

215

216 **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".

221

222 We analyzed only GPS positions calculated with ≥ 5 satellites from the first three nights of 223 tracking for behavioral segmentation. Afterwards, low batteries caused sporadic fixes. We then 224 interpolated GPS positions at 30s intervals, to account for the slight variation in GPS time-to-fix 225 (range: 1-18s; 23% of fixes required interpolation). We interpolated positions of missing fixes for 226 gaps ≤ 4 fixes (<120s; 3% of fixes). For slightly larger gaps (180-270s), we split the tracks and 227 ran segmentation separately (n=3 of 71 tracks). We calculated turning angle and speed using the 228 R package "move", then ran EMbC clustering on each track separately to account for variation 229 between individuals and nights ("EMbC" R package). The algorithm clusters GPS segments into 230 "high turning angle-high speed", "low turning angle-high speed", "high turning angle-low 231 speed", and "low turning angle-low speed". We did posterior smoothing on single instances of a 232 class nested within multiple instances of another class with the function smth(delta=1). We then 233 assigned behavioral states on tracks visualized in space. We assigned "low turning angle-high 234 speed" as "commuting-searching" and all three other clusters as "ARS (area restricted search)-

235	feeding". For final smoothing of remaining single instances of a behavioral state nested within
236	multiple instances of another state, we assigned the mode of the two states before and after.
237	
238	We used transitions between behavioral states to investigate fine-scale foraging behavior,
239	defining commuting-searching and ARS-feeding segments conservatively as stretches of ≥ 2
240	consecutive fixes (1min) of the same behavior. We calculated durations of segments at a
241	resolution of 30s (GPS inter-fix interval), and counted the number of ARS-feeding segments to
242	calculate 'number of insect patches visited' per bat foraging bout (one tracking night). We
243	summarized the total duration of each behavior, and calculated the proportion of ARS-feeding
244	relative to commuting-searching behavior for each bout.
245	
246	We calculated maximum distance from the roost and the total flight distance each night using the
247	as.ltraj() function (R package "adehabitatLT"). To estimate the area of concentrated feeding
248	activity, as a metric for estimating insect patch size, we calculated the minimum convex polygon
249	(MCP) around the GPS positions for each feeding segment >4 fixes (function requires min 5
250	locations) of each track (R packages "SpatialPoints", "Move", and "adehabitatHR"). We took the
251	square root of MCP values to report them in meters.
252	
253	Statistical analyses
254	We performed non-metric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity
255	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-

256

dimensional space (0.05-0.1 indicates very good representation in 2-D space). We fit numerical 257

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

260

261 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

263 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.

266

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 ARSfeeding, 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).

274

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.

281

282	We calculated 95% confidence intervals (CIs) around each metric's mean per season with
283	nonparametric bootstrapping (R package "boot", 5000 iterations). We compared the effect of
284	season on these metrics, with permutation t-tests (two-tailed t-statistic, 9999 permutations). We
285	adjusted P-values with sequential Bonferroni correction to control for multiple comparisons. We
286	calculated Hedge's g to estimate strength of effect sizes (small: 0.20, medium: 0.50, large: 0.80).
287	
288	We conducted all statistical analyses in R (version 4.2.2).
289	
290	RESULTS
291	Insect distribution in time and space
292	We analyzed the first 2.5h from seven nights in the dry season and ten in the wet season. Photos
293	from some locations for some monitoring nights were excluded due to rare camera malfunctions
294	or aquatic vegetation obscuring the lens, resulting in 22 and 31 location-monitoring nights for the
295	dry and wet seasons, respectively.
296	
297	Insect data clustered and diverged significantly in NMDS ordination space by season across all
298	numerical variables (stress level: 0.06; Figure S4; Table S3). Camera location had no significant
299	effect on ordinations (Figure S4, Figure S5, Table S4), supporting the hypothesis that insects
300	were spatially unpredictable. Season and monitoring night had significant effects on ordinations
301	(Figure S5, Table S4); however, PERMANOVA results revealed that season explained more
302	variation (R ²) and had a stronger relationship with the dissimilarity matrix of numerical variables
303	(F statistic) than monitoring date, indicating that insect distribution differed more strongly
304	between seasons than between nights within a season (Table S7). However, clustering of

305	individual monitoring nights was weaker during the wet season and likely reflects lower overall
306	predictability of the prey landscape, as nights were less similar across many metrics (Figure S5).
307	The mean and maximum number of insects per photo strongly decreased from the dry to the wet
308	season and the mean number of photos without insects strongly increased (Figure 2; Table 1).
309	The mean number of insect patches per monitoring night was also lower in the wet than in the dry
310	season and they persisted for less time (Figure 2; Table 1). The mean insect count was greater
311	and persistence longer in the dry season for all insect count threshold values. For most thresholds
312	the differences were significant, but less so with decreasing patch counts or sample sizes at
313	higher thresholds (Figure S2, Figure S3; Table S1, Table S2).
314	
315	Bat foraging effort in time and space
316	We GPS tracked bats in one wet season (Jun 2019) and two dry seasons (Feb 2019 and Feb
317	2020). We obtained 48 tracks from 16 individuals in the wet season, and 23 tracks from 9
318	individuals in the dry seasons. From each bat we obtained 1-3 nights of tracking data.
319	
320	Bat data clustered and diverged significantly in NMDS ordination space according to season
321	across all numerical variables (stress level: 0.08; Figure S6a, S6b; Table S5). Tracking night had
322	no significant effect on ordinations, suggesting that capture did not have a strong effect on
323	foraging behavior (Figure S6a, S6b; Table S6). Season, season-year, and bat ID all had
324	significant effects on ordinations (Figure S6a, S6b, S7; Table S6); however, PERMANOVA
325	results revealed that the relationship of season with the dissimilarity matrix of numerical
326	variables (F statistic) was stronger than bat ID and the relationship of season-year was not
327	significant. This indicates that bat foraging behavior differed more strongly between seasons than

328	years or individuals. Season and bat ID had similar R ² values, which may be driven by weaker
329	clustering overall between dry season individuals. The stronger clustering of individuals in the
330	wet season (Figure S7), indicating more similarity across many metrics, may reflect constraints
331	on foraging behavior caused by the less predictable prey landscape (and weak clustering between
332	insect monitoring nights, Figure S5). MRPP results revealed that in the dry season one individual
333	(BatG5b) diverged strongly from all others (delta>0.2; A: 0.191) and two individuals in the wet
334	season (Bat02 and Bat04; delta>0.2; A: 0.276), although the effects here were weak.
335	
336	In the wet season when insects were less predictable and more ephemeral, mean bat emergence
337	was 45% earlier relative to sunset (Figure 2; Table 2). Mean foraging bout duration was 44%
338	longer (Figure 2; Table 2). Bats spent less time in ARS-feeding per patch, and commuted-
339	searched longer for their next patch (Figure 2; Table 2). ARS-feeding time per foraging bout was
340	the same between seasons, but wet season commuting-searching lasted nearly three times longer
341	(Figure 2; Table 2). Because foraging bouts in the wet season were longer, the proportion of
342	ARS-feeding was 23% less (Figure 2; Table 2).
343	
344	In the wet season, bats flew nearly twice as far from the roost (0.9km) and in total distance
345	(5.1km; Figure 3; Table 3). They visited a mean of 1.7 more insect patches during the wet season
346	(Figure 3; Table 3). Area used for ARS-feeding was similar, suggesting similar patch sizes
347	between seasons (Figure 3; Table 3). In contrast, ARS-feeding time per insect patch was shorter
348	in the wet season, suggesting that patches were less dense and depleted more rapidly (Figure 2;
349	Table 2). Three wet season individuals on one night each, were still active when the GPS loggers
350	turned off. This means wet season summary metrics may be underestimated, and differences

351 between seasons could be even larger.

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352

353 **DISCUSSION**

354 Our results exemplify the importance of detailed mapping of the resource landscape for 355 understanding animal foraging behavior. Our insectivorous bats, specialized on patchy ephemeral 356 insect swarms, experienced substantial shifts in prey availability between seasons which strongly 357 affected their foraging behavior. Against our expectations, insect availability was significantly 358 lower and less predictable in the wet season. As wet season insect patches were apparently more 359 difficult to find, bats emerged 45% earlier, foraged 44% longer and increased distance and 360 duration of commuting and searching, likely also increasing energy expenditure. Feeding 361 behavior made up nearly 25% less time of each foraging bout in the wet season. Bats left patches 362 more quickly, matching that insect patches were more ephemeral, and searched longer for 363 subsequent patches. This overall pattern is corroborated by non-metric dimensional scaling 364 (NMDS), where insect monitoring nights were less clustered in the wet season, reflecting a less 365 predictable prey landscape. Correspondingly, individual bat data were more clustered in 366 ordination space in the wet season. This clustering may indicate bats were more constrained to 367 match the limited peaks of prey availability across many aspects of foraging behavior, whereas in 368 the dry season a more predictable prey landscape permitted greater liberty and flexibility without 369 jeopardizing foraging success.

370

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

376 reflected in the bats' foraging behavior. The difference may be related to the specific insects 377 exploited by *Noctilio albiventris*. In temperate zones, aquatic emerging insects synchronize mass 378 emergences during early summer months, but tropical insects may maintain less obvious seasonal 379 reproductive cycles (Brittain 1982; Sweeney & Vannote 1982). Our study site, the Chagres River 380 delta, experiences higher water levels, faster currents, and far more floating aquatic vegetation in 381 the wet season. These environmental conditions may limit the abundance of nymphs (Righi-382 Cavallaro et al. 2010) and may not be ideal for adult emergence and swarming, driving the 383 majority of species or populations to mate in the dry season (Corbet 1964; Brittain 1982). 384

385 Another reason we expected higher insect abundance during the wet season was because both 386 reproductive peaks of *N. albiventris* occur during this period of the year. During peak lactation, 387 when bat pups are close to fledging, energy demands for mothers can almost double compared to 388 just after parturition (Kurta et al. 1989; Kunz et al. 1995). Female N. albiventris synchronize 389 their primary birthing peak at the end of April and beginning of May, and lactate for up to three 390 months (Rasweiler 1977; Brown et al. 1983). Juveniles fledge after seven weeks of age, and 391 wean after three months, representing one of the longest periods of maternal care known for bats 392 (Brown et al. 1983). Due to extended lactation, females may be both pregnant and lactating in 393 August. Most bat species appear to time lactation (Racey 1982) or fledging (Fleming *et al.* 1972) 394 with high food abundance. For insectivorous bats, this is typically the onset of the rains and 395 lactation overlaps with the peak of the rainy season (Racey 1982; Racey & Entwistle 2000). 396 Thus, it was surprising that emerging aquatic insect availability was low during the reproductive 397 period for *N. albiventris* in the wet season. Emerging aquatic insects supply essential nutrients for 398 bats and other riparian predators (Baxter et al. 2005), namely long-chain omega-3 399 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 (MathieuResuge *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.

407

408 That bats flew further and longer in the wet season, likely expending more energy, while 409 spending proportionally less time feeding, suggests multiple non-mutually exclusive hypotheses 410 that warrant further investigation. First, foraging behavior in the dry season may represent 411 periods of energetic surplus because insects appear abundant and relatively easy to find. Only the 412 wet season may push bats close to their energetic edge. This is supported by the fact that in the 413 dry season bats ended foraging bouts and returned to the roost when insect abundance was still 414 relatively high. In contrast, New Zealand long-tailed bats (*Chalinolobus tuberculatus*) and parti-415 coloured bats (Vespertilio murinus) forage longer during nights of higher insect abundance 416 (O'Donnell 2000; Hałat et al. 2018), presumably investing more energy into foraging, to achieve 417 proportionally higher energy gain (Norberg 1977). Lactating female parti-coloured bats and 418 Leisler's bats (*Nyctalus leisleri*) also often forage longer, presumably to balance higher energetic 419 demands with greater prey intake (Shiel et al. 1999; Hałat et al. 2018). However, theory states 420 that animals should forage longer during less profitable periods, when food is limited and when 421 energetic requirements are higher (Schoener 1971). Only our high-resolution assessment of both 422 insect availability and bat foraging behavior allowed us to differentiate between these predictions. 423 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).

430

431 *Noctilio albiventris* may also use social foraging to overcome potentially higher energetic costs in 432 the less predictable and more ephemeral prey distribution in the wet season. In the wet season 433 subgroups of females from a roosting colony were consistently co-located for the majority of 434 their foraging bouts, and subgroups rarely overlapped in space and time (Dechmann *et al.* 2009). 435 Bats were also attracted to playbacks of conspecific feeding buzzes. By eavesdropping on group 436 members' feeding buzzes, N. albiventris can increase insect detection range tenfold (Dechmann et 437 al. 2009). According to our new understanding of how shifting prey distribution makes food 438 much more challenging to exploit, reproduction may only add to this challenge, rather than fully 439 drive it. Insect patches persist far less than the duration of a foraging bout of *N. albiventris*, only 440 8 min in the wet season, meaning social information about their presence has to be transferred in 441 situ (as opposed to in the roost). Noctilio albiventris may use social information flexibly, 442 increasing coordination when food is rare, difficult to find and energetic demands higher, in line 443 with predictions of the framework of Kohles et al. (2022). Interestingly, some wet season 444 individuals foraged for durations comparable to the dry season and non-metric multidimensional 445 scaling revealed some individuals diverging significantly in ordination space from others within 446 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 competitiveforagers, enabling them to exploit food patches more rapidly and or closer to the roost.

449

450 While studies assessing shifting food landscapes are rare, they have revealed novel insights into 451 the relationship of foraging behavior with energetic or nutritional needs, social constraints, and 452 predation pressure. Thick-billed murres (Uria lomvia) and black-legged kittiwakes (Rissa 453 *tridactyla*) increase foraging trip time and distance from colonies to compensate for lower fish 454 abundance, but only in kittiwakes this translated to decreased reproductive output. Even though 455 both birds experience the same prey landscape shift, only kittiwakes are pushed to their energetic 456 edge (Kitaysky et al. 2000; Piatt et al. 2007). When fluctuations in prey availability occur in non-457 seasonal patterns, such as larger scale climatic effects, species may not have strategies to 458 compensate, and suffer from reduced foraging success. Little penguins (*Eudyptula minor*) 459 increase foraging effort and lower prey encounter rates when fish are more challenging to find 460 and access (lower density and located lower in the water column), resulting in lower female mass 461 (Phillips *et al.* 2022). Even mapping prey distributions in conjunction with foraging effort for 462 animals exploiting somewhat predictable resources, and over smaller spatial scales, reveals 463 important insights. Bumblebees (Bombus terrestris) tracked over their entire foraging landscape, 464 often forage beyond closest available resources, which may indicate preference for quality over 465 quantity (Osborne *et al.* 1999). Indeed, bumblebees respond more to floral diversity than density, 466 indicating the complexity of understanding foraging decisions and how incorporating both food 467 distribution and abundance alters conclusions (Jha & Kremen 2013). Opposing spatial and 468 temporal resource distributions between simple and complex plant landscapes can even influence 469 the effort honeybees (Apis mellifera carnica) invest into their complex information sharing 470 strategy, the waggle dance (Steffan-Dewenter & Kuhn 2003). In the dry season of Costa Rica

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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).

477

478 It is clear that foraging ecology is complex and crucial for survival and reproduction. Especially 479 in seasonal environments, timing periods of increased energy demand with food availability 480 should be under strong selective pressure. Without quantifying prey distribution at scales relevant 481 for the foragers in question, we cannot disentangle how foraging effort is influenced by factors 482 beyond food distribution, such as behavioral or physiological states. Understanding the 483 relationships between dynamic resource landscapes and the foraging strategies animals use to 484 efficiently exploit them helps predict energetic and social requirements, behavioral plasticity, and 485 potential for adaptation to rapidly changing environments.

486

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- 655 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

658 cameras indicate locations of floating platforms with camera traps.

659

660 Figure 2. Insects are less predictable and more ephemeral in the wet season, and bats scale-661 up temporal foraging effort accordingly. Overview and summary metrics of temporal and 662 spatial insect distribution and bat foraging effort. In the wet season on average, (A) insect 663 abundance is almost 75% lower, (B) largest insect peaks are nearly 50% lower, (C) instances of 664 no insect availability are over 5x more common, (D) insect patches (≥ 10 insects per photo) are 665 over 2x rarer, and (E) insect patches are more ephemeral, persist for almost 15 min less. Bats in 666 the wet season on average, (A) forage almost 45% longer, (B) emerge 12 mins earlier relative to 667 sunset (45%), (C) feed 30% shorter in each insect patch and search nearly 70% longer for the 668 next insect patch, (D) spend the same total amount of time in ARS-feeding, but (E) spend more 669 time commuting-searching in total, (F) decreasing the proportion of ARS-feeding by nearly 25%. 670 Overview plot: lines represent insects detected in photos (every 5 min) over the night per

671 platform for single nights of monitoring at identical locations during the wet (N=31) and dry 672 seasons (N=22). Horizontal bars represent foraging bouts of individual bats, for each date they 673 were tracked, colored by behavioral state: light colors represent commuting-searching and dark 674 colors, ARS-feeding. N=23 foraging bouts in the dry season and N=48 foraging bouts in the wet 675 season. For insect summary metric plots, each point represents a calculation (A-C, E) per photo 676 for one of the same four locations between seasons or (D) for photos across all locations, on each 677 monitoring night. For bat summary metric plots, points represent (A-B, D-F) each night of 678 tracking for every bat, or (C) a segment of a behavioral state within a bat's track. Diamonds 679 represent bootstrapped means and bars represent bootstrapped 95% confidence intervals around 680 means.

681

682 Figure 3. Bats scale-up spatial foraging effort in the wet season. Overview of bat foraging 683 tracks in space per season, along with summary metrics quantifying spatial foraging effort. In the 684 wet season on average, bats flew nearly twice as far in (A) maximum distance from roost and (B) 685 total distance, (C) visited close to 2 more insect patches, but (D) but performed ARS-feeding in 686 same-sized areas. Overview plots: tracks are individual foraging bouts of bats, colored by 687 behavioral state: light colors represent commuting-searching and dark colors represent ARS-688 feeding. N=23 tracks in the dry season and N=48 tracks in the wet season. For summary metric 689 plots, points are (A-C) each track for each bat, or (D) each segment of ARS-feeding within each 690 track of each bat. Diamonds are bootstrapped means and bars bootstrapped 95% confidence 691 intervals. 692

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695 FIGURES



697 Figure 1.

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- 707 Figure 2.



- 718 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	Ν	Mean Change	р	adj. p	Hedge's g
Mean	Dry	5.1	6.4	7.8	22	171	<0.0002	<0.0002	1 013
Weall	Wet	1.2	1.7	2.2	31	-4.74	<0.0002	<0.0002	-1.913
Monimum	Dry	15.8	19.2	22.4	22	0.16	<0.0002	0.0005	1 095
Maximum	Wet	7.1	10.1	12.9	31	-9.10	<0.0002	0.0005	-1.083
Zana Count	Dry	1.5	2.9	4.1	22	12.21	<0.0002	<0.0002	2 162
Zero Count	Wet	13.6	16.2	18.6	31	15.51	<0.0002	<0.0002	2.162
	Dry	6.3	9.9	13.4	7	7.20	0.000		1.025
Patch Count	Wet	1.3	2.6	3.8	10	-7.28	0.002	0.012	-1.835
Patch Duration	Dry	12.5	22.7	31.4	22	12.05	0.010	0.049	0.602
(min)	Wet	5.9	9.4	12.2	16	-13.25	0.010	0.048	-0.092

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

Motrio	Secon	Lower	Maan	Linner		Mean	р	ad: D	Hedge's
Metric	Season	Lower	Mean	Upper	п	change	r	auj. P	g
Emergence (min after	Dry	26.0	26.9	28.0	27	12 11	<0.0002	<0.0002	1 706
sunset)	Wet	12.2	14.8	16.7	48	-12.11	<0.0002	<0.0002	-1.790
Foraging bout	Dry	42.5	47.5	51.8	27	20.70	<0.000 2	×0.0002	1.056
duration (min)	Wet	62.9	68.2	72.9	48	20.70	<0.0002	<0.0002	1.256
Duration commuting-	Dry	2.2	2.5	2.7	69				
searching segments						1.62	< 0.0002	< 0.0002	0.524
(min)	Wet	3.7	4.1	4.5	282				
Duration ARS-feeding	Dry	7.3	8.9	10.4	94	2.60	0.004	0.022	0.419
segments (min)	Wet	5.7	6.3	7.0	274	-2.00	0.004	0.035	-0.418
Total time	Dry	7.0	9.1	11.1	23				
commuting-searching						16.8	< 0.0002	< 0.0002	1.402
(min)	Wet	21.9	26.0	29.8	47				
Total time ARS-	Dry	32.8	37.2	41.3	23	1.20	0.571	1.000	0.172
feeding (min)	Wet	36.8	38.6	40.3	47	1.39	0.371	1.000	0.175
Proportion of time	Dry	0.8	0.8	0.8	23	0.19	<0.0002	<0.0002	1 627
ARS-feeding	Wet	0.6	0.6	0.7	47	-0.16	<0.0002	<0.0002	-1.037

- Table 3. Means and their bootstrapped 95% confidence intervals, and sample sizes for bat
- 751 foraging effort summary metrics in space by season.
- 752

Metric	Season	Lower	Mean	Upper	n	Mean	Р	adj. P	Hedge's
						change			g
Maximum	Dry	0.8	1.0	1.1	23				
distance travelled						0.89	0.0004	0.0008	0.650
from roost (km)	Wet	1.3	1.8	2.3	47				
Total distance	Dry	4.5	5.8	6.8	23	5 1 1	<0.0002	<0.0002	1 120
flown (km)	Wet	9.4	10.9	12.3	47	5.11	<0.0002	<0.0002	1.129
N feeding	Dry	3.3	4.1	4.8	23	1 73	0.0003	0.002	0.966
patches visited	Wet	5.3	5.8	6.3	47	1.75	0.0005	0.002	0.700
MCP of feeding	Dry	91.2	112.5	129.9	85	-0.18	0.976	_	-0.004
patches (m)	Wet	101.3	112.2	122.2	204	-0.10	0.970		-0.004

SUPPLEMENT



Figure S1. Two example photos from camera trapping method representing insects of either different sizes or different distances from the camera.



Sensitivity Analysis for Count of Dense Insect Patches

Figure S2. For most insect count threshold values (for signifying the occurrence of an insect patch or "swarm" in a single photo), the number of insect patches per monitoring night across all locations is significantly larger in the dry season, and this difference narrows steadily with

increasing thresholds values, so our choice of a threshold of ≥ 10 insects in our analyses represents a conservative approach.

Table S1. As the threshold value increases from 3 to 17, the difference between the dry and wet season means peaks at a threshold of 6 insects, and then decreases overall, with some fluctuations at certain threshold values. The largest fluctuations, however, do not occur at the threshold of ≥ 10 insects, so our results in number of patches per monitoring night across all locations are conservative.

	Dry-Wet Mean	% Change in	# Obser	rvations
Threshold	Difference	Difference	Dry Season	Wet Season
3	0.99		7	10
4	5.30	437.14%	7	10
5	7.66	44.6%	7	10
6	10.09	31.7%	7	10
7	9.40	-6.8%	7	10
8	8.51	9.4%	7	10
9	8.06	-5.4%	7	10
10	7.26	-9.9%	7	10
11	7.14	-1.6%	7	10
12	6.69	-6.4%	7	10
13	5.50	-17.8%	7	10
14	5.03	-8.6%	7	10
15	4.71	-6.3%	7	10
16	3.57	-24.2%	7	10
17	3.77	5.6%	7	10



Sensitivity Analysis for Persistence of Dense Insect Patches

Figure S3. For most insect count threshold values (for signifying the occurrence of an insect patch or "swarm" in a single photo), the persistence or duration of the patch is significantly longer in the dry season, and this difference narrows with decreasing sample size at higher thresholds values, so our choice of a threshold of ≥ 10 insects in our analyses represents a conservative approach.

Table S2. As the threshold value increases from 3 to 17, the difference between the dry and wet season means decreases overall, with some fluctuations at certain threshold values. The largest fluctuations, however, do not occur at the threshold of ≥ 10 insects, so our results of persistence of insect patches are conservative.

	Dry-Wet Mean	% Change in	# Obser	rvations
Threshold	Difference	Difference	Dry Season	Wet Season
3	60.00		23	23
4	46.33	-22.8%	23	22
5	36.73	-20.7%	23	20

6	25.26	-31.2%	23	19
7	21.32	-15.6%	23	18
8	16.87	-20.8%	23	18
9	14.23	-15.7%	23	16
10	13.35	-6.1%	22	16
11	11.68	-12.5%	21	13
12	10.75	-8.0%	20	10
13	11.06	2.9%	18	10
14	9.00	-18.5%	15	10
15	10.45	16.1%	14	8
16	9.73	-6.8%	14	8
17	8.90	-8.6%	13	7

NMDS for Insects



Figure S4. Insect location-monitoring nights cluster separately in Non-metric Multidimensional Scaling (NMDS) ordination space (stress = 0.06) along both axes according to season (color), indicating its strong effect on the variation in summary metrics, (1) mean and (2) maximum insects per photo per location-monitoring night, (3) number of photos with zero insects per location-monitoring night, (4) number of swarms per monitoring night across all locations, (5) persistence of swarms in single locations for photos. Location (point shape), however, do not cluster in ordination space, indicating its lack of effect on summary metrics. Ellipses are 95% confidence intervals of the standard deviation of the weighted averages of season. Permutation testing of season confirms that the factor of season is significant (P < 0.001; see Table S7).



Figure S5. Insect location-monitoring nights cluster in NMDS ordination space (stress = 0.06) by season (color family; warm colors = dry, cool colors = wet) more strongly than monitoring night (individual color). Ellipses are 95% confidence intervals of the standard deviation of the weighted averages of monitoring night (factored sequentially within season). However, permutation testing of monitoring night shows that the factor is significant (P = 0.004; see Table S7).

Intrinsic variables	NMDS1	NMDS2	r ²	Р
Mean	0.68	-0.74	0.84	0.001
Maximum	0.76	-0.65	0.79	0.001
Zero Count	-0.94	-0.34	0.94	0.001
Patch Count	0.39	-0.92	0.78	0.001
Patch Duration (min)	0.89	-0.46	0.66	0.001

Table S3. Results for NMDS of intrinsic variables for insect data.

Table S4. Results for NMDS of extrinsic variables for insect data.

Extrinsic varia	bles	NMDS1	NMDS2	r ²	Р
FACTORS					
Centroids					
Season					
	Dry	0.55	0.00		
	Wet	-0.39	-0.00		
Location					
	Location 1	-0.11	-0.06		
	Location 2	0.09	0.04		

0.37

0.007

	Location 3	0.09	-0.04		
	Location 4	-0.09	0.06		
Monitoring nigh	nt				
(factored sequer	ntially within season)				
	Monitoring night 1	-0.32	0.15		
	Monitoring night 2	0.08	0.14		
	Monitoring night 3	0.56	0.08		
	Monitoring night 4	0.22	-0.50		
	Monitoring night 5	0.00	0.32		
	Monitoring night 6	-0.13	-0.12		
	Monitoring night 7	0.08	-0.04		
	Monitoring night 8	0.34	-0.25		
	Monitoring night 9	-1.02	-0.18		
	Monitoring night 10	-0.39	-0.07		
Goodness of fit					
Season				0.39	0.001
Location				0.02	0.893

Monitoring night

NMDS for Bats



Figure S6a. Bat tracking nights cluster separately in NMDS ordination space (stress = 0.08) along both axes according to season (color), indicating its strong effect on the variation in summary metrics, (6) emergence time after sunset, (7) foraging bout duration, (8) duration of commutingsearching segments, (9) duration of ARS-feeding segments, (10) total commuting-searching duration per bout, (11) total ARS-feeding duration per bout, (12) proportion of foraging bout spent in ARS-feeding per bout, (13) maximum distance traveled from roost per bout, (14) total distance flown per bout, (15) minimum convex polygon around GPS points in ARS-feeding segments, and (16) number of patches visited per bout for each bat track. Consecutive tracking night (point shape), however, does not cluster in ordination space, indicating its lack of effect on summary metrics. Ellipses are 95% confidence intervals of the standard deviation of the weighted averages of season. Permutation testing of seasons shows that the factor is significant (P < 0.001; see Table S8).



Figure S6b. Bat tracking nights cluster separately in NMDS ordination space (stress = 0.08) along both axes according to season but not year. The dry seasons from 2019 and 2020 overlap unlike the wet season from 2019. Ellipses are 95% confidence intervals of the standard deviation of the weighted averages of Season.Year. Permutation testing of Season.Year confirms that the factor is not significant (P = 0.061; see Table S8).



Figure S7. Bat individuals cluster in NMDS ordination space (stress = 0.08) according to the season in which they were tracked. Warm colors represent bats tracked in the dry season, and

cool colors, bats in the wet season. Bat201 was tracked in both seasons and its dry season data (dark red) clusters separately from its wet season data (dark blue). Ellipses could not be calculated for individuals with only 2 nights of tracking data and were excluded from this plot. Ellipses are 95% confidence intervals of the standard deviation of the weighted averages of bat ID. Permutation testing of bat ID, however, shows that the factor is significant (P < 0.001; see Table S8). Bat02 and Bat04 have the highest within and out-of-group disagreement in the wet season, and BatG5b in the dry season according to MRPP analysis (see Table S9 and S10).

Intrinsic variables	NMDS1	NMDS2	r^2	Р
Emergence (min after sunset)	0.17	0.98	0.68	0.001
Foraging bout duration (min)	-0.96	0.29	0.97	0.001
Total time commuting-searching (min)	-0.98	-0.20	0.80	0.001
Total time ARS-feeding (min)	-0.55	0.84	0.54	0.001
Proportion of time ARS-feeding	0.74	0.67	0.65	0.001
Maximum distance travelled from roost (km)	-0.84	0.54	0.46	0.001
Total distance flown (km)	-0.97	0.25	0.88	0.001
N visited feeding patches	-0.97	-0.25	0.49	0.001

Table S5. Results for NMDS of intrinsic variables for bat data.

Table S6. Results for NMDS of extrinsic variables for bat data. Bat 200 and Bat 201 in red were tracked in both seasons.

Extrinsic variables	NMDS1	NMDS2	r ²	Р
FACTORS				

Centroids			
Season			
	Dry	0.23	0.09
	Wet	-0.11	-0.04
Season-year			
	Dry 2019	0.12	0.12
	Dry 2020	0.32	0.06
	Wet 2019	-0.11	-0.04
Tracking night			
	Night 1	0.00	0.03
	Night 2	0.02	-0.02
	Night 3	-0.03	-0.01
Bat ID			
	Bat01	-0.31	-0.10
	Bat02	-0.06	-0.06
	Bat04	-0.32	0.08
	Bat06	0.10	-0.11
	Bat07	-0.37	0.06
	Bat09	0.11	0.04
	Bat10	-0.08	-0.07
	Bat13	-0.20	-0.03
	Bat14	-0.05	-0.09
	Bat15	0.18	-0.09
	Bat16	-0.06	-0.10
	Bat17	-0.50	0.07
	Bat19	-0.00	-0.11

	Bat21	-0.18	-0.03		
	Bat200	-0.00	-0.01		
	Bat201	0.21	-0.03		
	Bat100	0.49	0.06		
	Bat102	0.21	0.10		
	Bat104	0.26	0.08		
	Bat105	0.36	0.03		
	BatG1	0.23	0.08		
	BatG5a	-0.03	0.22		
	BatG5b	0.14	0.13		
Goodness of fit					
Season				0.34	0.001
Season-year				0.38	0.001
Tracking night				0.01	0.790
Bat ID				0.75	0.001

PERMANOVA Results

Insect data

Table S7. Permutation test for adonis under reduced model. Terms added sequentially (first to

last). Permutation: free; number of permutations: 999.

insects)

	Degrees of	Sum of	R ²	F	Р
	freedom	squares			
Season	1	1.07	0.44	55.80	0.001 ***

Monitoring night	9	0.57	0.23	3.30	0.004 **
(factored sequentially within season)					
Location	3	0.06	0.02	1.04	0.388
Residual	39	0.75	0.31		
Total	52	2.45	1.00		

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Bat data

Table S8. Permutation test for adonis under reduced model. Terms added sequentially (first to

last). Permutation: free; number of permutations: 999.

adonis2(formula = dissimilarity_matrix ~ Season + Season + BatID, data = bats)

	Degrees of	Sum of	\mathbb{R}^2	F	Р
	freedom	squares			
Season	1	0.61	0.276	46.32	0.001 ***
Season-year	1	0.04	0.019	3.17	0.061
Bat ID	22	0.97	0.437	3.34	0.001 ***
Residual	45	0.60	0.268		
Total	69	2.22	1.000		

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

MRPP Results

Dry season bat data

Call: mrpp(dat = bat.num.mrpp.dry, grouping = batid, distance = "bray")

Dissimilarity index: bray.

Weights for groups: n.

Table S9. Class means and counts.

	Bat100	Bat102	Bat104	Bat105	Bat200	Bat201	BatG1	BatG5a	BatG5b
Delta	0.154	0.070	NaN	0. 117	0.082	0.053	0.036	0. 171	0. 233
N	3	3	1	2	2	3	3	3	3

Chance corrected within-group agreement A: 0.191

Based on observed delta 0.1068 and expected delta 0.1433

Significance of delta: 0.023

Permutation: free

Number of permutations: 999

Wet season bat data

Call: mrpp(dat = bat.num.mrpp.wet, grouping = batid, distance = "bray")

Dissimilarity index: bray

Weights for groups: n

Table S10.	Class	means	and	counts.
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	Bat01	Bat02	Bat04	Bat06	Bat07	Bat09	Bat10	Bat13	Bat14	Bat15	Bat16	Bat17
Delta	0.118	0.221	0.216	0.197	0.137	0.162	0.097	0.094	0.097	0.087	0.068	0.136

Ν	3	3	3	3	3	2	3	3	3	3	3	3

	Bat19	Bat200	Bat201	Bat21
Delta	0.105	0.050	0.139	0.092
Ν	3	3	3	3

Chance corrected within-group agreement A: 0.2758

Based on observed delta 0.1251 and expected delta 0.1728

Significance of delta: 0.001

Permutation: free

Number of permutations: 999

Table S11. We recaptured only a proportion of GPS-tagged bats. From these recaptures we calculated percent change in mass (g) to evaluate the effect of tagging. Percent change mean \pm sd: $-5.9 \pm 4.2\%$.

					Logger attachment
Season	Bat PIT-tag ID	Final mass (g)	Mass change (g)	Percent change	duration (days)
dry	7B8103E	22.5	-1.0	-4.3%	9
dry	7B8E6E8	21.5	-3.0	-12.2%	10
dry	7B8E196	24.5	-2.0	-7.5%	fell off pre recapture
wet	7B8E0CB	24.5	-1.0	-3.9%	9
wet	7B8E196	25.5	1.0	4.1%	2
wet	7B97EF2	23.0	-3.5	-13.2%	18
wet	7BA3BD0	23.0	0.0	0.0%	10
wet	7B8E196	24.5	-2.0	-7.5%	9

wet	7B996D4	22.5	-2.5	-10.0%	fell off pre recapture
wet	7B98C6F	23.0	-2.0	-8.0%	fell off pre recapture
wet	7B8E34A	21.5	-2.5	-10.4%	fell off pre recapture
wet	7BC8129	23.5	-1.5	-6.0%	fell off pre recapture
wet	7B97CD6	24.0	-0.5	-2.0%	fell off pre recapture
wet	7B98F76	23.5	-1.5	-6.0%	fell off pre recapture
wet	7BA3625	23.5	-1.5	-6.0%	fell off pre recapture
wet	7B982AF	23.5	-1.5	-6.0%	fell off pre recapture
wet	7B8F063	22.0	-1.5	-6.4%	fell off pre recapture
wet	7BA37D8	23.5	-0.5	-2.1%	fell off pre recapture
wet	7B98277	25.5	-1.0	-3.8%	fell off pre recapture