

1 **TITLE**

2 **Severe seasonal shifts in tropical insect ephemerality drive bat foraging effort**

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16 **STATEMENT OF AUTHORSHIP**

17 J.E.K. and D.K.N.D conceived the study, J.E.K collected the data, J.E.K. performed the analyses,

18 J.E.K. wrote the first draft of the manuscript and all authors contributed to the final manuscript.

19 **DATA ACCESSIBILITY STATEMENT**

20 All data and code required to replicate the present study are publicly available in the Movebank

21 Data Repository, <https://doi.org/10.5441/001/1.297> (Kohles et al., 2023) and the Figshare

22 repositories, data: 10.6084/m9.figshare.24543688 [available with this link for editors/reviewers:

23 <https://figshare.com/s/2e8b660eb285df17198b>]; code: 10.6084/m9.figshare.24543550 [available
24 with this link for editors/reviewers: <https://figshare.com/s/5ff3ed5667f86afaa835>].

25 **RUNNING TITLE**

26 Insect ephemerality drives bat foraging effort

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47 **ABSTRACT**

48 Food distribution and availability fundamentally shape foraging. Yet spatiotemporal distribution
49 of mobile prey and its proximate effects on animals have rarely been assessed. The neotropical
50 bat, *Noctilio albiventris*, forages on aquatic swarming insects which peak just one to two hours
51 after dusk. We matched seasonal insect distribution at high spatiotemporal resolution to the
52 foraging behavior of adult female bats. Surprisingly, insect abundance was lower in the wet
53 season, and insect patches dispersed more rapidly. Correspondingly, bats emerged 45% earlier,
54 foraged over 40% longer, and flew almost twice as far compared to the dry season. Wet season
55 bats also spent less time at each patch, suggesting that patches, though the same size, were less
56 dense and depleted more rapidly. Our results highlight the tight link between foraging and sharp
57 seasonal shifts in the spatial unpredictability and temporal ephemerality of resources, shedding
58 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 100km² (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

116 Bats are exceptionally energetically constrained while foraging (Schmidt-Nielsen 1972). Those
117 that 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
131 quantification of spatiotemporal variation in seasonal food landscapes can provide insights into
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
136 The lesser bulldog bat (*Noctilio albiventris*), a neotropical insectivore, primarily forages low over
137 water for a wide range of primarily small flying insects in a single short bout after dusk (Hooper
138 & Brown 1968; Brown *et al.* 1983; Aguirre *et al.* 2003; Dechmann *et al.* 2009). At our study site
139 in central Panama the long wet season is interrupted by a dry season from January through April,
140 likely providing a dynamic resource landscape. To investigate the relationship between food
141 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

166 platforms, and after learning that our bats foraged primarily on the west side of the river delta.
167 This resulted in four locations that overlapped exactly between the wet and dry seasons (Figure
168 1). Cameras detect insects of *N. albiventris*' typical prey size (5-15mm length; Aguirre *et al.*
169 2003) up to a height of ca. 8m (volume 125m³; Ruczyński *et al.* 2020), thus encompassing prey
170 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**

189 We counted the number of insects per photo via a machine learning algorithm (Choinski *et al.*
190 2023). We compared the algorithm's insect counts with manual counts by JEK for a subset of
191 1,177 photos that spanned a range of conditions and insect numbers (Spearman Rank Correlation
192 0.80; Choinski *et al.* 2023). We excluded nights with rain, or manually counted photos where rain
193 occurred for 10-15min.

194
195 To assess differences in spatiotemporal insect availability during the dry and wet seasons within a
196 bat foraging bout, and break the temporal autocorrelation of insect counts, we calculated mean
197 and maximum insects per photo and counted the number of photos without insects during the first
198 2.5h of photos for each location and each monitoring night. These metrics estimate average
199 abundance, the largest peak, and instances of no insect availability, respectively, for single
200 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

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

215

216 **Bat foraging effort in time and space**

217 We calculated foraging durations from the difference in minutes between the first and last GPS
218 fix on each tracking night (GPS did not function inside the roost, and outside the roost bats fly
219 continuously). We calculated emergence time as minutes after sunset with the R package
220 “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 (< 120 s; 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
256 stress metric, which indicates how easily the multidimensional data could be condensed into 2-
257 dimensional space (0.05-0.1 indicates very good representation in 2-D space). We fit numerical

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

260

261 Insects: ordinations included the intrinsic variables (vectors) mean/maximum insects per photo,
262 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
264 insect patches at locations. We then visualized how the extrinsic variables (factors) season,
265 location (1-4), and monitoring date contributed to the ordination's structure.

266

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

274

275 We assessed the effects of season, camera location, and monitoring night for insect data, and of
276 season, season-year, and bat ID for bat data with a permutation multivariate analysis of variance
277 (PERMANOVA) on dissimilarity matrices of insect and bat data. We calculated dissimilarity
278 matrices using Gower's distance, with numerical and categorical variables. We showed which
279 individuals diverged significantly within each season with a Multi Response Permutation
280 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.

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

371 We predicted that insect abundance would be lower and patches less predictable and more
372 ephemeral in the dry season, as tropical insect abundance usually peaks during the transition to,
373 or in the wet season, including for nocturnal flying insects in Panama (Ricklefs 1975; Tanaka &
374 Tanaka 1982; Rautenbach *et al.* 1988; Kishimoto-Yamada & Itioka 2015). In contrast, we
375 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

400 offspring performance than food quantity (Twining *et al.* 2016, 2019), and the levels of
401 LCPUFAs available to predators from aquatic prey can vary by insect taxonomy (Mathieu-
402 Resuge *et al.* 2021). *Noctilio albiventris* may time reproduction with a period of exceptional
403 nutritional gain if the wet season supports prey species with higher LCPUFA content, despite
404 lower prey abundance. Future studies should sample insects to elucidate the way resource
405 distribution interacts with both energetic and nutritional requirements for reproductive output in
406 *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

424 energy-rich insects, as they spent less time performing ARS-feeding in each patch. This could
425 compensate for the energy expenditure of increased searching behavior. Thirdly, flight and or
426 echolocation may be less costly under shifting environmental conditions like lower wind speeds
427 and higher relative humidity in the wet season (Sapir *et al.* 2014; Chaverri & Quirós 2017;
428 O'Mara *et al.* 2019), and, finally, bats may compensate by using additional energy-saving
429 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

447 strategies. Alternatively, these bats may simply be more experienced, skilled, or competitive
448 foragers, 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

471 when many trees are leafless, foraging Seba's short-tailed bats (*Carollia perspicillata*) often
472 invest into commuting back to their day roost between foraging bouts, rather than use nearby
473 night roosts on trees that without leaves probably do not provide enough protection from
474 predators. However, fruit is also less abundant and dispersed during the dry season, which likely
475 contributes to greater foraging commutes in addition to increased predation pressure (Fleming &
476 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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492

493 **REFERENCES**

- 494 Aguirre, L.F., Herrel, A., Van Damme, R. & Matthysen, E. (2003). The implications of food
495 hardness for diet in bats. *Funct. Ecol.*, 17, 201–212.
- 496 Aikens, E.O., Kauffman, M.J., Merkle, J.A., Dwinell, S.P.H., Fralick, G.L. & Monteith, K.L.
497 (2017). The greenscape shapes surfing of resource waves in a large migratory herbivore.
498 *Ecol. Lett.*, 20, 741–750.
- 499 Ashmole, N.P. (1971). Seabird ecology and the marine environment. In: *Avian Biology*. pp. 223–
500 286.
- 501 Baxter, C. V., Fausch, K.D. & Saunders, W.C. (2005). Tangled webs: Reciprocal flows of
502 invertebrate prey link streams and riparian zones. *Freshw. Biol.*, 50, 201–220.
- 503 Bell, W.J. (1990). Central place foraging. In: *Searching Behaviour*. Springer Netherlands, pp.
504 171–187.
- 505 Boonman, A., Fenton, B. & Yovel, Y. (2019). The benefits of insect-swarm hunting to
506 echolocating bats, and its influence on the evolution of bat echolocation signals. *PLoS*
507 *Comput. Biol.*, 15, 1–18.
- 508 Brittain, J.E. (1982). Biology of Mayflies. *Annu. Rev. Entomol.*, 27, 119–147.
- 509 Brown, P.E., Brown, T.W. & Grinnell, A.D. (1983). Echolocation, Development, and Vocal
510 Communication in the Lesser Bulldog Bat, *Noctilio albiventris*. *Behav. Ecol. Sociobiol.*, 13,
511 287–298.
- 512 Chaverri, G. & Quirós, O.E. (2017). Variation in echolocation call frequencies in two species of
513 free-tailed bats according to temperature and humidity. *J. Acoust. Soc. Am.*, 142, 146–150.
- 514 Choinski, M., Zegarek, M., Hałat, Z., Borowik, T., Kohles, J., Dietzer, M., *et al.* (2023). Insect
515 detection on high-resolution images using Deep Learning. In: *Proceedings of the 22nd*

- 516 *International Computer Information Systems and Industrial Management Conference* (eds.
517 Saeed, K., Dvorský, J., Nishiuchi, N. & Fukumoto, M.). Springer Nature Switzerland AG,
518 Tokyo, pp. 225–239.
- 519 Corbet, P.S. (1964). Temporal Patterns of Emergence in Aquatic Insects. *Can. Entomol.*, 96,
520 264–279.
- 521 Dechmann, D.K., Ehret, S., Gaub, A., Kranstauber, B. & Wikelski, M. (2011). Low metabolism
522 in a tropical bat from lowland Panama measured using heart rate telemetry: an unexpected
523 life in the slow lane. *J. Exp. Biol.*, 214, 3605–3612.
- 524 Dechmann, D.K.N., Heucke, S.L., Giuggioli, L., Safi, K., Voigt, C.C. & Wikelski, M. (2009).
525 Experimental evidence for group hunting via eavesdropping in echolocating bats. *Proc. R.*
526 *Soc. B Biol. Sci.*, 276, 2721–2728.
- 527 Egert-Berg, K., Hurme, E.R., Greif, S., Goldstein, A., Harten, L., Herrera M., L.G., *et al.* (2018).
528 Resource Ephemerality Drives Social Foraging in Bats. *Curr. Biol.*, 28, 3667–3673.
- 529 Fagan, W.F., Gurarie, E., Bewick, S., Howard, A., Cantrell, R.S. & Cosner, C. (2017). Perceptual
530 ranges, information gathering, and foraging success in dynamic landscapes. *Am. Nat.*, 189,
531 474–489.
- 532 Fauchald, P. & Tveraa, T. (2006). Hierarchical patch dynamics and animal movement pattern.
533 *Oecologia*, 149, 383–395.
- 534 Fleming, T.H. & Heithaus, E.R. (1986). Seasonal Foraging Behavior of the Frugivorous Bat
535 *Carollia perspicillata*. *J. Mammal.*, 67, 660–671.
- 536 Fleming, T.H., Hooper, E.T. & Wilson, D.E. (1972). Three Central American Bat Communities:
537 Structure, Reproductive Cycles, and Movement Patterns. *Ecology*, 53, 556–569.

- 538 Florko, K.R.N., Shuert, C.R., Cheung, W.W.L., Ferguson, S.H., Jonsen, I.D., Rosen, D.A.S., *et*
539 *al.* (2023). Linking movement and dive data to prey distribution models: new insights in
540 foraging behaviour and potential pitfalls of movement analyses. *Mov. Ecol.*, 11, 1–14.
- 541 Fukui, D., Murakami, M., Nakano, S. & Aoi, T. (2006). Effect of emergent aquatic insects on bat
542 foraging in a riparian forest. *J. Anim. Ecol.*, 75, 1252–1258.
- 543 Gonsalves, L., Law, B., Webb, C. & Monamy, V. (2013). Foraging Ranges of Insectivorous Bats
544 Shift Relative to Changes in Mosquito Abundance. *PLoS One*, 8.
- 545 Gutenkunst, R., Newlands, N., Lutcavage, M. & Edelstein-Keshet, L. (2007). Inferring resource
546 distributions from Atlantic bluefin tuna movements: An analysis based on net displacement
547 and length of track. *J. Theor. Biol.*, 245, 243–257.
- 548 Hałat, Z., Dechmann, D.K., Zegarek, M., Visser, A.E. & Ruczyński, I. (2018). Sociality and
549 insect abundance affect duration of nocturnal activity of male parti-colored bats. *J.*
550 *Mammal.*, 99, 1503–1509.
- 551 Hooper, E.T. & Brown, J.H. (1968). Foraging and Breeding in Two Sympatric Species of
552 Neotropical Bats, Genus *Noctilio*. *J. Mammal.*, 49, 310–312.
- 553 Hurme, E., Fahr, J., Eric-Moise, B.F., Hash, C.T., O'Mara, M.T., Richter, H., *et al.* (2022). Fruit
554 bat migration matches green wave in seasonal landscapes. *Funct. Ecol.*, 36, 2043–2055.
- 555 Jha, S. & Kremen, C. (2013). Resource diversity and landscape-level homogeneity drive native
556 bee foraging. *Proc. Natl. Acad. Sci. U. S. A.*, 110, 555–558.
- 557 Jones, T.B., Green, J.A., Patrick, S.C., Evans, J.C., Wells, M.R., Rodríguez-Malagón, M.A., *et al.*
558 (2020). Consistent sociality but flexible social associations across temporal and spatial
559 foraging contexts in a colonial breeder. *Ecol. Lett.*, 23, 1085–1096.

- 560 Kalko, E.K.V., Schnitzler, H.U., Kaipf, I. & Grinnell, A.D. (1998). Echolocation and foraging
561 behavior of the lesser bulldog bat, *Noctilio albiventris*: Preadaptations for piscivory? *Behav.*
562 *Ecol. Sociobiol.*, 42, 305–319.
- 563 Keicher, L., Shipley, J.R., Schaeffer, P.J. & Dechmann, D.K.N. (2023). Contrasting Torpor Use
564 by Reproductive Male Common Noctule Bats in the Laboratory and in the Field. *Integr.*
565 *Comp. Biol.*, 1–12.
- 566 Kishimoto-Yamada, K. & Itioka, T. (2015). How much have we learned about seasonality in
567 tropical insect abundance since Wolda (1988)? *Entomol. Sci.*, 18, 407–419.
- 568 Kitaysky, A.S., Hunt, J., Flint, E.N., Rubega, M.A. & Decker, M.B. (2000). Resource allocation
569 in breeding seabirds: Responses to fluctuations in their food supply. *Mar. Ecol. Prog. Ser.*,
570 206, 283–296.
- 571 Kohles, J.E., O’Mara, M.T. & Dechmann, D.K.N. (2022). A conceptual framework to predict
572 social information use based on food ephemerality and individual resource requirements.
573 *Biol. Rev.*, 97, 2039–2056.
- 574 Kotliar, N.B. & Wiens, J.A. (1990). Multiple Scales of Patchiness and Patch Structure: A
575 Hierarchical Framework for the Study of Heterogeneity. *Oikos*, 59, 253.
- 576 Kunz, T.H., Whitaker, J.O. & Wadanoli, M.D. (1995). Dietary energetics of the insectivorous
577 Mexican free-tailed bat (*Tadarida brasiliensis*) during pregnancy and lactation. *Oecologia*,
578 101, 407–415.
- 579 Kurta, A., Bell, G., Nagy, K. & Kunz, T. (1989). Energetics of Pregnancy and Lactation in
580 Freeranging Little Brown Bats (*Myotis lucifugus*). *Physiol. Zool.*, 62, 804–818.
- 581 Mathieu-Resuge, M., Martin-Creuzburg, D., Twining, C.W., Parmar, T.P., Hager, H.H. & Kainz,

- 582 M.J. (2021). Taxonomic composition and lake bathymetry influence fatty acid export via
583 emergent insects. *Freshw. Biol.*, 66, 2199–2209.
- 584 Moretto, L. & Francis, C.M. (2017). What factors limit bat abundance and diversity in temperate,
585 north American urban environments? *J. Urban Ecol.*, 3, 1–9.
- 586 Norberg, R.A. (1977). An Ecological Theory on Foraging Time and Energetics and Choice of
587 Optimal Food- Searching Method. *J. Anim. Ecol.*, 46, 511–529.
- 588 O’Donnell, C.F.J. (2000). Influence of season, habitat, temperature, and invertebrate availability
589 on nocturnal activity of the new zealand long-tailed bat (*Chalinolobus tuberculatus*). *New*
590 *Zeal. J. Zool.*, 27, 207–221.
- 591 O’Mara, M.T., Scharf, A.K., Fahr, J., Abedi-Lartey, M., Wikelski, M., Dechmann, D.K.N., *et al.*
592 (2019). Overall Dynamic Body Acceleration in Straw-Colored Fruit Bats Increases in
593 Headwinds but Not With Airspeed. *Front. Ecol. Evol.*, 7, 1–12.
- 594 Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., *et al.* (1999). A
595 landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *J.*
596 *Appl. Ecol.*, 36, 519–533.
- 597 Phillips, L.R., Carroll, G., Jonsen, I., Harcourt, R., Brierley, A.S., Wilkins, A., *et al.* (2022).
598 Variability in prey field structure drives inter-annual differences in prey encounter by a
599 marine predator, the little penguin. *R. Soc. Open Sci.*, 9.
- 600 Piatt, J.F., Harding, A.M.A., Shultz, M., Speckman, S.G., Van Pelt, T.I., Drew, G.S., *et al.*
601 (2007). Seabirds as indicators of marine food supplies: Cairns revisited. *Mar. Ecol. Prog.*
602 *Ser.*, 352, 221–234.
- 603 Racey, P.A. (1982). Ecology of Bat Reproduction. In: *Ecology of Bats* (ed. Kunz, T.H.). Plenum

- 604 Press, New York, pp. 57–104.
- 605 Racey, P.A. & Entwistle, A.C. (2000). *Life-history and Reproductive Strategies of Bats. Reprod.*
606 *Biol. Bats.*
- 607 Rasweiler, J.J. (1977). Preimplantation development, fate of the zona pellucida, and observations
608 on the glycogen-rich oviduct of the little bulldog bat, *Noctilio albiventris*. *Am. J. Anat.*, 150,
609 269–299.
- 610 Rautenbach, I.L., Kemp, A.C. & Scholtz, C.H. (1988). Fluctuations in availability of arthropods
611 correlated with microchiropteran and avian predator activities. *Koedoe*.
- 612 Real, L. & Caraco, T. (1986). Risk and foraging in stochastic environments. *Annu. Rev. Ecol.*
613 *Syst. Vol. 17*, 371–390.
- 614 Ricklefs, R.E. (1975). Seasonal Occurrence of Night-Flying Insects on Barro Colorado Island,
615 Panama Canal Zone. *J. New York Entomol. Soc.*, 83, 19–32.
- 616 Righi-Cavallaro, K.O., Roche, K.F., Froehlich, O. & Cavallaro, M.R. (2010). Structure of
617 macroinvertebrate communities in riffles of a Neotropical karst stream in the wet and dry
618 seasons. *Acta Limnol. Bras.*, 22, 306–316.
- 619 Roeleke, M., Blohm, T., Hoffmeister, U., Marggraf, L., Schlägel, U.E., Teige, T., *et al.* (2020).
620 Landscape structure influences the use of social information in an insectivorous bat. *Oikos*,
621 129, 912–923.
- 622 Ruczyński, I., Hałat, Z., Zegarek, M., Borowik, T. & Dechmann, D.K.N.D.K.N. (2020). Camera
623 transects as a method to monitor high temporal and spatial ephemerality of flying nocturnal
624 insects. *Methods Ecol. Evol.*, 11, 294–302.
- 625 Safi, K. & Kerth, G. (2007). Comparative analyses suggest that information transfer promoted

- 626 sociality in male bats in the temperate zone. *Am. Nat.*, 170, 465–472.
- 627 Sapir, N., Horvitz, N., Dechmann, D.K.N., Fahr, J. & Wikelski, M. (2014). Commuting fruit bats
628 beneficially modulate their flight in relation to wind. *Proc. R. Soc. B Biol. Sci.*, 281.
- 629 Schmidt-Nielsen, K. (1972). Locomotion: Energy cost of swimming, flying, and running.
630 *Science*, 177, 222–228.
- 631 Schoener, T.W. (1971). Theory of Feeding Strategies. *Annu. Rev. Ecol. Syst.*, 2, 369–404.
- 632 Shiel, C.B., Shiel, R.E. & Fairley, J.S. (1999). Seasonal changes in the foraging behaviour of
633 Leisler’s bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. *J. Zool.*, 249,
634 347–358.
- 635 Steffan-Dewenter, I. & Kuhn, A. (2003). Honeybee foraging in differentially structured
636 landscapes. *Proc. R. Soc. B Biol. Sci.*, 270, 569–575.
- 637 Sweeney, B.W. & Vannote, R.L. (1982). Population Synchrony in Mayflies: A Predator Satiation
638 Hypothesis. *Ecology*, 36, 810–821.
- 639 Tanaka, L.K. & Tanaka, S.K. (1982). Rainfall and Seasonal Changes in Arthropod Abundance on
640 a Tropical Oceanic Island. *Biotropica*, 14, 114.
- 641 Teague O’Mara, M., Wikelski, M. & Dechmann, D.K.N. (2014). 50 years of bat tracking: Device
642 attachment and future directions. *Methods Ecol. Evol.*, 5, 311–319.
- 643 Twining, C.W., Brenna, J.T., Lawrence, P., Shipley, J.R., Tollefson, T.N. & Winkler, D.W.
644 (2016). Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore
645 performance more than food quantity. *Proc. Natl. Acad. Sci. U. S. A.*, 113, 10920–10925.
- 646 Twining, C.W., Brenna, J.T., Lawrence, P., Winkler, D.W., Flecker, A.S. & Hairston, N.G.
647 (2019). Aquatic and terrestrial resources are not nutritionally reciprocal for consumers.

648 *Funct. Ecol.*, 33, 2042–2052.

649 Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep. Res. Part II*
 650 *Top. Stud. Oceanogr.*, 54, 211–223.

651 Wiens, J.A. (1976). Population Responses to Patchy Environments. *Annu. Rev. Ecol. Syst.*, 7, 81–
 652 120.

653 Wilkinson, G.S. (1992). Information transfer at evening bat colonies. *Anim. Behav.*, 44, 501–518.

654

655 **FIGURE CAPTIONS**

656 Figure 1. Study site in Gamboa, Panama, where the Chagres River meets the Panama Canal. Blue
 657 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.

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695 **FIGURES**



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697 Figure 1.

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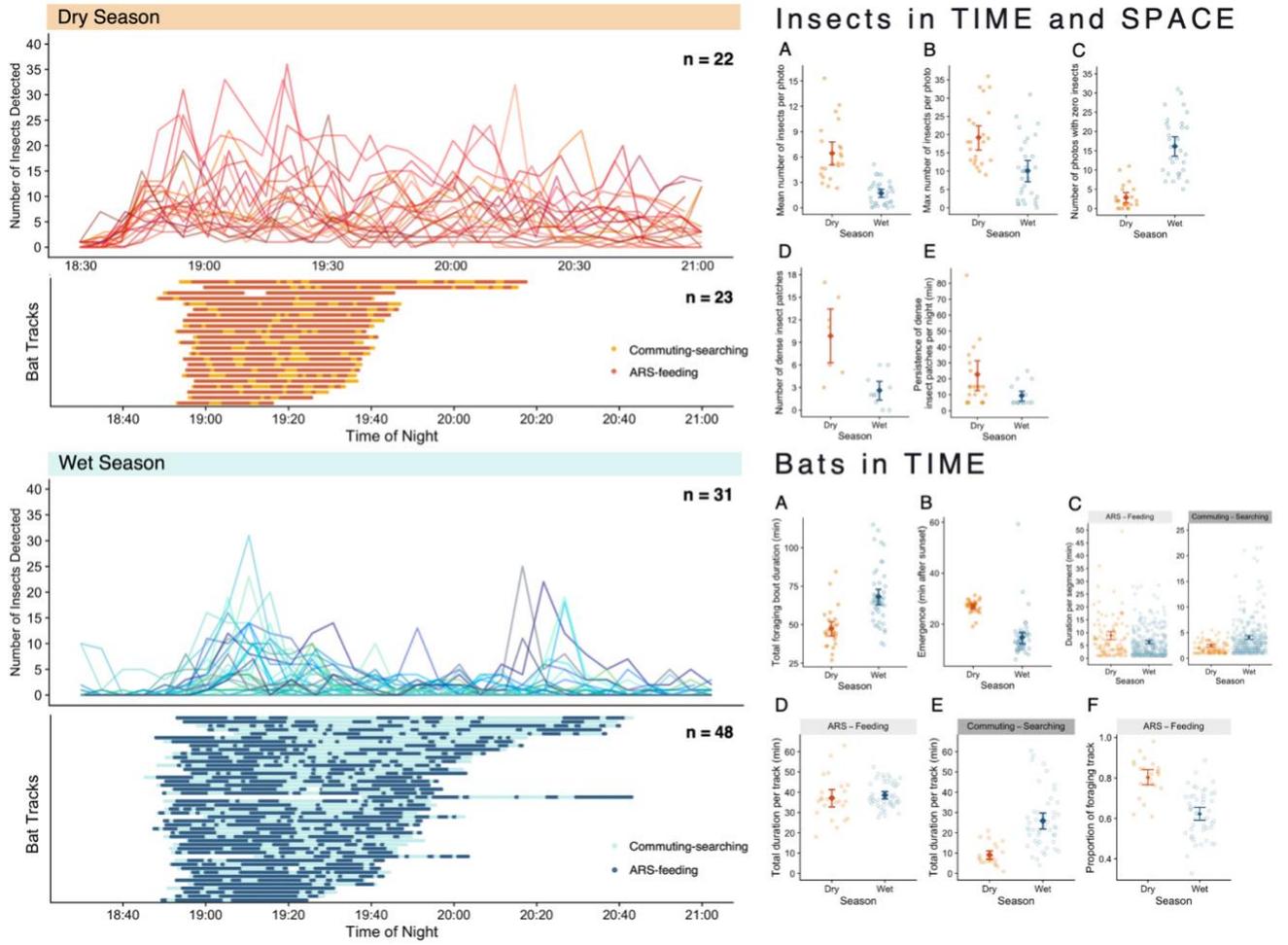
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707 Figure 2.

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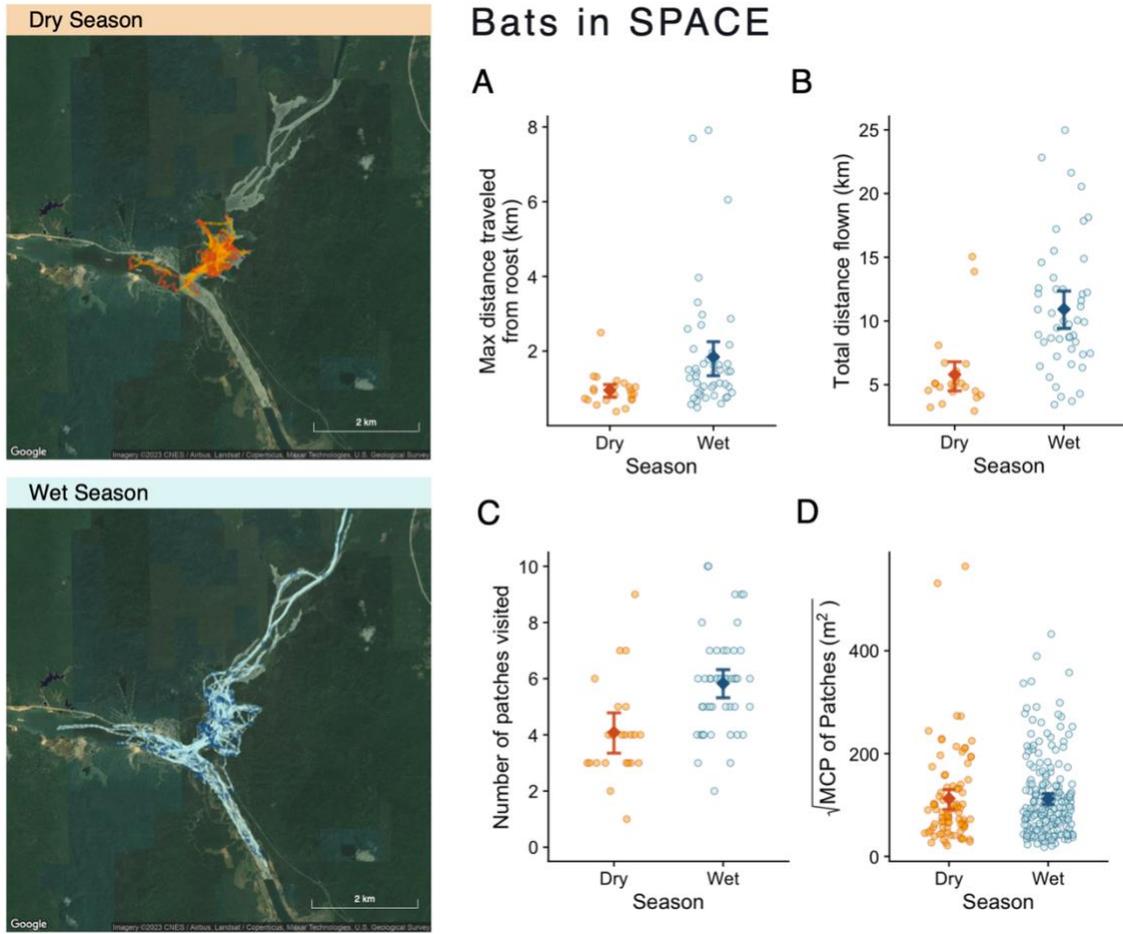
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718 Figure 3.

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728 **TABLES**

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

732

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

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

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

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