

1 **Title: A trait-based understanding of the vulnerability of a paleotropical moth community to**
2 **predation by a sympatric bat with flexible foraging strategies**

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6 **Abstract**

- 7 **1.** Prey profitability for a predator hunting diverse prey varies with species and seasons. Whereas
8 prey selection by aerial-hawking or gleaning bats is well established, this is challenging to
9 establish in species that adopt both these strategies flexibly. Measurable prey traits coupled
10 with availability in the foraging grounds help characterize the vulnerability of prey species to
11 predation.
- 12 **2.** In the Western Ghats of India, a global biodiversity hotspot, we studied an anthropogenic
13 landscape, where insectivorous bats are abundant and diverse, but their impact on moth
14 communities is little understood. We investigated the morphological traits of a sympatric moth
15 community that make them more vulnerable to predation by *Megaderma spasma*, a bat with
16 flexible foraging strategies. We also established the seasonal composition of moth prey in the
17 diet of the bat.
- 18 **3.** We analyzed the discarded prey remains from several roosts, collected over three years, for
19 seasonal patterns in the diet and selective hunting. Through light-trapping, we collected moth
20 specimens in different seasons to assess the morphological traits of the moth community
21 available in the foraging area of the bat.
- 22 **4.** The traits likely to affect the profitability of prey moths were measured: forewing length,
23 hindwing length, wingspan, and body length (a proxy for body size); forewing area, hindwing
24 area, maneuverability, and wing loading (as a proxy for evasive flight capability), and forewing
25 aspect ratio (as a proxy for wing shape).

- 26 5. Our results showed that consumed moth prey diversity varies seasonally, with moths belonging
27 to the Hepialidae family being preferred in the wet season. Moths belonging to the Sphingidae
28 family were the most abundant in the diet, followed by Erebididae and Hepialidae. Sphingid
29 moths have the lowest maneuverability, and highest forewing aspect ratio; the Hepialidae
30 moths have the maximum body size followed by Sphingids thus confirming our hypothesis that
31 larger moths with low evasive capabilities are more vulnerable to predation.
- 32 6. Assessing vulnerability at the prey community level, we establish a framework for future
33 research on moth-bat interactions from the diverse and less-explored paleotropical
34 communities. Additionally, the study reiterates the usefulness of trait-based approaches to
35 understanding prey-predator dynamics.

36

37 **Keywords:** megadermatid bats, morphological traits, moths, prey-predator, Western Ghats

38

39 **Introduction**

40 Predator–prey relationships are central to community dynamics. The relationship involves strategies
41 that predators adopt to become efficient hunters and those that prey adopt to avoid getting eaten (
42 Schmitz, 2017). Recent studies have investigated these interactions as an evolutionary battle through
43 functional traits which are measurable morphological, behavioural, physiological, or life history traits
44 of organisms associated with their ecological functions (Ferry-Graham, 2002; Violle et al., 2007).
45 Functional prey-predator relationships are based on the presumption that prey characteristics rather
46 than prey taxonomy should drive prey selection by predators (Spitz et al., 2014).

47 Morphological traits related to flight efficiency and maneuverability help characterise the prey’s
48 profitability to a predator based on how difficult it is to catch them or how much effort goes into
49 searching for them. For example, hunting prey that are too large is energetically costly to predators
50 and too small a prey is not worth the chase (Schmitz, 2017). Selecting a prey based on size is quite
51 common (Brose, 2010; Nakazawa, 2017; Ortiz & Arim, 2016), but in addition, prey evasive tactics

52 determine predator preference and its impact on the prey assemblage (Klecka & Boukal, 2013).
53 Therefore, this trait-based approach is an important connection between evolutionary and community
54 ecology that allows ecologists to study predator-prey dynamics at the scale of a community rather than
55 a simple paired prey-predator model (Moore & Biewener, 2015; Schmitz et al., 2015; Schmitz &
56 Trussell, 2016).

57 For 65 million years, moths and bats have been engaged in aerial warfare replete with stealth and
58 deception (reviewed in ter Hofstede & Ratcliffe, 2016). As highly skilled and acrobatic hunters, bats
59 choose prey that are energetically profitable and suited to their hunting skills (Arrizabalaga-Escudero
60 et al., 2018; Mata et al., 2016; Vesterinen et al., 2016). Successful foraging by bats depends on the age
61 and sex of the individual (Arrizabalaga et al., 2019; Mata et al., 2016), prey abundance (Wray et al.,
62 2021), and prey accessibility due to habitat structure (Almenar et al., 2013). Selection of larger prey
63 has been observed in insectivorous bats (reviews in Almenar et al., 2008; Burles et al., 2008; Fenton
64 et al., 1990; Jones, 1990; Siemers & Schnitzler, 2000; Vesterinen et al., 2016) and attributed to prey
65 profitability (energy gained/prey handling time) (Catania & Remple, 2005). Arrizabalaga-Escudero et
66 al. (2019) provided a better understanding of prey resources using trait-based analyses, establishing
67 that in a temperate ecosystem, a combination of functional traits of moths (wing loading and body
68 mass) and life-history traits of bats (age and sex) governs predation risk from the insectivorous
69 horseshoe bat *Rhinolophus euryale*. Fundamental to prey-predator interactions, these hypotheses are
70 untested from the diverse tropical systems and from bats that follow different hunting strategies, such
71 as megadermatid gleaning bats. Tropical arthropod communities are extremely high in species richness
72 (Basset et al., 2012) which gives predators much to choose from and also allows them to specialize on
73 profitable moths of certain species or traits.

74 Prey species have to be faster and have high maneuverability to escape predators successfully
75 (Howland, 1974) and evasive flight is a common anti-predator tactic known in moths (Roeder, 1964,
76 1967). They “turn away” (directional flight) and/or “dive” (erratic flight) toward the ground in response
77 to a distant bat or close bat respectively (Roeder, 1962). Depending on their auditory capabilities

78 (Minnaar et al., 2015; Schoeman & Jacobs, 2011) and size (Surlykke et al., 1999), moths show species-
79 specific strategies that are a functional consequence of the morphological differences that contribute
80 to maneuverability (Hügel & Goerlitz, 2019). It is known that the hindwings in the flapping flight of
81 moths and butterflies are more important for take-off, acceleration, and maneuverability than for
82 sustained flight (Jantzen & Eisner, 2008; Stylman et al., 2020). However, it is yet to be investigated
83 how different morphological traits make moths of different sizes vulnerable to predation, especially
84 by bats with flexible foraging strategies.

85 Our focal predator is the lesser false vampire bat, *Megaderma spasma*, found mostly across south-east
86 Asia, NE India, and in the Western Ghats. The insect order Lepidoptera (mostly moths) forms about
87 10-12% of the diet of *M. spasma* (Davison & Zubaid, 1992; Raghuram et al., 2015) and does not vary
88 across seasons (Prakash, 2020). Usually, moth species with audible wing beats and nocturnal flight
89 (e.g Sphingidae, Saturniidae) are abundant in the diet (Balete, 2010). *Megaderma spasma* hunt within
90 a kilometer of their daytime roost (Prakash et al., 2021) and return to the roost with prey, thereby
91 providing culled remains through which the prey species can be identified (Brosset, 1962). Their large
92 ears make them capable of detecting low-frequency, directional sounds due to prey movement (Wang
93 & Müller, 2009). However, *M. spasma* most likely uses multiple foraging tactics as their short,
94 broadband, multi-harmonic, frequency-modulated calls are more suited to catching prey by perch
95 hunting ('flycatching'), in high clutter habitats rather than surface gleaning (Tyrell, 1990).

96 The predator is well-studied in our study area and its roost locations have been mapped, from which
97 we reliably know that it feeds mostly on orthopteran prey (Prakash et al., 2021; Raghuram et al., 2015).
98 Given its foraging tactics and size, it is capable of handling larger prey. Lepidoptera (especially moths)
99 is the most diverse insect group that it feeds on. It remains to be known what kind of moths are chosen,
100 in which season, and what traits drive this decision.

101 In this paper, our goal was to investigate, in a paleotropical ecosystem, the following questions: 1) Is
102 there a seasonal difference in the diversity of moth species hunted by *M. spasma* ? and 2) Which
103 morphological traits of a sympatric moth community make them more vulnerable to predation? We

104 predicted that the consumed moth prey diversity would change with seasons and that larger moths with
105 low evasive capabilities would be preferred by *M. spasma*. Overall, our study aims to bridge the gap
106 in prey-predator interaction research from the tropics with a community-level trait-based analysis to
107 understand the functional demands on the moth assemblages imposed by a sympatric bat species. This
108 study establishes a model prey-predator system for further exploring the bat-moth arms race from this
109 part of the globe.

110 **Materials and Methods**

111 *Study Area*

112 The study was conducted in the human-modified landscape just outside Kudremukh National Park, in
113 and around Kadari Village, Udipi district, Karnataka, India (13°21'N–75°08'E) in the Western Ghats,
114 a global biodiversity hotspot (Fig. 1). The annual rainfall ranges from 600-800 cm, with the maximum
115 rain from June to September. The maximum temperature varies from 21-34°C (April to July) and the
116 minimum temperature from 12-18 °C (January to May) (Nagaraja et al., 2005). The Western Ghats, a
117 1600 km long chain of mountains along the west coast of India, are unique because of their
118 geographical location, stable geological history, heavy rainfall, and good soil conditions, crucial to
119 maintaining a variety of tropical forest ecosystems (Pascal et al., 2004). The natural vegetation (below
120 300 m), i.e our core study area, is semi-evergreen and human-influenced (Subramanian et al., 2005).
121 The Areca nut (*Areca catechu*), Rubber (*Hevea brasiliensis*) plantations, and agricultural lands have
122 replaced the natural forests. *Megaderma spasma* roosts predominantly in human habitation in this
123 landscape and the roosts are regularly monitored.

124 *Culled remains collection*

125 Prey remains discarded by bats on the floor of the roosts (referred to as 'culled remains') were collected
126 weekly (2018-20, 2021) or every two weeks (2016-17). The collection was made from 21, 24, and 21
127 roosts in 2016-17, 2018-20, and 2021 respectively (details in Table 1 and Fig 1 in Supporting
128 information). Some of the roosts become unavailable for collection for some parts of the year as they

129 are private properties or they get damaged due to heavy rainfall. The culled remains collection was
130 restricted to 8 selected roosts during the month of May-July 2021, due to a nationwide lockdown amidst
131 the global COVID-19 pandemic, so the comparisons are done only among those 8 roosts for the wet
132 season in the third year.

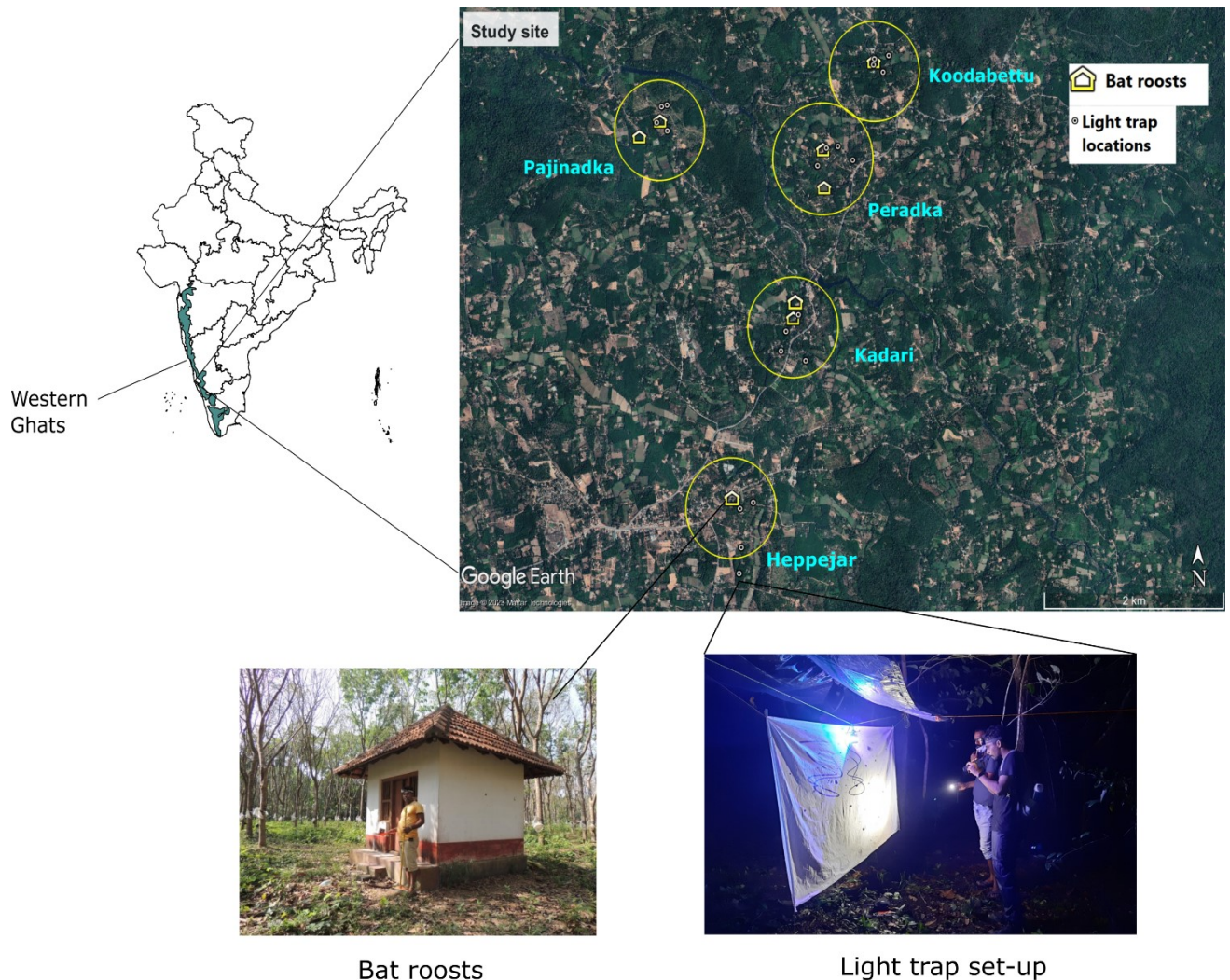
133 Most insect parts were classified to the order level, but the moth wing remains were identified to
134 species level, whenever possible. We also identified each forewing as a left or right wing. By matching
135 the left and right wings, we arrived at the minimum number of individuals for all insect orders. A
136 database was created with segregated insect orders and the identified moth species over the years.
137 About 40% of the culled remains could not be identified, as they were torn, or damaged due to rain or
138 the wing patterns were not visible due to loss of scales.

139 *Light trapping*

140 We used light traps to study moths at random points around 8 bat roosts at five sites (Field Station,
141 Peradka, Pajinadka, Koodabettu, and Heppejar) (Fig. 1) for documenting the available moth diversity.
142 The light trapping was done by the vertical sheet method (a white sheet measuring ~90 x 190 cm),
143 illuminated by LepiLED (Brehm, 2017) (Fig.1). LepiLED consists of power LEDs with peaks at 368
144 nm (ultraviolet), 450 nm (blue), 530 nm (green), and 550 nm (cool white), corresponding to the peak
145 sensitivity of most Lepidoptera eye receptors (Brehm, 2017).

146 Light-trapping was done for 10 nights/month (each site was sampled twice a month) for 7 months from
147 the fading moon to the new moon cycle (Jan-April; Aug-Oct) in 2021. We sampled moths with two
148 traps running for different periods of the night because the storage life of portable batteries was a
149 maximum of only 5 hours (details in Table 2 and Fig. 2 in the Supporting Information). The traps were
150 placed within a radius of 1 km from a bat roost. The effective attraction distance of moths to light traps
151 used in our study is about 50 m; thus, we spaced our traps by 100 m to minimize bias and maximize
152 efficiency within a night at a sampling site.

153 The number of individuals of moth species having >40 mm wingspan were counted every hour, as the
154 smallest moth species identified from the culled remains collection of previous years had around 40
155 mm wingspan.



156
157 Figure 1. The map shows the location of the study area with details of the light traps around the bat
158 roosts

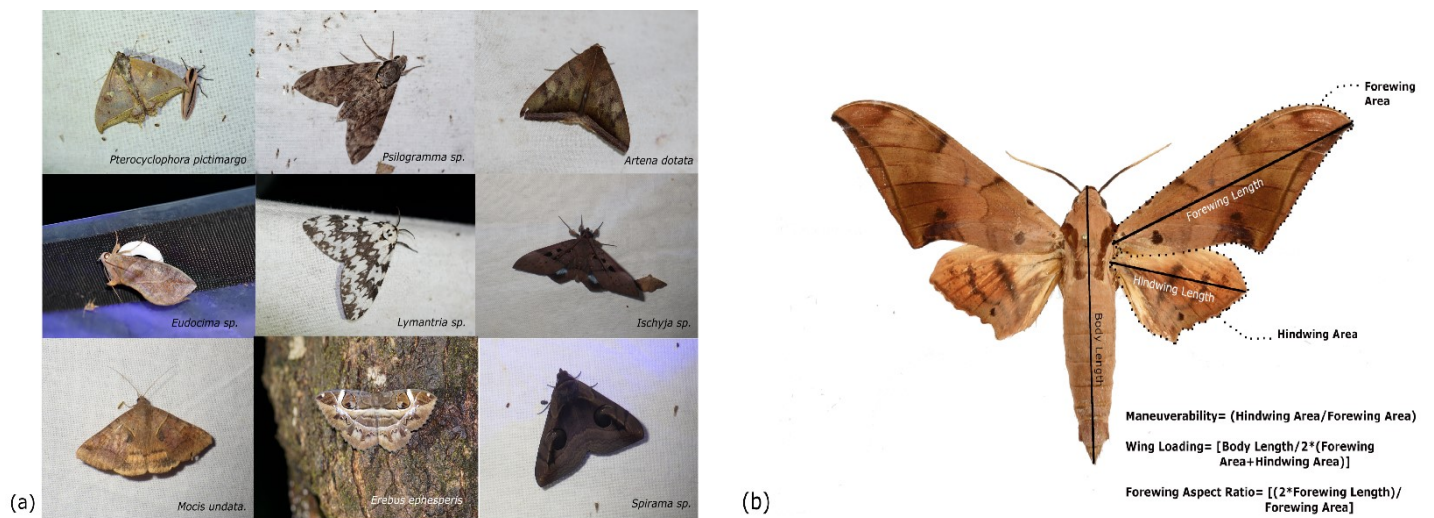
159 *Measuring morphological traits*

160 The specimens collected from the light traps were deposited as voucher specimens at The Research
161 and Collections Facility of the National Centre for Biological Sciences, Bangalore, India. Fig. 2a
162 shows a representative moth species diversity of the light traps. We photographed the voucher
163 specimens with their wings outstretched and with a reference scale. From these photographs, we

164 measured the following traits using the software ImageJ (Schneider et al., 2012): Forewing length
165 (FWL); Hindwing length (HWL); Body length (BL) (a proxy for body size); Wingspan; Forewing
166 area (FWA); Hindwing area (HWA); Maneuverability= HWA/FWA (as a proxy for evasive flight
167 capability, higher value equals higher capability) (Arrizabalaga-Escudero et al., 2019; Jantzen &
168 Eisner, 2008); Wing loading = $BL/2(FWA+HWA)$ and Forewing aspect ratio = $(2*FWL)/FWA$ (as a
169 proxy for wing shape) (Shi et al., 2015) (Fig. 2b). These traits were chosen as they are likely to affect
170 the profitability of prey moths for *M. spasma*.

171 Only specimens having wingspan >40 mm were considered for the analyses. Each trait was measured
172 from 2 to 5 specimens per species to obtain an average value. We had only one individual from the
173 Family Crambidae, which was not included in the analyses. A total of 418 specimens of 158
174 morphospecies belonging to 14 families were measured.

175



176

177 Figure 2. a) Representative moth species that were collected from the light traps and b) the
178 morphometric traits measured from voucher specimens that were collected from the light traps and
179 stored in the NCBS research collection

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185 Replication Statement:

Section	Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Culled remains collection	Roost	Year	21, 24, and 21 roosts in 2016-17, 2018-20, and 2021 respectively
Light trapping	Location	Location	4, 4, 4, 4, 4 (for each of the 7 months)
Morphometry	Specimen	Family	418 specimens of 158 morphospecies in 14 families

186

187 *Statistical Analyses*

188

189 We used the light-trapping data as a proxy of the moth species pool present in the study area, and
190 compared species found in the culled remains with those not found in the culled remains for further
191 analyses. To understand sample completeness, we computed rarefied and extrapolated species
192 accumulation curves for all the five sites sampled, using the iNEXT package (Hsieh et al., 2016) in R.

193 Culled remains: The diversity of moth species (Shannon Diversity Index) and the proportions of moth
194 individuals belonging to different families found in the culled remains were calculated across seasons
195 and for three years. As the proportion of individuals belonging to the three families Sphingidae,

196 Erebidae (in all seasons), and Hepialidae (in the wet season) were higher, we compared the proportions
197 of individuals in these families across seasons using a two-proportions z-test.

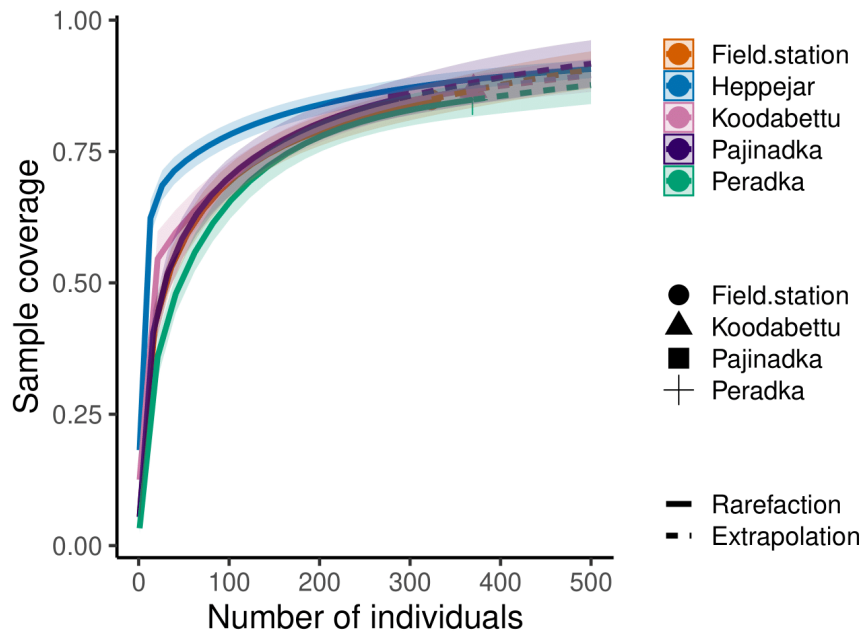
198 Morphological traits: All 9 morphological traits were compared among the species present and absent
199 in the diet using a Wilcoxon Rank Sum Test. To compare the morphological trait space of the three
200 most abundant families present or absent in the diet (Erebidae, Sphingidae, Hepialidae), we carried out
201 a Principal Coordinates Analysis (PCoA) followed by PERMANOVA (Permutational multivariate
202 analysis of variance) on a Euclidean distance matrix. The proportion of species present in the diet from
203 the other families was low and thus was not considered for comparing the trait space. We also
204 performed a multivariate beta diversity analysis to test for the homogeneity of dispersion within the
205 trait space of each of the families. Both analyses were done with the *betadisper* and *adonis* functions
206 in the Vegan package (Oksanen et al., 2009) in R.

207 To understand the effect of different morphological traits on the selection of prey by *M. spasma*, we
208 performed logistic linear regression (binomial function) with the presence or absence in the diet as the
209 response variable and the Body length, Maneuverability, Forewing Aspect Ratio, and Wing Loading
210 as the predictors. Predictor variables that were correlated above 0.8 were not considered, to avoid
211 multicollinearity in the models (Fig. 3 in Supplementary material). All statistical analyses and
212 visualizations were performed using R (“R Development Core Team: R: A language and environment
213 for statistical computing,” 2008).

214 **Results**

215 *Species pool at the foraging grounds*

216 We carried out light-trapping for 7 months in 2021, to establish the prey moth species pool available
217 for *M. spasma* around their roosts. Our sampling was adequate at the five sampling sites based on the
218 abundance-based sample completeness curve of species sampled at each site (Fig. 3).

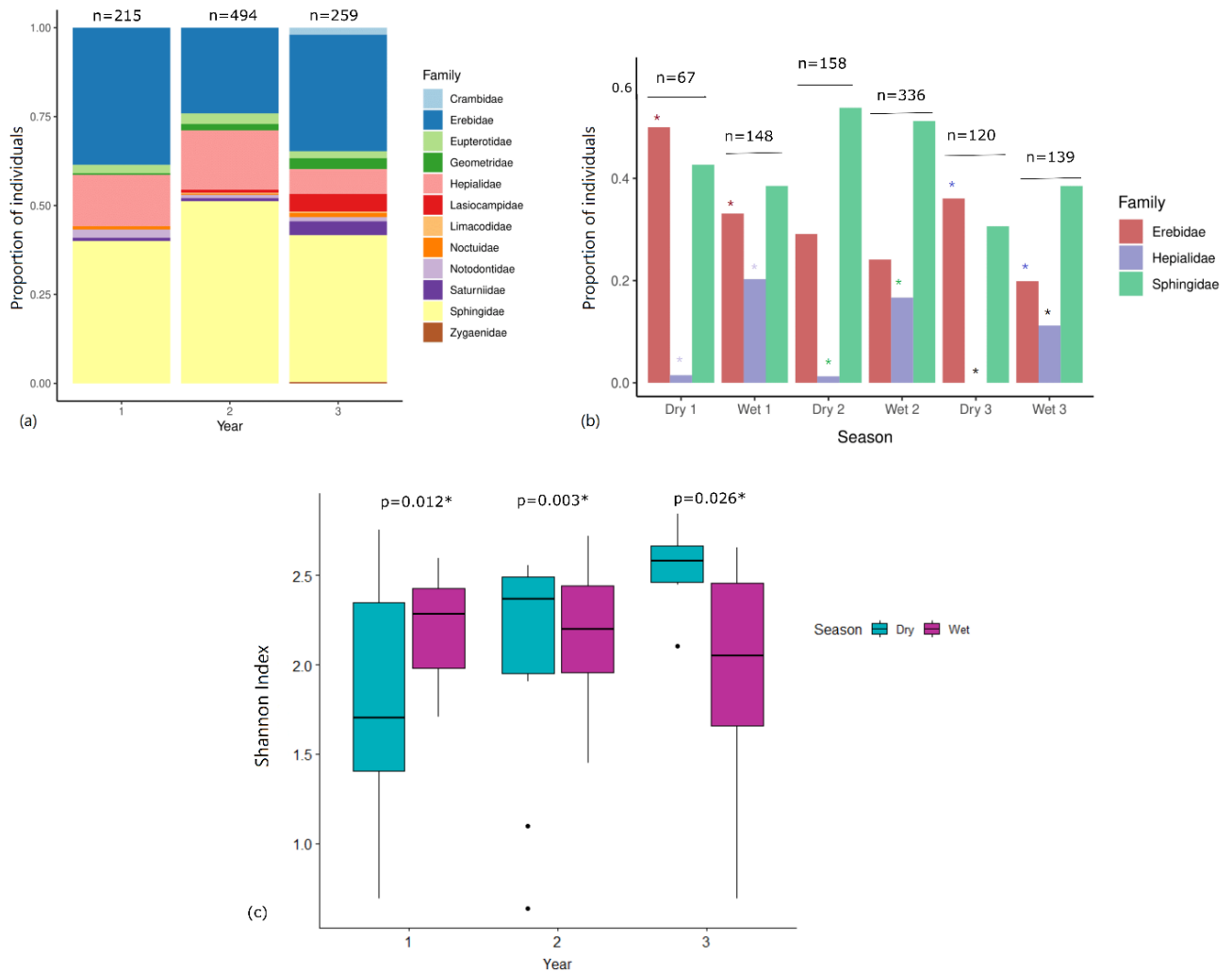


219
220 Figure 3: The graph shows an abundance-based rarefied and extrapolated species accumulation curve
221 for the light trapping of moth species in the study area.

222
223 *Lepidoptera families consumed by M. spasma*

224 Proportions of different families in the diet from the culled remains
225 In all the years, individuals of the family Sphingidae were found in proportionately higher numbers in
226 the culled remains, followed by Erebidae, then Hepialidae (Fig. 4a). Geometridae species were found
227 the least in Year 1; Limacodidae and Noctuidae in Year 2 and; Limacodidae and Zygaenidae in the
228 last year.

229 The proportions of the most abundant families in the diet (Sphingidae, Erebidae and Hepialidae) in
230 the diet varied significantly across dry and wet seasons in the sampling years. Erebids were eaten more
231 in the dry season, in Year 1 and 2 and Hepialids were significantly eaten more in the wet season in all
232 the years. Sphingids were found comparably in the diet throughout the seasons across years (Fig. 4b).
233 We observed a significant difference in the overall diversity of moth species in the culled remains
234 between the seasons each year (Fig. 4c).



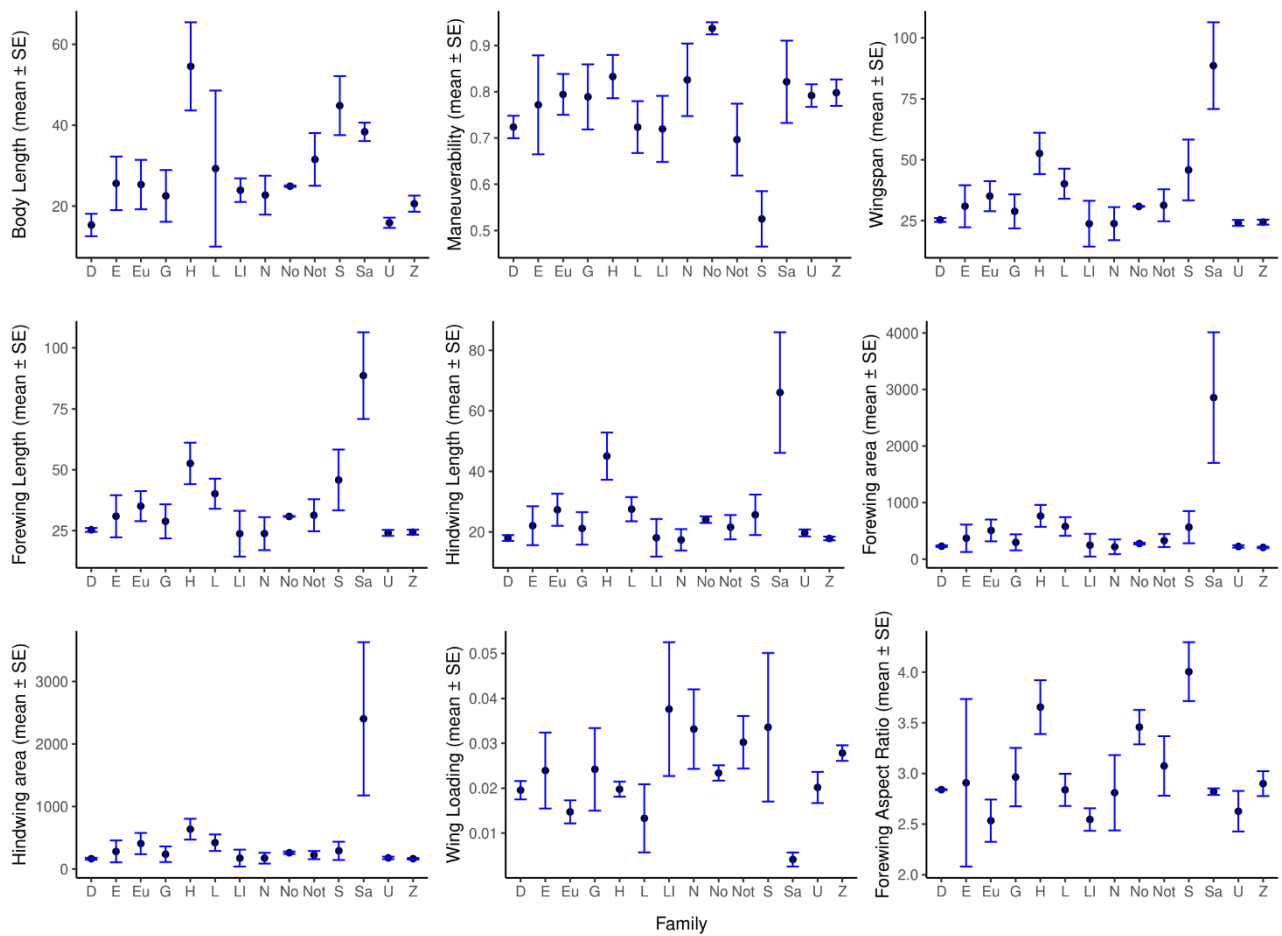
235

236 Figure 4: The proportion of individuals belonging to (a) different families of moths found in the culled
 237 remains across the years (b) Erebiidae, HEPIALIDAE, and SPHINGIDAE families across seasons each year
 238 (* of similar colour denotes significant difference), (c) The diversity (Shannon Index) of moths found
 239 in the culled remains across the years in the Dry and Wet season (the plots show significant differences
 240 with Wilcoxon signed rank exact test)

241

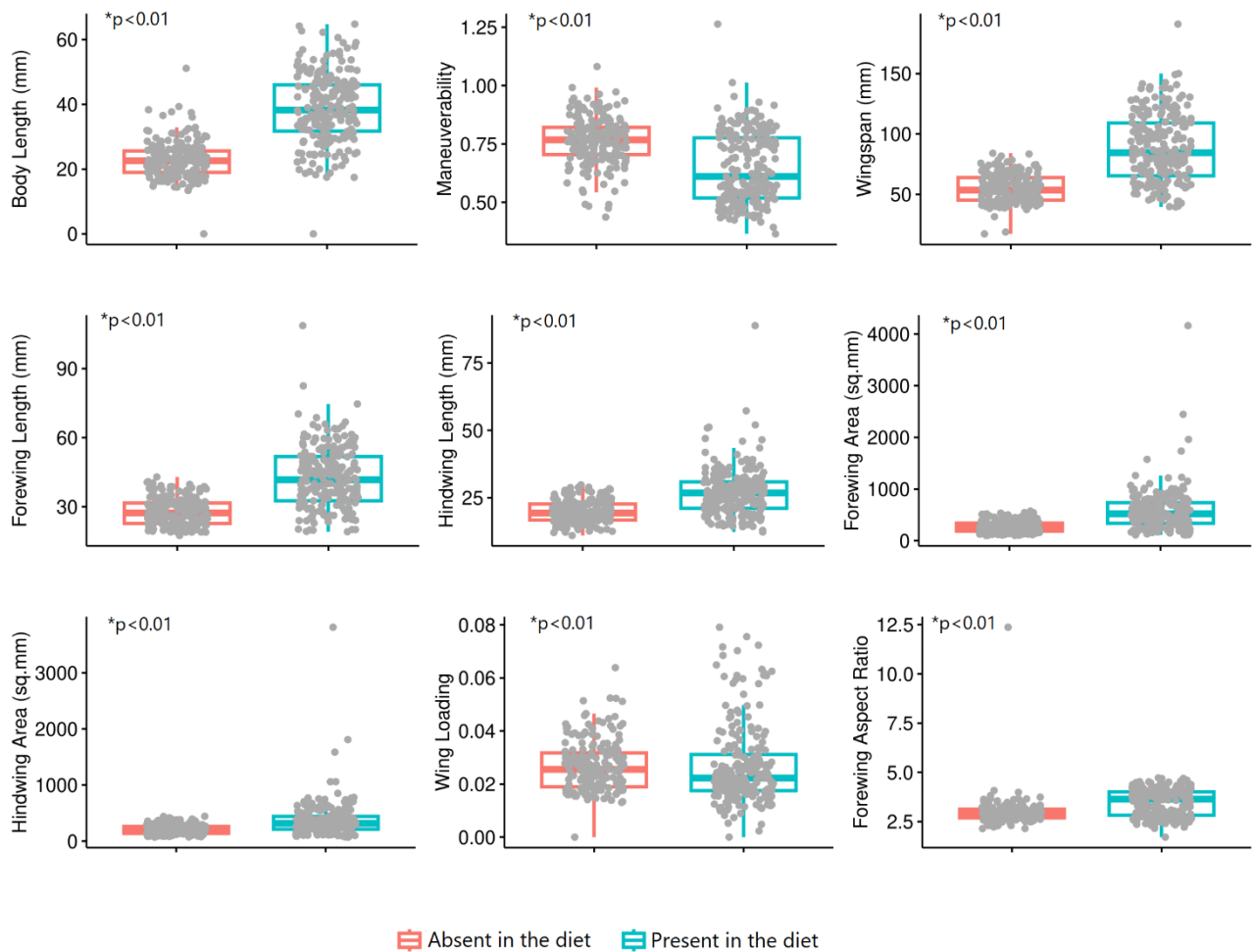
242 Species belonging to the Saturniidae family had the largest wingspan (159.55 ± 16.13 mm), forewing
 243 area (2856.45 ± 667.8 mm²), hindwing area (2402.40 ± 707.7 sq. mm), forewing length (88.60 ± 10.27
 244 mm), and hindwing length (66.02 ± 11.49 mm). HEPIALID moths showed the highest body length
 245 (54.55 ± 5.45 mm), Limacodids the highest Wing Loading (0.037 ± 0.007), and SPHINGIDAE moths

246 showed the highest Forewing Aspect Ratio (4.00 ± 0.02) and the lowest Maneuverability (0.52 ± 0.005)
 247 (Fig. 5).



248
 249 Figure 5. The 9 morphological trait values (in mm) (mean \pm SE) measured across the families
 250 (wingspan >40mm) that were found in the diet. (D=Drepanidae, n=2; E=Erebidae, n=159;
 251 Eu=Eupterotidae, n=21; G=Geometridae, n=52; H=Hepialidae, n=4; L=Lasiocampidae, n=4;
 252 Li=Limacodidae, n=4; N=Noctuidae, n=12; No=Nolidae, n=2; Not=Notodontidae, n=22;
 253 S=Spingidae, n=124; Sa=Saturniidae, n=3; U=Uraniidae, n=3; Z=Zygaenidae, n=5).
 254
 255 These traits were compared among the species present and absent in the diet (above ~40 mm wingspan)
 256 from all the families. The species present in the diet were significantly larger, with higher Body
 257 Length, and other correlated traits like Wingspan, Forewing Area, Hindwing Area, Forewing Length
 258 and Hindwing length (Wilcoxon Rank sum test with continuity correction, $p < 0.01$, for each of the

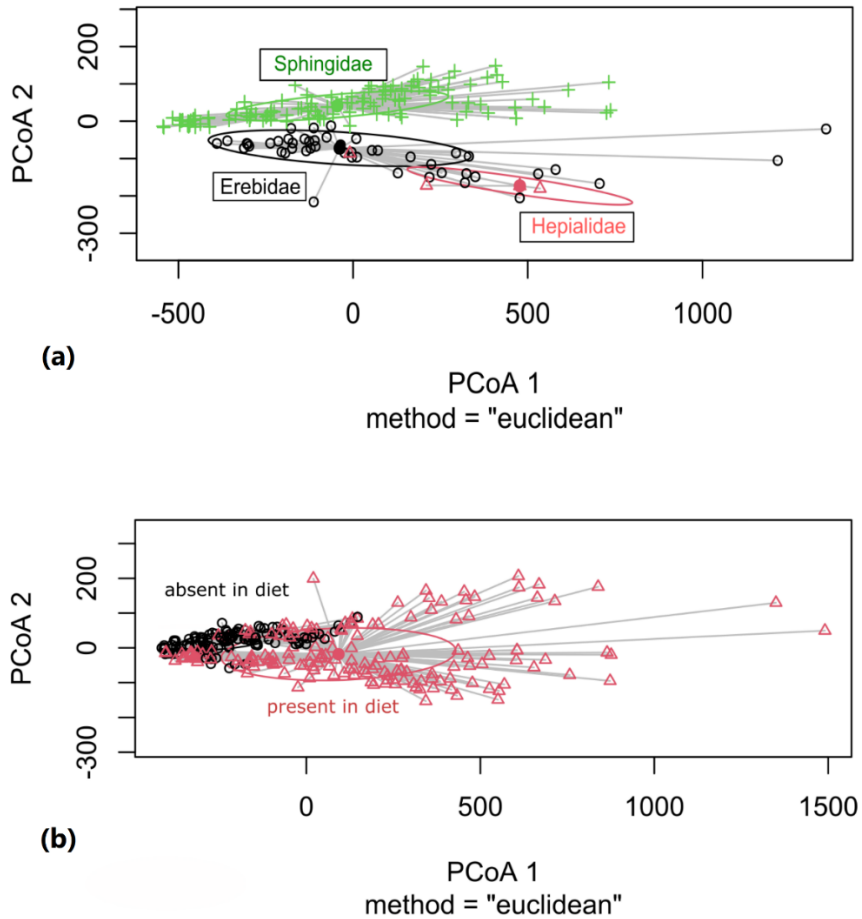
259 traits). They also had higher Forewing Aspect Ratio ($p < 0.01$), lower Wing Loading ($p < 0.01$) and lower
260 Maneuvrability ($p < 0.01$) (Fig. 6).



261
262 Figure 6. Comparison of the 9 morphological traits measured and pooled among the species that were
263 present or absent in the diet of *M. spasma* (all the plots show significant differences with Wilcoxon
264 Rank sum test).

265
266 There was a significant difference in the trait-space distances among the most abundant taxonomic
267 groups found in the diet, i.e. Sphingidae, Erebidae and Hepialidae (PERMANOVA, $df=1$, $R^2=0.168$,
268 $P < 0.01$) (Fig. 7a). Also, beta dispersion showed that the group dispersion, or variance, is significantly
269 different from each other ($p < 0.01$). When we looked into the traits of the species present or absent in
270 the diet from these three taxonomic groups, we observed a significant difference in the trait-space

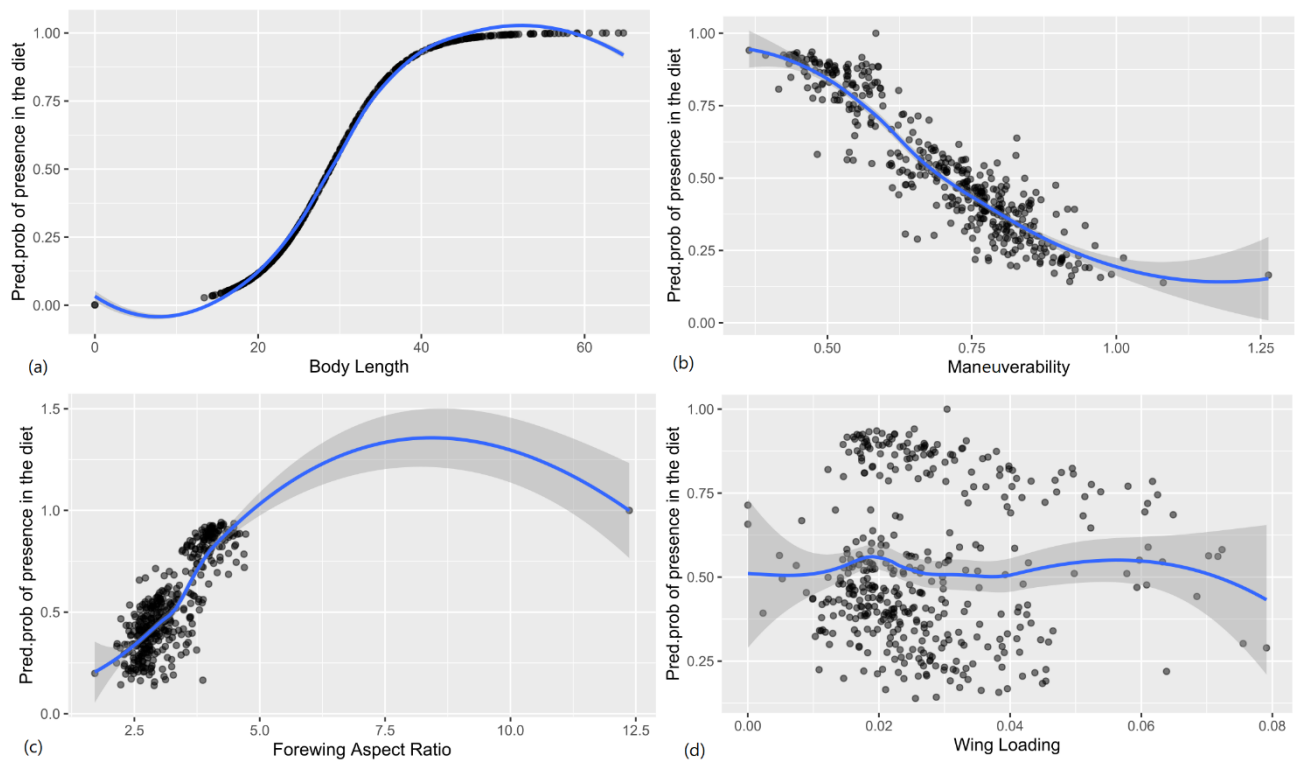
271 distances (PERMANOVA, $df=1$, $R^2=0.274$, $P<0.01$) (Fig. 7b) and the variance is significantly low
272 ($p=0.001$) in the 'absent' group suggesting there is a specific range of traits that the bat is avoiding.



273
274 Figure 7. The Principal Coordinates Axes comparing the dispersion of traits a) the three most abundant
275 families present in the diet (Erebidae, Sphingidae, and Hepialidae) and b) among species present and
276 absent in the diet from these three subfamilies.

277
278 Body length ($p<0.01$, McFadden's Pseudo R-square=0.45, Maneuverability ($p<0.01$, Mc Fadden's
279 Pseudo R-square=0.132), and Forewing Aspect Ratio ($p<0.001$, McFadden's Pseudo R-square=
280 $3.463261e-07$), were found to be significant with Diet (present/absent) as a response variable in a
281 Logistic regression model (model parameters in Supporting information Table 3). Predicted values
282 from the Logistic Regression model showed that the higher the body size, Forewing Aspect Ratio, and
283 lower the Maneuverability, there is increased probability of being present in the diet, wherein body

284 size and maneuverability have the best fit (Fig. 8 a,b,c). Wing loading did not show any significant
285 effect on the species being present or absent in the diet (Fig. 8d).



286
287 Figure 8: The logistic regression model plots show the predicted probabilities (with 95% CI) of the
288 species to be present or absent in diet, with changing (a) Body Length, (b) Maneuverability, (c)
289 Forewing Aspect Ratio, and (d) wing loading.

290

291 Discussion

292 Our results show a seasonal variation in the overall moth species diversity in the diet of *M. spasma*,
293 with Hepialid moths being preyed upon significantly more in the wet season in all the years. Our results
294 also support the hypothesis that larger moths with weaker evasive capabilities are more vulnerable to
295 predation by a sympatric bat predator. The study thus establishes a foundation for trait-based
296 elucidation of the vulnerability of paleotropical moth communities to insectivorous bats.

297 *Seasonal variation in bat diet*

298 Seasonal variation in diet is governed by food availability and how bats adapt to these changes (Bhartiy
299 & Elangovan, 2021; Catto et al., 1995; Shiel et al., 1991) among others). Though Erebidae and

300 Sphingidae were the most abundant moth families found overall in culled remains, we found seasonal
301 variation in the composition of the diet of *M. spasma* across the years. This variation can be attributed
302 to the availability of the moths of the family Hepialidae in the months of May and June every year
303 (during the wet season) and also that they have the largest body size in our dataset. These moths emerge
304 around the summer solstice and are known to be crepuscular or nocturnal (Andersson et al., 1998).
305 Males are known to show lekking behaviour at dusk (for around 30 min) to avoid bird predators and
306 late-emerging insectivorous bat species (Andersson et al., 1998; Rydell, 1998). Lekking behaviour in
307 ‘acoustic’ moths is associated with reduced predation risk and increased mating success (Rydell, 1998),
308 but the Hepialid moths are a primitive group of non-tympanate moths and do not produce ultrasound,
309 mimetic coloration, or flight maneuvers to combat bat predation (Scoble, 1992), which places them at
310 high risk of bat predation (Rydell, 1998). *M. spasma* is known to emerge at dusk, shortly after sunset
311 (Balete, 2010; Prakash et al., 2021) and presumably hunts Hepialid moths due to their body size, and
312 high detection during the months that they emerge, probably because of the male lekking behaviour.
313 Amidst the global pandemic, due to a state-wide lockdown in the state of Karnataka, India, fieldwork
314 could not be done in May and June 2021; hence we do not have light-trapping data from those months
315 to account for the presence of these moths in the foraging area.

316 *Prey traits influencing vulnerability to predation*

317 Insectivorous bats are known to detect and hunt prey in flight in a matter of seconds, during which the
318 energy profit (Koselj et al., 2011), flight pattern, and ease of capture (Barclay & Brigham, 1994) of
319 the prey would be prioritized over taxonomic predisposition (Arrizabalaga-Escudero et al., 2019).
320 Although there was a shift in the local moth assemblage seasonally, our results show that prey body
321 size is an important criterion for prey selection by *M. spasma*.

322 We did not find any Arctiinae moth body parts in the culled remains. These moths, commonly known
323 as Tiger moths or Lichen moths are known to employ aposematic colouration and acoustic defence
324 (warning, mimicry, or sonar-jamming) against bats (Miller & Surlykke, 2001; Ratcliffe et al., 2011;
325 Ratcliffe & Fullard, 2005). Noctuid moths, also known for their anti-predatory flight maneuvers

326 against bats (Roeder, 1962, 1964, 1967; Surlykke et al., 1999; ter Hofstede et al., 2013), scored pretty
327 high on the maneuverability index (Fig. 4) and were less represented in the culled remains. Both these
328 groups have >40mm wingspan and were abundant in our light traps.

329 Interestingly, moths of the Sphingidae family (commonly called hawkmoths) were recorded the most
330 in the culled remains of *M. spasma*. Sphingid moths are known to have agile and maneuvering flight
331 performance among flying insects (Greeter & Hedrick, 2016), with an increased ability to change the
332 speed and direction of movement (Dudley, 2002). Such maneuverability may be beneficial for mate
333 choice (Thornhill & Alcock, 2013) and defence. They show rapid turning-away flight when ‘visually’
334 startled to avoid ambush predators during flower visitation (Cheng et al., 2011; Wasserthal, 1993), but
335 are not able to initiate escape flight as quickly as other ‘eared’ moths (that can detect bat echolocation),
336 in response to bat echolocation calls (Morrill & Fullard, 1992). Here, using a morphological trait-based
337 framework, we indeed find that Sphingids have the lowest hindwing-to-forewing area ratio, and highest
338 forewing aspect ratio, which probably leads to less effective maneuvers against echolocating bats
339 (correlation of form to function still needs detailed behavioural studies), and higher vulnerability to
340 predation.

341 Also, certain species of hawkmoths (in two distantly related subtribes, the Choerocampina and the
342 Acherontiina, (Göpfert et al., 2002) have non-tympanal hearing organs in the mouthparts that are
343 capable of receiving ultrasound, but these groups were quite abundant in the culled remains in our
344 results. Possibly, 1) Flying hawkmoths are detected by *M. spasma* from a longer distance due to their
345 size (Surlykke et al., 1999), and audible wing beats (Baete, 2010), and 2) Hawkmoth ‘ears’ while
346 flying or perching, are not able to detect the soft ‘low intensity’ echolocation calls of *M. spasma*
347 (Fenton & Bell, 1981; Schmidt et al., 2000). Therefore, they are too late at initiating an escape flight.

348 Moths of the Erebidae family represented the second most abundant group in the diet of *M. spasma*.
349 We found species from the genera *Erebus*, *Eudocima*, *Artena*, most commonly in the diet, which are
350 the larger moths in the family, and possibly capable of anti-bat acoustic defence (Barber et al., 2022).
351 Moths from the genus *Erebus* are not effectively attracted to light (Holloway, 2005) and hence were

352 not attracted to our light traps, except in the months of August and September, (with few individuals)
353 while moths of the genus *Artena* were quite abundant in our light traps. *Eudocima* moths are fruit-
354 piercing moths and are generally found sucking on ripened citrus and other fruit crops (Reddy et al.,
355 2007) during the evening, and could be easy targets for substrate-gleaning by bats. The study area is a
356 human-dominated landscape with ample guava, cashewnut, *Areca*, and other fruiting trees, which are
357 common hosts of the fruit piercers. The high occurrence of these groups in the culled remains could
358 be due to their abundance in the foraging range of the bats and easy detectability by *M. spasma* (large
359 size with audible wingbeats, (Balete, 2010). Not much has been established in the literature to clarify
360 the acoustic or behavioural defences against bats for these groups of moths.

361 *Prey selection by the bat predator*

362 Our study showed some degree of selective hunting of moth species, previously unknown for a
363 megadermatid bat, which is not a moth specialist. *M. spasma* and related bats with similar foraging
364 strategies rely more on prey-generated sound for prey detection at long range (Balete, 2010; Denzinger
365 & Schnitzler, 2013; Raghuram et al., 2015; Schnitzler et al., 2003), but can also hunt through
366 echolocation similar to its closest relative *Lyroderma lyra* (Marimuthu et al., 1995; Ratcliffe et al.,
367 2005; Schmidt et al., 2000). Given the broad range in diet (Raghuram et al., 2015), this bat most likely
368 adopts a flexible strategy of hawking and gleaning (Gordon et al., 2019). In our study, it was, however,
369 not possible to establish if the moths found in the diet were gleaned from a surface or caught in the air.
370 Even though the diet might be largely conserved in sympatric predators, each species might segregate
371 temporally, spatially, or through different hunting strategies (Divoll et al., 2022). How is the trophic
372 niche of moths shaped in this landscape, in adaptation to the range of hunting strategies of different
373 species of their most formidable predator? Following (Arrizabalaga-Escudero et al., 2019); using both
374 prey and predator traits, we aim in future studies to generate a deeper understanding of prey selection
375 in this biodiverse landscape. In the face of the alarming decline of insect populations (Wagner et al.,
376 2021), we could potentially identify predators that are affected by the loss of key prey traits when there
377 is a decline in prey populations.

378

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Supplementary material

Table 1: The bat roosts sampled across the years

#	Name of roost	Year 1	Year 2	Year 3
1	Abbenjal	✓		
2	Anni temple_keravashe		✓	✓
3	Aravind_joshi	✓		
4	Babu Nalluru	✓	✓	
5	Babu Poojari Miyar	✓	✓	✓
6	Bogu Shetty_Panjala Kare			✓
7	Cement_Shed_house_kadari		✓	✓
8	Chowki	✓		
9	Field_station_Kadari		✓	✓
10	Forest_house Keravashe	✓	✓	✓
11	Ganesh_Poojari_Kera		✓	✓
12	Garadi house_Keravashe		✓	✓
13	Gopala Mullur		✓	
14	Hermunde_house	✓		
15	Hukkuratte house	✓		
16	Karate Manjalthur	✓	✓	✓
17	Kittamulya Mullur		✓	
18	Kittu house Keravashe	✓	✓	✓
19	Leela House	✓		
20	Madhava_Prabhu	✓		
21	Madhusudan Joshi			✓
22	Malayalee_house_Heppejar		✓	✓
23	Malayalee house_Pajinadka	✓	✓	✓
24	Manjalnath	✓		
25	Nagesh_temple	✓	✓	
26	Nayak Temple	✓		
27	Nellikatte_house	✓		
28	Peradka_house	✓	✓	✓
29	Prashanth_Pejattaguri		✓	
30	Praveen_house	✓		
31	Praveen new roost Hukkurate			✓
32	Sadashivnayak pajinadka		✓	✓
33	Sanjeeva Hekunje		✓	
34	Sarojini Peradka		✓	✓
35	Satish House Panjala Kare			✓
36	Satish house Yedapadi	✓		
37	Satish Mala		✓	
38	Shailesh Temple Nallur	✓	✓	✓
39	Udaya Bhat_koodabetta		✓	✓
40	Vishwanath Padella			✓
41	Wilfred_Kera		✓	



Figure 1: Spatial roost locations for culled remains collection in the study area. The numbers correspond to the roost numbers in the Table 1.

Table 2: Details of the light traps

Sites	Total no. of nights sampled (sampling months)	Plots	Plot type	Total no. of species recorded
Field station	14 (Jan-April; Aug-Oct)	P1	Forest	94
		P2	Plantation	
		P3	Forest	
		P4	Forest	
Peradka	14 (Jan-April; Aug-Oct)	P1	Forest	111
		P2	Forest	
		P3	Forest	
		P4	Forest	
Pajinadka	14 (Jan-April; Aug-Oct)	P1	Forest	85
		P2	Plantation	
		P3	Forest	
		P4	Forest	
Koodabettu	14 (Jan-April; Aug-Oct)	P1	Plantation	94
		P2	Forest	
		P3	Forest	
		P4	Forest	
Heppejar	14 (Jan-April; Aug-Oct)	P1	Plantation	100
		P2	Forest	
		P3	Forest	
		P4	Forest	

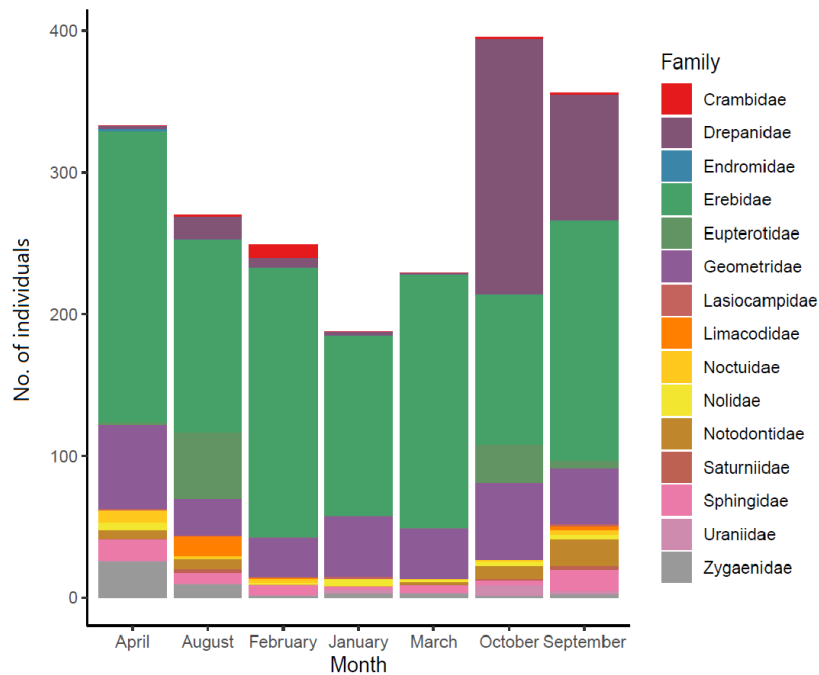


Figure 2: The number of individuals from each family (>40mm wingspan) counted at the light traps across 7 months in 2021.

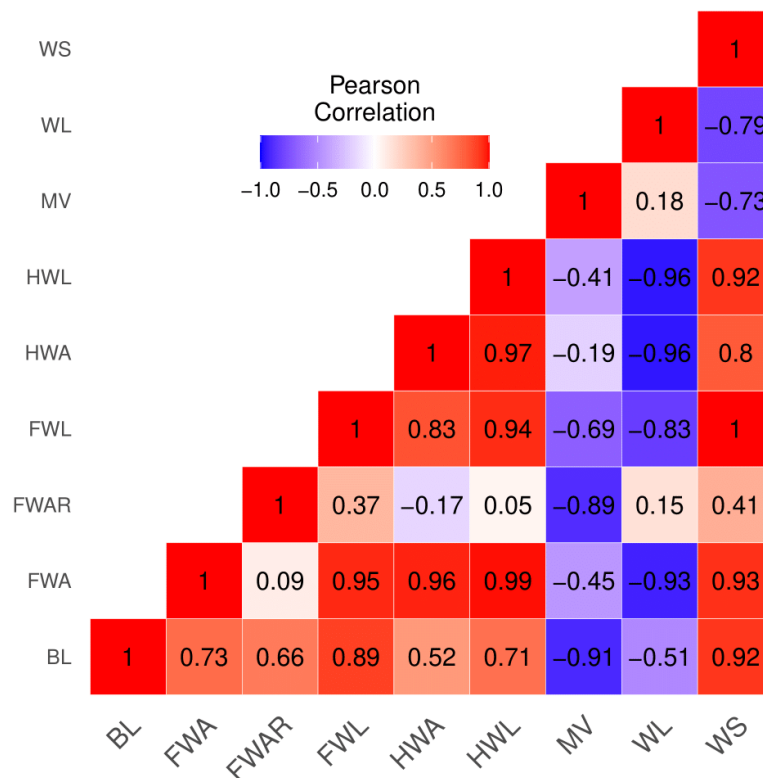


Figure 3: Correlation matrix for the morphological traits measured from the moth specimens (Forewing length (FWL); hindwing length (HWL); Body length (BL) (a proxy for body size); Wingspan; Forewing area (FWA); Hindwing area (HWA); Maneuverability= HWA/FWA ; Wingloading= $BL/2(FWA+HWA)$ and Forewing aspect ratio = $(2*FWL)/FWA$ (as a proxy for wing shape)

Table 3: Model parameters for the Logistic Regression models (binomial function) for each of the traits

Trait	Model	Estimate	std. error	Z-value	p-value
Body Length	glm(formula = Diet ~ BL, family = binomial, data = Trait_family)	0.2309	0.0221	10.44	0.001
Hindwing Area/Forewing Area=Maneuverability	glm(formula = Diet ~ MV, family = binomial, data = Trait_family)	-6.7912	0.8689	-7.816	0.001
(2*Forewing Length)/Forewing Area =Forewing Aspect Ratio	glm(formula = Diet ~ FWAR, family = binomial, data = Trait_family)	1.3809	0.1924	7.179	0.001
Body Length/2(Forewing Area+Hindwing Area)=Wing Loading	glm(formula = Diet ~ WL, family = binomial, data = Trait_family)	0.11	7.7737	0.014	0.98