

1 **RUNNING HEADER:** *Seasonal morphology in Malagasy bats*

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3 **TITLE:** Reproduction, seasonal morphology, and juvenile growth in three Malagasy fruit bats

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36 The island nation of Madagascar is home to three endemic species of Old World Fruit Bat in the
37 family Pteropodidae: *Pteropus rufus*, *Eidolon dupreanum*, and *Rousettus madagascariensis*, all
38 three of which are IUCN Red Listed under some category of threat. To inform conservation efforts
39 to model population viability for these threatened species, as well understand the mechanisms
40 underpinning persistence of several potentially zoonotic pathogens hosted by these bats, we here
41 define the seasonal limits of a staggered annual birth pulse across the three species. Our field
42 studies in central-eastern Madagascar indicate that this annual birth pulse takes place in
43 September/October for *P. rufus*, November for *E. dupreanum*, and December for *R.*
44 *madagascariensis*. Juvenile development periods vary across the three Malagasy pteropodids,
45 resulting in near-synchronous weaning of pups for all species in late January-February at the height
46 of the fruiting season for Madagascar, a pattern characteristic of most mammalian frugivores on

47 the island. We here document the size range in morphological traits for the three Malagasy fruit
48 bat species; these traits span the range of those known for pteropodids more broadly, with *P. rufus*
49 and *E. dupreanum* among the larger of recorded species and *R. madagascariensis* among the
50 smaller. All three species demonstrate subtle sexual dimorphism in observed traits with larger-
51 bodied males vs. females. We explore seasonal variation in adult body condition by comparing
52 observed body mass with body mass predicted by forearm length, demonstrating that pregnant
53 females add weight during staggered gestation periods and males lose weight during the
54 nutritionally-deficit Malagasy winter. Finally, we quantify forearm, tibia, and ear length growth
55 rates in juvenile bats, demonstrating both faster growth and more protracted development times
56 for the largest *P. rufus* species. The longer development period for the already-threatened *P. rufus*
57 further jeopardizes this species' conservation status as human hunting of bats for subsistence is
58 particularly detrimental to population viability during reproductive periods. The more extreme
59 seasonal variation in the mass to forearm relationship for *P. rufus* may also modulate immune
60 function, an important consideration given these bats' roles as reservoir hosts for several high
61 profile viral families known to cause severe disease in humans. Our work highlights the importance
62 of longitudinal field studies in collecting critical data for mammalian conservation efforts and
63 human public health alike.

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93 The Old World Fruit Bat family Pteropodidae, known colloquially as the ‘flying foxes,’
94 makes up one of the most endangered groups of mammals on Earth, with some 35% of species
95 either extinct or threatened with extinction, a proportion almost three times higher than that
96 reported (12%) for all other bat families combined (Species IUCN Red List Threat. 2018). Fruit
97 bats experience disproportionate rates of persecution, likely as a result of their propensity for small
98 island endemism (Jones et al. 2009) and their large sizes (fruit bat wingspans can reach up to two
99 meters in the case of *Pteropus vampyrus*, the world’s largest bat; Corbet and Hill 1992), which
100 make them targets for the bushmeat trade (Craig et al. 1994; Brooke 2002; Oleksy et al. 2003;
101 Jenkins and Racey 2008; Kamins et al. 2011; Openshaw et al. 2016; Peel et al. 2017). Pteropodid
102 bats offer critical services to surrounding ecosystems, playing important roles in the pollination
103 and seed dispersal of numerous plant species across the Old World, particularly in island
104 ecosystems often depauperate in other frugivores (McConkey and Drake 2006; Kunz et al. 2011).

105 Madagascar is one such island ecosystem recognized for its unusually depauperate
106 frugivorous fauna (Dewar and Richard 2007). Primates (lemurs), rather than birds, are considered
107 the primary seed dispersers on the island (Langrand 1990; Wright et al. 2011), in contrast to
108 otherwise comparable tropical ecosystems in the New World (Terborgh 1983, 1986). In addition
109 to lemurs, Madagascar is home to three endemic species of frugivorous bats from the family
110 Pteropodidae—*Pteropus rufus*, *Eidolon dupreanum*, and *Rousettus madagascariensis*—all of
111 which are known to pollinate flowers and disperse seeds from both native Malagasy and exotic
112 plants (Bollen and Elsacker 2002; Andriafidison et al. 2006; Long and Racey 2007; Picot et al.
113 2007; Andrianaivoarivelo et al. 2011; Oleksy et al. 2015, 2017). Importantly, *E. dupreanum* may
114 be the only extant pollinator of the endangered, endemic Malagasy baobab, *Adansonia suarezensis*
115 (Andriafidison et al. 2006).

116 Despite their ecosystem value, Madagascar’s fruit bats are heavily persecuted. All three
117 species are consumed across the island as a source of human food (Oleksy et al. 2003; Jenkins and
118 Racey 2008; Cardiff et al. 2009; Randrianandrianina et al. 2010; Golden et al. 2014; Fernández-
119 Llamazares et al. 2018; Brook et al. 2019a), and *P. rufus*, the largest and most heavily hunted, is
120 sometimes targeted in response to its largely inaccurate characterization as a predator of human
121 fruit crops (Raharimihaja et al. 2016). Respectively, *P. rufus*, *E. dupreanum*, and *R.*
122 *madagascariensis* are currently IUCN Red-listed as ‘Vulnerable,’ ‘Vulnerable,’ and ‘Near-
123 Threatened’ species (Species IUCN Red List Threat. 2018), though recent population viability
124 analyses suggest that *P. rufus*, in particular, may be experiencing more severe population declines
125 than have been previously reported (Brook et al. 2019a). Bats are reservoir hosts for a majority of
126 the world’s most virulent zoonotic viruses (Guth et al. 2019, 2021), as well as hosts for
127 coronaviruses ancestral to the recently emerged SARS-CoV-2 (Zhou et al. 2020; Temmam et al.
128 2021). Globally, anti-bat sentiments have been on the rise as a result of the COVID-19 pandemic
129 (Rocha et al. 2020); though no specific instances of COVID-related persecution have yet been
130 documented for the Malagasy fruit bats, all three species are known to host potentially zoonotic
131 pathogens (Iehlé et al. 2007; Razafindratsimandresy et al. 2009; Reynes et al. 2011a; Wilkinson et
132 al. 2012a; Brook et al. 2015, 2019b; Razanajatovo et al. 2015; Ranaivoson et al. 2019), posing
133 risks that negative public reactions may arise in the future.

134 Previous work suggests that roost population sizes and survival rates vary across the year
135 for these three species (Brook et al. 2019a; Noroalintseheno Lalarivoniaina et al. 2019). Temporal
136 fluctuations in nutritional status may alter bat immune responses, thus influencing pathogen
137 dynamics (Brook et al. 2019b), as well as modulate bats’ vulnerability to seasonally variable
138 hunting pressures (Brook et al. 2019a). All three Malagasy fruit bats are thought to reproduce

139 seasonally in species-specific annual birth pulses (MacKinnon et al. 2003; Brook et al. 2019a).
140 Documentation of the timing of these birth pulses for Malagasy fruit bats is important for
141 understanding their vulnerability to seasonally-varying population pressures: previous work
142 describes how seasonal variation in hunting pressure for Malagasy lemurs poses elevated risks to
143 species when directly overlapping their annual birth pulse (Brook et al. 2018).

144 In addition to its importance for conservation efforts to quantify fruit bat population
145 viability, defining the temporal limits of each fruit bat species-specific birth pulse is essential to
146 understanding the mechanisms which underpin the maintenance and persistence of numerous
147 infectious agents that these bats host (Iehlé et al. 2007; Razafindratsimandresy et al. 2009; Reynes
148 et al. 2011b; Wilkinson et al. 2012b; Brook et al. 2015, 2019b; Ranaivoson et al. 2019). Isolated
149 *E. helvum* populations on islands off the west coast of Africa have been shown to support
150 circulation of potentially zoonotic henipaviruses at population sizes well below the established
151 critical community size for closely-related paramyxoviruses in other systems (Bartlett 1957, 1960;
152 Swinton et al. 1998; Peel et al. 2012). Some work has suggested that seasonally-staggered births
153 allowing for a protracted introduction of juvenile susceptibles into the host population could play
154 a role in pathogen persistence in these systems (Peel et al. 2013, 2014; Hayman 2015).

155 We sought to expand existing knowledge of seasonal variation in the reproductive calendar
156 and nutritional status of all three Malagasy fruit bat species, to facilitate future conservation
157 assessments and studies aimed at deciphering the dynamics of bat-hosted infections. In particular,
158 we aimed to (a) quantify life history traits needed for population modeling for these species, (b)
159 document seasonal variation in morphometrics and body conditions for these bats, and (c) calculate
160 juvenile growth rates throughout the post-reproductive period. Our work emphasizes the
161 importance of longitudinal field studies in accurately describing the ecology of frugivorous bats.

162 MATERIALS AND METHODS

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165 *Study periods and sites*—Field studies were carried out between 2013 and 2020 in part
166 with previously published work examining population viability and the dynamics of potentially
167 zoonotic infections in Malagasy fruit bats (Brook et al. 2015, 2019b; a; Ranaivoson et al. 2019).
168 Bats were captured periodically throughout each year, with sampling spanning all months and all
169 seasons (dry, wet, shoulder), interspersed with some gaps in temporal continuity. Captures took
170 place in several regions of Madagascar: (1) Ankarana National Park in the northwest (-12.9S,
171 49.1E), (2) Makira Natural Park in the northeast (-15.1S, 49.6E), (3) Mahabo forest in the center-
172 west (-20.5S, 44.7E), and (4) several sub-localities of the Moramanga District in the center-east,
173 including: the fragmented forests of Ambakoana (-18.5, 48.2), Mangarivotra (-18.3S, 48.2E),
174 Marotsipohy (-18.4S, 48.1E), Marovitsika (-18.8S, 48.1E), Lakato (-19.2S, 48.4E), and
175 Mahialambo (-18.1S, 48.2E), the special reserves of Angavokely (-18.9S, 47.8E) and Angavobe
176 (-18.9S), 47.9E, and the new protected area of Maromizaha (-18.9S, 48.5E).

177 *Netting*—Mist nets were deployed from 6:00 p.m. to midnight and from 3:00 a.m. to 8:00
178 a.m. around roosting or feeding sites of *P. rufus*, *E. dupreanum* and *R. madagascariensis* and
179 monitored continuously. Captured bats were placed in individual clean cloth bags while awaiting
180 processing for infectious disease studies, as has been previously described (Brook et al. 2015,
181 2019b; Ranaivoson et al. 2019). For each sampling session, we conducted between 1 and 10 nights
182 of netting, ending sessions early when 30 individuals of each species present at the site were
183 captured. Upon capture, all bats were weighed (in grams) with a Pesola scale attached to the cloth
184 bag and forearm, tibia, and ear were measured with a caliper or tape measure (in mm). Bats were

185 classed by sex and age (juvenile vs. adult) and, for females, reproductive class (non-reproductive,
186 pregnant, lactating). For females captured approximately within the period of possible gestation
187 for each species, abdominal palpitation was used to determine whether or not females were
188 pregnant. All raw data used in this study are accessible in our open-access GitHub repository at:
189 github.com/brooklabteam/Mada-Bat-Morphology.

190 This study was carried out in strict accordance with research permits obtained from the
191 Madagascar Ministry of Forest and the Environment (permit numbers 251/13, 166/14, 075/15,
192 258/16, 170/18, 019/18, 170/18, 007/19, 14/20) and under guidelines posted by the American
193 Veterinary Medical Association. All field protocols employed were pre-approved by the Princeton
194 University and UC Berkeley Institutes for Animal Care and Use Committees (respectively, IACUC
195 Protocol #1926 and ACUC Protocol # AUP-2017-10-10393), and every effort was made to
196 minimize discomfort to animals.

197 *Literature review*—To place our Malagasy bats in a broader context, we compiled
198 information from the literature concerning the morphology of other bats in the family
199 Pteropodidae. From the ‘Bat Species of the World’ database (Simmons and Cirranello 2020), we
200 compiled a list of 201 previously described pteropodid species, then searched GoogleScholar and
201 Web of Science for any records documenting the mass, forearm, tibia, and ear length of each
202 species. We only collected records that were sex-specific, and where possible, we documented the
203 sample size from which those records were derived, if reported as an average. In cases where no
204 sample size was reported, we assumed sample size to be one individual. All raw data and references
205 are accessible in our open-access GitHub repository at: [github.com/brooklabteam/Mada-Bat-](https://github.com/brooklabteam/Mada-Bat-Morphology)
206 [Morphology](https://github.com/brooklabteam/Mada-Bat-Morphology).

207 *Statistical analysis*—Data analysis was performed using R v.4.0.3 (R Core Team, 2020).
208 All raw data and corresponding code for these analyses can be accessed in our GitHub repository.
209 Additional details of statistical output are compiled in supplementary tables in Appendix 2.

210 First, we aimed to define the seasonal limits of the reproductive calendar for each of the
211 three Malagasy fruit bat species. To this end, we restricted our analyses to our most complete
212 cross-species time series from roost sites in the District of Moramanga, Madagascar and queried
213 the data subset for the following metrics, unique for each species: (a) the earliest calendar day on
214 which a pregnant female was observed, (b) the earliest calendar day on which a juvenile was
215 observed, and (c) the latest calendar day on which a lactating female was observed. Metrics (a)
216 and (b) corresponded to the date limits of gestation for each species, while metrics (b) and (c)
217 corresponded to the date limits of lactation for each species. Because fruit bats of many species
218 are known to delay embryonic implantation and fetal development for months after fertilization
219 (Mutere 1967; Heideman 1988; Heideman and Powell 1998; Meenakumari and Krishna 2005), we
220 assumed that abdominal palpitation to determine reproductive status in the field would likely miss
221 early-stage pregnancies in the three Malagasy species. To this end, we additionally searched the
222 literature for records of gestation length in closely-related pteropodids to compare against our
223 records of observed gestation in Malagasy species.

224 We next sought to document morphological variation in adult *P. rufus*, *E. dupreanum*, and
225 *R. madagascariensis*, as compared with other bats in family Pteropodidae. To this end, we
226 calculated the sex-specific median and interquartile range of reported measurements of mean tibia
227 and ear length (in mm) for adult pteropodids globally, as well as the range of values recorded for
228 individuals within our dataset. To investigate any potential sexual dimorphism in our dataset, we
229 compared mean forearm, tibia, and ear length for male vs. female distributions across the global

230 dataset and the three Malagasy species using *Welch's 2-sample t-tests* for independent distributions
231 of unequal sample size.

232 We additionally compared the relationship between sex-specific forearm length and mass
233 for adult pteropodids surveyed in the literature against the ranges recorded in our own field data
234 for the three Malagasy species. We first fit a linear regression to \log_{10} -transformed values for both
235 forearm length (predictor variable) and mass (response variable), separated by sex, both to species-
236 level averages for pteropodids globally and to individual datapoints for adults of the three
237 Malagasy species.

238 Next, we explored seasonal variation in the relationship between adult body mass and
239 forearm length within our Malagasy fruit bat field data. To facilitate this analysis, we refit a
240 composite linear regression using \log_{10} -transformed values for forearm length as predictors of
241 \log_{10} -transformed values for mass. We included a fixed effect of bat species as an additional
242 predictor to control for differences in skeletal structure:mass ratios across the different species,
243 then calculated the residual of each individual's observed mass in the data against that predicted
244 from the regression. This generated a body condition index metric for bats: individuals with
245 positive mass:forearm residuals corresponded to those with higher masses than predicted by body
246 size (broadly indicative of better nutritional condition), while individuals with negative
247 mass:forearm residuals corresponded to those with lower masses than predicted by body size
248 (broadly indicative of poorer nutritional condition). Because all individuals included in these
249 analyses were adults, and previous work indicates that up to 96% of reproductively mature fruit
250 bats give birth annually (Hayman et al. 2012; Brook et al. 2019a), we assumed all females observed
251 during the defined gestation period for each species to be pregnant, regardless of reproductive class
252 recorded from abdominal palpitation.

253 To assess seasonal variation in body condition, we restricted our analysis to data collected
254 from the longitudinally-monitored Moramanga sites only, and fit a generalized additive model
255 (GAM), using the *mgcv* package in R (Wood 2001), to the seasonal time series of mass:forearm
256 residual, separately across each discrete species-sex subset of the data. We modeled mass:forearm
257 residual as the response variable predicted by day of year as a cyclic cubic ("cc") spline, with the
258 number of smoothing knots ("k") fixed at seven, as recommended by the package author (Wood
259 2001). Cyclic cubic splines can be used to capture annual seasonality, as the seasonal smoother on
260 January 1 is modeled as a continuation from December 31. Because some previous work has
261 questioned the effectiveness with which body condition indices represent bat nutritional status
262 (McGuire et al. 2018), we computed an additional set of supplementary GAMs which included the
263 predictor variables of day of year (as a cyclic cubic smoothing spline) and forearm length (as a
264 random effect) against the response variable of mass (in grams) for both sexes and all three species.

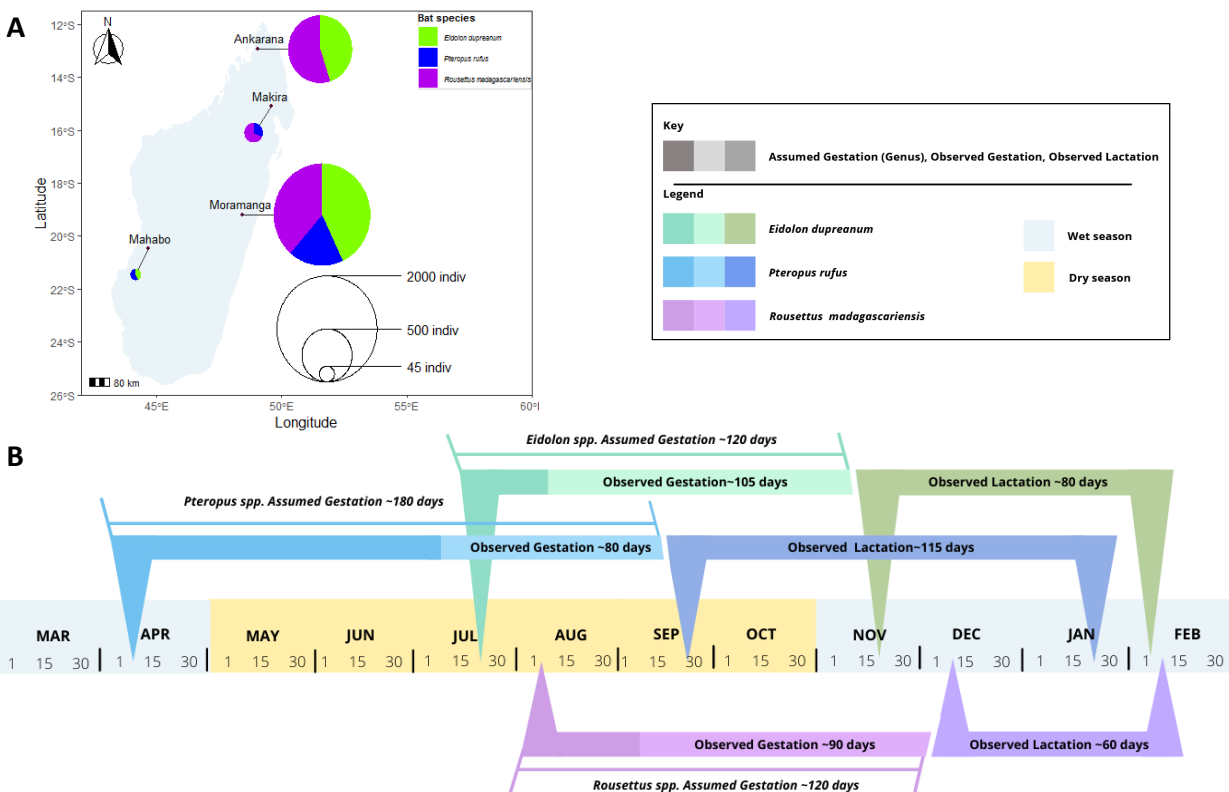
265 Finally, we explored juvenile growth rates for forearm, tibia and ear across all three
266 Malagasy fruit bat species, calculating the age in days since birth of each juvenile bat in our dataset
267 with "day 0" set equal to the first date of an observed juvenile in the dataset for each species, as
268 described above, up to one year of life (day 365). Using GAMs, we then modeled the response
269 variables of forearm length, tibia length, and ear length against the smoothing predictor of age in
270 days, using a thinplate smoothing spline ("tp") with the number of smoothing knots fixed again at
271 seven. After fitting each model, we then calculated the age-varying derivative of each fitted curve
272 using the 'gratia' package in R to facilitate comparison of growth rates across different species and
273 morphological features.

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RESULTS

Field captures— In total, 2160 fruit bats were captured and processed between August 2013 and March 2020 (**Fig. 1A**). The majority of bats ($n=1700$) were captured in roost sites located in the District of Moramanga in central-eastern Madagascar (*P. rufus* $n=316$; *E. dupreanum* $n=732$; *R. madagascariensis* $n=652$), followed by Ankarana National Park in the northwest ($n=380$; *E. dupreanum* $n=172$; *R. madagascariensis* $n=208$), Makira Natural Park in the northeast ($n=47$; *P. rufus* $n=15$; *R. madagascariensis* $n=32$), and Mahabo forest in the center-west ($n=33$; *P. rufus* $n=19$; *E. dupreanum* $n=14$) (**Table S1**).



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Fig. 1. B. Map of field sites and distribution of bat captures for *P. rufus*, *E. dupreanum*, and *R. madagascariensis* in Madagascar. Pie size corresponds to total bats captured at each site: 1700 in the District of Moramanga (*P. rufus* $n=317$; *E. dupreanum* $n=732$; *R. madagascariensis* $n=653$), 380 in Ankarana National Park (*E. dupreanum* $n=172$; *R. madagascariensis* $n=208$), 47 in Makira Natural Park (*P. rufus* $n=15$; *R. madagascariensis* $n=32$), and 33 in Mahabo forest (*P. rufus* $n=19$; *E. dupreanum* $n=14$). **B.** Gestation and lactation periods across the three Madagascar fruit bat species, calculated from the field data (observed) and reported in the literature (assumed). Respectively, for *P. rufus*, *E. dupreanum*, and *R. madagascariensis*, observed gestation begins on: July 7, August 3, and September 11; birth occurs on: September 29, November 16, and December 12; and lactation ceases on: January 21, February 2, and February 19 (**Table S1**).

Fruit bat reproductive calendars—Longitudinal data collected in the District of Moramanga allowed us to define the seasonal limits of a single annual reproduction event for all three fruit bat species (**Fig. 1B**). We calculated the earliest calendar day on which a pregnant female was observed, respectively, for *P. rufus*, *E. dupreanum*, and *R. madagascariensis*, as July

304 7, August 3, and September 11; the earliest calendar day on which a juvenile was observed as
305 September 29, November 16, and December 12; and the latest calendar day on which a lactating
306 female was observed as January 21, February 2, and February 19 (**Table S1**). These dates allowed
307 us to define the approximate duration of the observed gestation and lactation period for each
308 species (observed gestation: *P. rufus* = ~80 days, *E. dupreanum* = ~105 days, and *R.*
309 *madagascariensis* = ~90 days; observed lactation: *P. rufus* = ~115 days, *E. dupreanum* = ~80 days,
310 and *R. madagascariensis* = ~60 days). Because gestation was observed through abdominal
311 palpitation in the field, we presumed that early stage pregnancies for all three species might not be
312 visible. To account for this, we compared our observed gestation period for all three fruit bat
313 species against that which has been previously described for closely-related species: *Pteropus*
314 *alecto*, *Pteropus policephalus*, and *Pteropus scapulatus* (sister species to *P. rufus*) demonstrate a
315 ~180 day gestation period on the Australian continent (McIlwee and Martin 2002), while *Eidolon*
316 *helvum* (sister species to *E. dupreanum*) and *Rousettus aegyptiacus* (sister species to *R.*
317 *madagascariensis*) both demonstrate gestation periods of ~120 days on the African continent
318 (Odukoya et al. 2008; Barclay and Jacobs 2011). Extension of the gestation period for the three
319 Malagasy species back in time from the birth pulse to match those recorded for sister species
320 elsewhere would place the mating period for *P. rufus* in the month of April, for *E. dupreanum* in
321 the month of July, and for *R. madagascariensis* in the month of August. These estimates of mating
322 period are consistent with previous reporting for *P. rufus* (Long and Racey 2007) and *R.*
323 *madagascariensis* (Noroalintseho Lalarivoniaina et al. 2019); to our knowledge, no previous
324 records of the reproductive calendar for *E. dupreanum* have been published.

325 In sum, we observed the longest gestation and lactation period for *P. rufus*, which births
326 first of the three Malagasy fruit bat species, followed by *E. dupreanum*, and *R. madagascariensis*,
327 in order of decreasing body size. Despite differences in the timing and duration of gestation,
328 lactating mothers for all three species weaned pups around the same time of the year (~late January
329 – February), at the onset of peak fruit abundance in the hot-wet season in the District of
330 Moramanga.

331 *Morphological patterns*—After searching the literature, we successfully compiled adult
332 mass records from 103 pteropodid species for females and 106 species for males; adult forearm
333 records from 146 species for females and 140 species for males; adult tibia records from 64 species
334 for females and 64 species for males; and adult ear length records from 101 species for females
335 and 99 species for males. We compared these records against morphological patterns witnessed in
336 our own longitudinally-collected field data.

337 For Malagasy fruit bats, we observed large differences in adult morphology across species
338 and more subtle differences by sex. The Malagasy fruit bat species ranked in size, from largest to
339 smallest: *P. rufus*, *E. dupreanum*, and *R. madagascariensis*, with the size ranges of each species
340 roughly spanning the range in ear length, tibia length, and forearm length captured across mean
341 values for all non-Malagasy pteropodid bats surveyed in the literature (**Fig. 2A-C**). Specific
342 morphological ranges for tibia length and forearm length matched the size distributions of the three
343 Malagasy species, scaling downward from *P. rufus* to *E. dupreanum* to *R. madagascariensis*. For
344 ear lengths, *P. rufus* and *E. dupreanum* distributions were largely overlapping, while *R.*
345 *madagascariensis* were smaller; species-specific interquartile ranges for each morphological trait
346 are summarized in **Table S2**. Global data for comparison roughly approximated the range spanned
347 from the *R. madagascariensis* minimum to the *P. rufus* maximum, with the median falling in
348 between that of *R. madagascariensis* and *E. dupreanum* across all three metrics.

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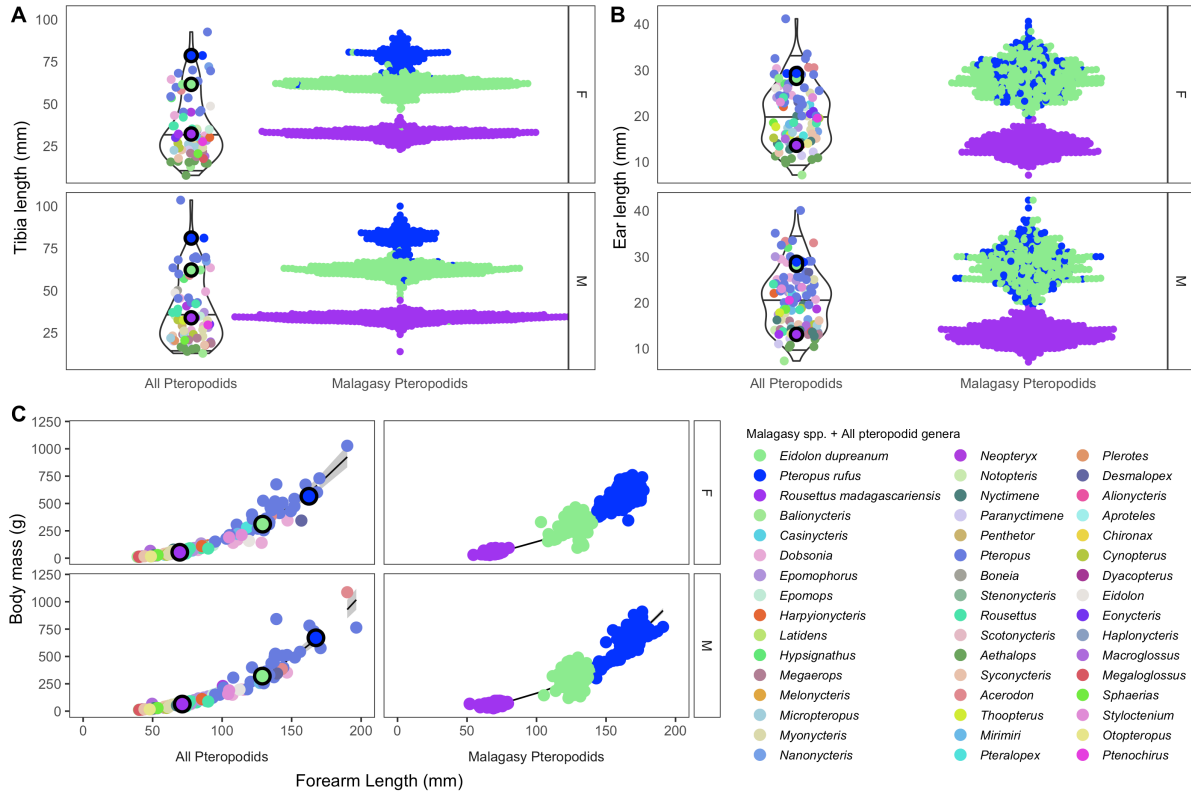


Fig. 2. A. Tibia, and **B.**, ear length across fruit bat species from the literature (left) and from our Madagascar field data (right), colored by genera according to legend; data are grouped by sex (upper=females, lower=males). Violin plots show range and 25, 50, and 75% quantiles for each distribution. **B.** Linear regression of \log_{10} body mass (in grams, y-axis) by \log_{10} forearm length (in mm, x-axis) across pteropodids from the literature (left) and from our Madagascar field data (right), colored by genera according to legend; data are grouped by sex (upper=females, lower=males). Solid line corresponds to predictions from the fitted model (R^2 : All Pteropodids, M= .96, F=.95; Malagasy Pteropodids, M=.96, F=.97). Data are summarized in Table S2, S3.

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Welch's 2-sample t-test comparisons indicated that length distributions for tibia and forearm length were significantly longer in adult males vs. females for both *P. rufus* and *R. madagascariensis* ($p < 0.001$; Table S2; **Fig. S1**). For *E. dupreanum*, only tibia length was different between the sexes, with males again larger than females ($p < 0.029$). Ear lengths showed sexual dimorphism only in *R. madagascariensis* bats, for which observed female ear lengths were actually larger than those of males. Nonetheless, given that both tibia and forearm length were larger in *R. madagascariensis* males vs. females, we conclude that all three Malagasy fruit bat species demonstrated slight sexual dimorphism characterized by larger-bodied males and smaller females.

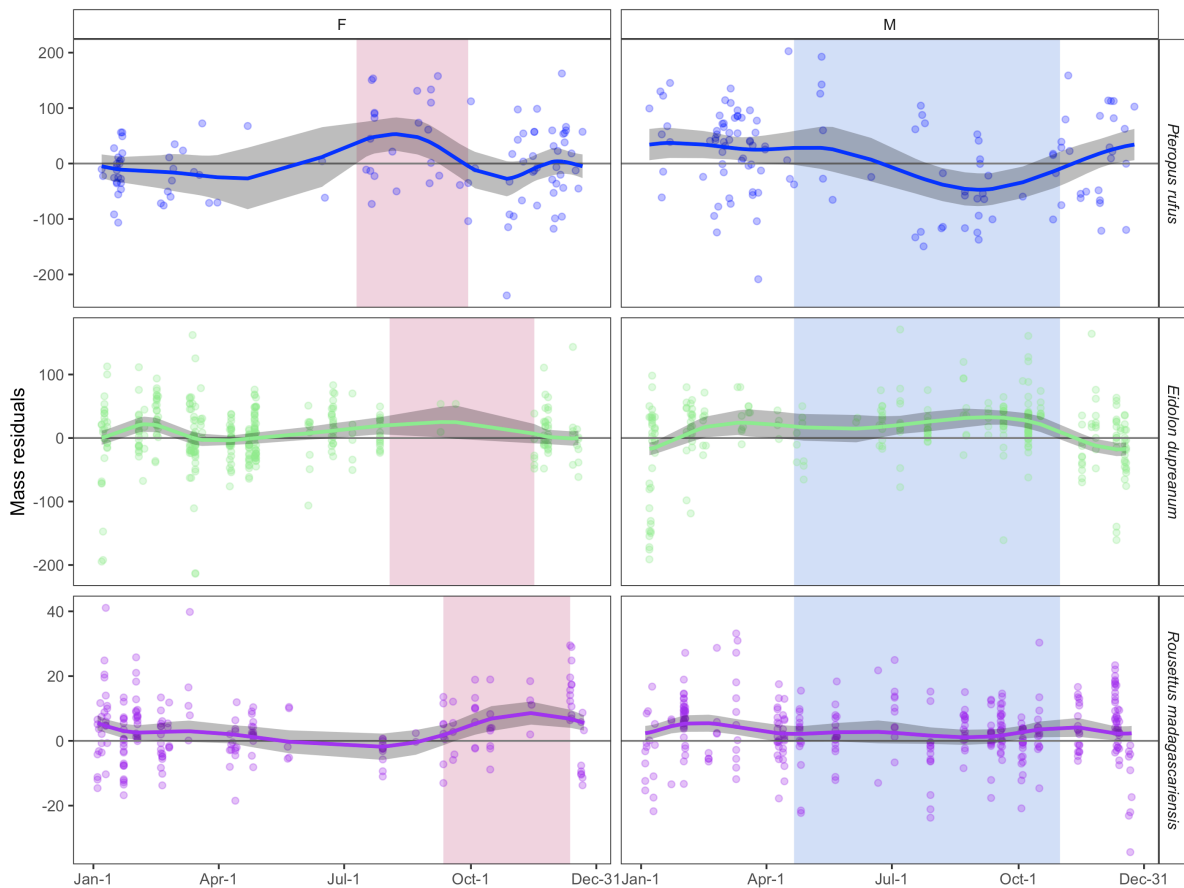
Linear regressions of \log_{10} body mass as predicted by \log_{10} forearm length for both all-pteropodid and Malagasy-specific datasets, separated by sex, demonstrated a good fit to the data with R^2 values $> .95$. Roughly comparable slopes across all four models indicated 20-30 fold increases in bat mass (in grams) corresponding to every 10-fold increase in forearm length (in mm) across all species and sexes (Fig 2C; **Table S3**).

Seasonality of mass:forearm relationships—Restricting our analyses to the Madagascar field data only, we refit the regression of mass:forearm length across both sexes, incorporating bat species as a second fixed predictor of mass (**Table S4; Fig. S2**), then computed mass:forearm residuals from the resulting regression models for each individual. We explored seasonal variation

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377 in these residuals from the longitudinally-monitored Moramanga site only, using GAMs. GAM
378 results indicated significant seasonality in bat body condition for both male and female subsets of
379 the *P. rufus* and *E. dupreanum* data and for the female subset of the *R. madagascariensis* data (p -
380 $value < 0.001$; **Table S5**). Only male *R. madagascariensis* demonstrated no seasonal variation in
381 mass:forearm residual. Finally, we plotted the GAM-predicted mass for each species and sex
382 across, respectively, the reproductive and nutritional calendars for female and male fruit bats of
383 the three Malagasy species (**Fig. 3**). As expected, we observed a seasonal peak in adult female
384 mass:forearm which overlapped the staggered period of observed gestation for each species from
385 Fig. 1, followed by a deficit overlapping the corresponding, species-specific lactation period.
386 These results supported our assumption that the vast majority of female bats in our dataset could
387 be considered reproductive.

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390 **Fig. 3.** Seasonal variation in mass:forearm residual by sex (females = left, males = right) and species. Raw data are
391 shown as open circles with prediction from fitted GAM model as solid line; 95% confidence intervals by standard
392 error are shown by shading in gray (Table S5). For female plots, pink shading corresponds to the species-specific
393 gestation period; for male plots, blue shading corresponds to the winter dry season in Madagascar.

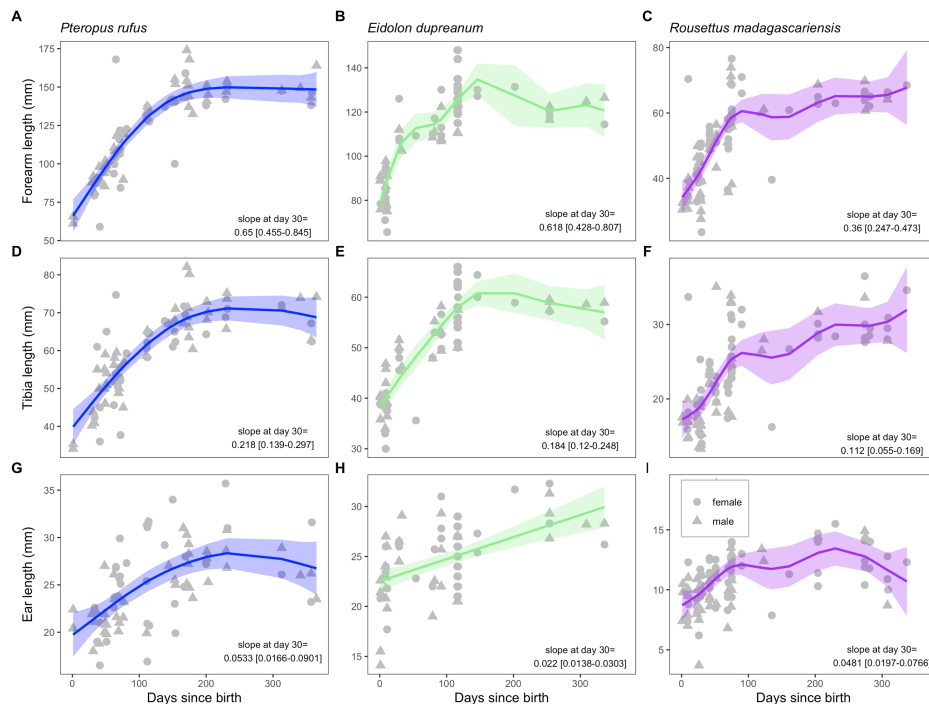
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395 We also observed a less extreme mass deficit which overlapped the resource-poor winter
396 for male *P. rufus* and *E. dupreanum* but occurred earlier in the season for *E. dupreanum* than for
397 *P. rufus*. Notably, GAMs for *R. madagascariensis* males, which showed no significant seasonality
398 in body condition, predicted positive mass:forearm residuals across the entire calendar year,
399 suggesting that bats in the Moramanga site had high mass:forearm ratios, as compared with those
400 across the entire dataset (sites outside of Moramanga were not included in seasonal analyses).

401 These results are logical, considering that, outside of Moramanga, *R. madagascariensis* were
 402 predominantly captured in Ankarana National Park, an arid, desert environment where bats are
 403 much more likely to experience food stress. Finally, supplementary GAMs used to model seasonal
 404 mass directly demonstrated comparable results to patterns for mass:forearm residuals across all
 405 three species and both sexes, with female masses peaking across gestation and male masses
 406 declining through the winter season (**Fig. S3**).

407 *Juvenile growth rates*—In our final analysis, we compared juvenile growth rates in
 408 forearm, tibia, and ear length across all three Malagasy fruit bat species in the first year of life.
 409 GAMs fitted to the response variable of each morphological trait demonstrated highly significant
 410 smoothing predictors of days since birth across all three metrics and all three species (**Fig. 4; Table**
 411 **S6**). Quantification of the derivative of each fitted GAM across the range of observed days since
 412 birth allowed us to compare growth rates across traits and species: in general, we observed the
 413 largest slopes, corresponding to the fastest growth rates for forearm lengths, then tibia lengths, and
 414 finally, ear lengths of all three species. *P. rufus* grew at the fastest rate (largest slope in growth
 415 curve) for all three morphological traits, followed by *E. dupreanum* and then *R. madagascariensis*.
 416 Despite faster growth rates, as the largest of the three species, *P. rufus* also demonstrated the most
 417 protracted development phase, approaching adult size (10-day average slope for forearm growth
 418 $<.1$) approximately six months after birth (180 days), as compared to two months (53 days) for *E.*
 419 *dupreanum* and 2.5 months (81 days) for *R. madagascariensis*. Species- and metric-specific
 420 growth rates from our fitted GAMs across the first year of life are summarized in **Table S7**; all
 421 raw values are available on our open-access GitHub repository.

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423 **Fig. 4.** Variation in juvenile forearm, tibia, and ear length with days since birth, corresponding to the date of first
 424 observed juvenile for each of three Madagascar species (Sep-29 for *P. rufus*, Nov-16 for *E. dupreanum*, Dec-12 for
 425 *R. madagascariensis*). Raw data are shown in grey (females = triangles, males = circles), with predictions fitted
 426 GAM model overlain as colored lines; 95% confidence intervals by standard error are shown by translucent shading
 427 (Table S6). The slope (derivative) of each fitted GAM at day 30 is identified in the bottom right; derivative results
 428 across the first year are summarized in Table S7.

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DISCUSSION

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Here, we explore spatial-temporal and seasonal variation in morphological features for three endemic Malagasy bats in the Old World Fruit Bat family, Pteropodidae: *P. rufus*, *E. dupreanum*, and *R. madagascariensis*. Our work confirms that *P. rufus*, *E. dupreanum*, and *R. madagascariensis* birth in a single annual, species-specific pulse in Madagascar, which is temporally staggered across the three species. In the District of Moramanga in Madagascar's center-east where we conducted the bulk of our field studies, the *P. rufus* birth pulse occurred first in the months of September/October, followed by *E. dupreanum* in November, and *R. madagascariensis* in December. It is possible that the timing of this birth pulse may vary latitudinally based on climatic differences across the island (e.g. occurring earlier in warmer climates or later in cooler regions), though our birth pulse projections align well with previous records of the mating season for *P. rufus* in southeastern Madagascar (Long and Racey 2007) and *R. madagascariensis* in northwestern Madagascar (Noroalintseho Lalarivoniaina et al. 2019); to our knowledge, no previous records defining the reproductive calendar for *E. dupreanum* have been published (Shi et al. 2014). Nonetheless, climate-related variation in birth pulse timing is well-described for populations of *Eidolon helvum*, which range across the entirety of the African continent (Peel et al. 2013, 2017).

This birth timing of Malagasy fruit bats likely increases their vulnerability to seasonally-varying population pressures. In particular, fruit bats are legally hunted during the Malagasy winter (1 May – 1 September), which overlaps the gestation period observed here for all three species, but most significantly for *P. rufus*, a species already known to be experiencing severe population declines due to anthropogenic threats (Golden et al. 2014; Brook et al. 2019a). Critically, the Malagasy fruit bat lactation periods are varied in duration such that, despite staggered birth pulses, juvenile weaning occurs largely coincidentally at the onset of the peak fruiting season in the hot-wet Malagasy summer, a pattern recapitulated across numerous species of frugivorous lemur, as well (Wright et al. 2005). As a result, Malagasy fruit bat population viability will likely be sensitive to future shifts in fruiting phenology, which are predicted to accompany changing climates (Dunham et al. 2018). Importantly, our study quantifies life history traits needed to assess population viability for these species into the future (Dobson and Lyles 1989; Brook et al. 2019a).

In Madagascar, seasonally-staggered birth pulses across the three fruit bat species could support the persistence of multi-species pathogens, such as bat-borne coronaviruses, which frequently transmit and recombine amongst different species of bats that co-roost in the same caves (Hu et al. 2017). Among Malagasy pteropodids, *E. dupreanum* and *R. madagascariensis* are known to share cave roosts, sometimes with insectivorous bats, while *P. rufus* inhabits single-species arboreal roosts (MacKinnon et al. 2003). Previous work suggests that sympatric cave-roosting likely plays a role in pathogen-sharing of diverse paramyxoviruses among Malagasy bats (Mélade et al. 2016), but considerable evidence also supports a largely single-host-species-to-single-pathogen relationship for many other bat-borne infections, including those described in Madagascar (Ng et al. 2015; Lagadec et al. 2016; Brook et al. 2019b; Joffrin et al. 2019). It is likely that diverse inter- and intra-species dynamics underpin the population-level persistence of different pathogen types.

Because the dynamics of pathogen shedding and zoonotic spillover have been linked to reproductive and nutritional calendars across several bat-virus systems (Plowright et al. 2008; Amman et al. 2012; Schmidt et al. 2017; Brook et al. 2019b), documentation of seasonal variation

476 in bat body condition and nutrition also has important implications for understanding immunity
477 and pathogen maintenance. We here highlight significant seasonal changes observed in body
478 condition for Malagasy fruit bats, apparently modulated by reproduction for females and
479 corresponding more closely to the nutritional calendar for males. Further research confirming the
480 reproductive status of adult female bats in this system—by either ultrasound in the field or assay
481 of plasma progesterone from field-collected samples (Buchanan and Younglai 1986)—is needed
482 to confirm this hypothesis of reproductive regulation of seasonal female bat masses. Additionally,
483 future work elucidating seasonal and cross-species variation in fruit bat diet—and its impact on
484 bat health—would do much to elucidate the observed discrepancy in the timing of the seasonal
485 mass: forearm deficit for in *E. dupreanum* (June-July) vs. *P. rufus* (September) males. No seasonal
486 pattern was found for male *R. madagascariensis* bats in our dataset, which could result from a lack
487 of statistical power to identify differences across a smaller body size range for this species, or
488 which may signify perpetually abundant food resources for this species in the Moramanga District.

489 Beyond the observed seasonality in body mass:forearm residual, which tracked
490 reproduction for females and nutrition for males, we also documented sexual dimorphism (larger
491 males vs. females) in tibia and forearm lengths for Malagasy fruit bats, a pattern that is common
492 to pteropodids more generally and has been previously reported for *R. madagascariensis* (McNab
493 and Armstrong 2001; Goodman et al. 2017). Our study confirms that the size distribution of
494 Malagasy pteropodids spans the range of that documented globally, with *P. rufus* and *E.*
495 *dupreanum* falling among the larger 50% of previously described species and *R. madagascariensis*
496 among the smaller. Mirroring adult size distributions, juvenile growth rates were highest and
497 developmental periods longest in *P. rufus*, followed by *E. dupreanum* and *R. madagascariensis*.
498 Critically, the longer development period for *P. rufus* further jeopardizes this species' already-
499 threatened conservation status—which recent analysis suggests may be even more vulnerable than
500 previously reported (Brook et al. 2019a). The rapid ~two month juvenile growth window witnessed
501 for *E. dupreanum* in our dataset suggests that this species may actually birth earlier than is recorded
502 here; additional, intensive sampling throughout the reproduction period is needed to confirm the
503 seasonal limits of each developmental stage for these three fruit bat species.

504 In conclusion, we quantify life history traits needed for population modeling, document
505 seasonal variation in body condition, and elucidate the Malagasy fruit bat reproductive calendar,
506 contributing important resources for future efforts to quantify both conservation trajectories and
507 zoonotic pathogen transmission in his system. This work emphasizes the importance of
508 longitudinal field studies in uncovering seasonal variability in ecological data, with critical
509 implications for understanding of both population viability and infectious disease dynamics alike.

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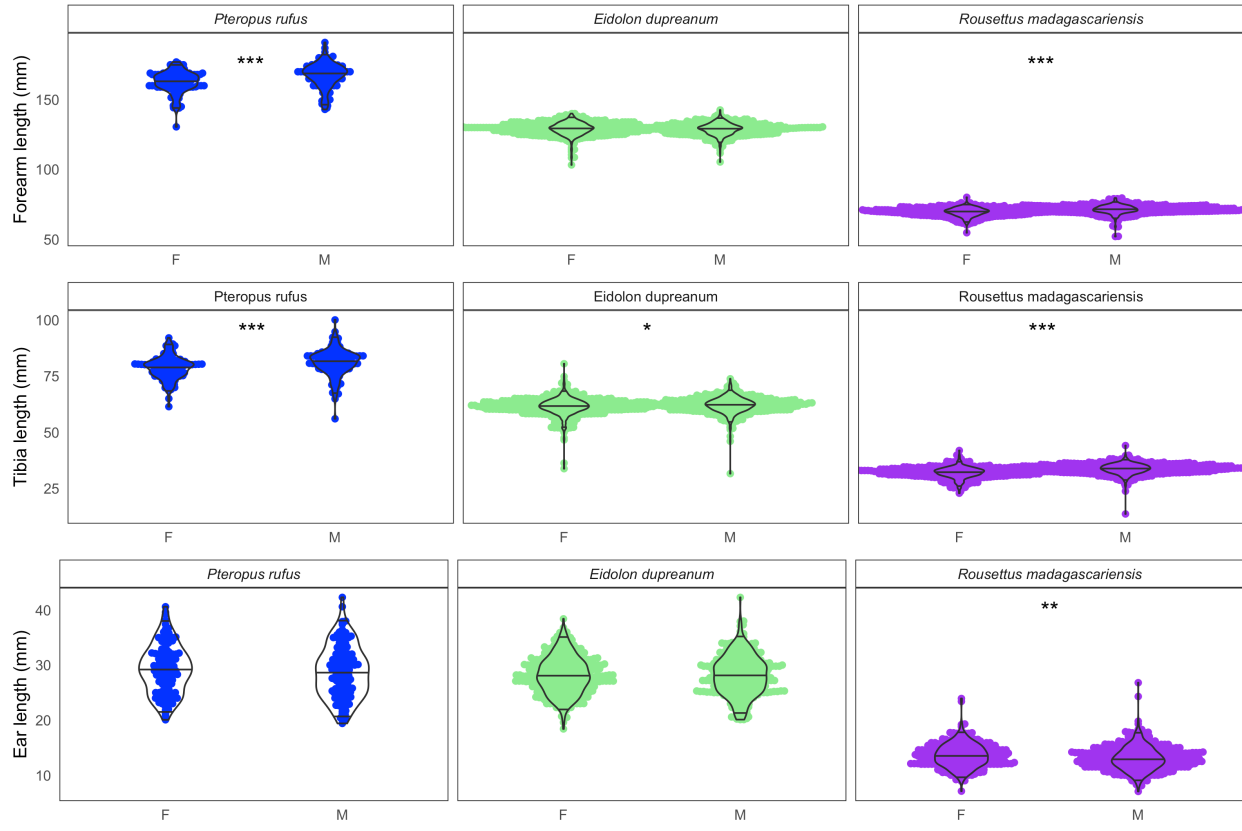
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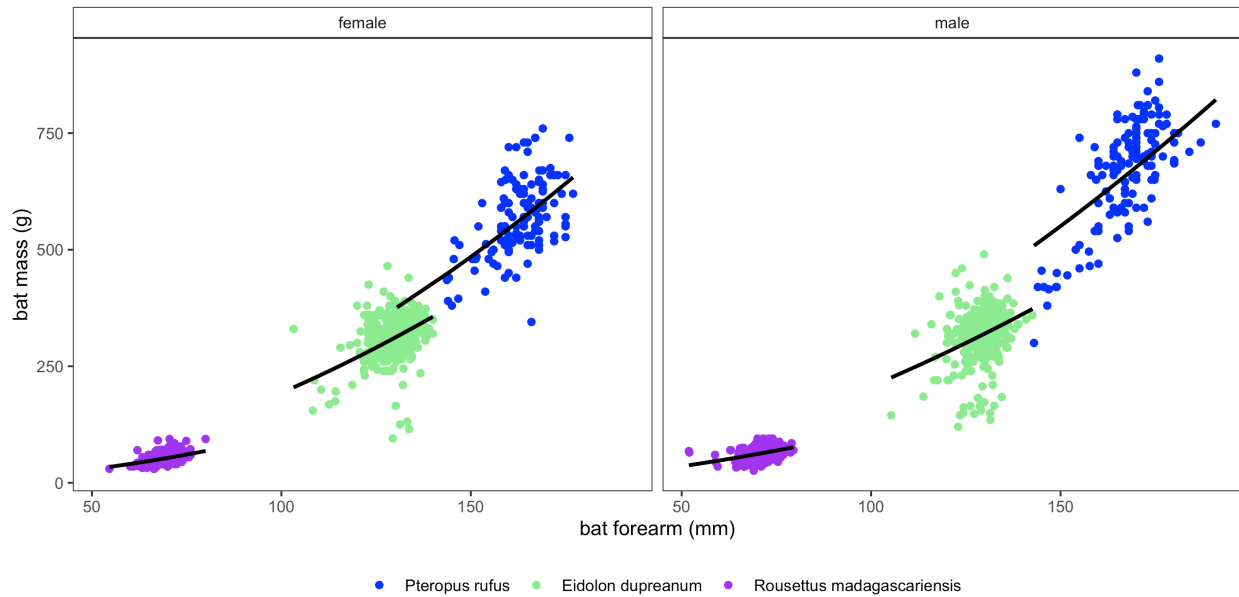
APPENDIX 1: SUPPLEMENTARY FIGURES

Fig. S1. Morphological trait distributions in forearm, tibia, and ear length for *Pteropus rufus*, *Eidolon dupreanum*, and *Rousettus madagascariensis*. Each panel compares distributions from females (F) vs. males (M). Asterisks indicate significance in *Welch's 2-sample t-tests* from data within each panel, based on significance codes: ***=0.001; **=0.01; *=0.05; . = 0.1.



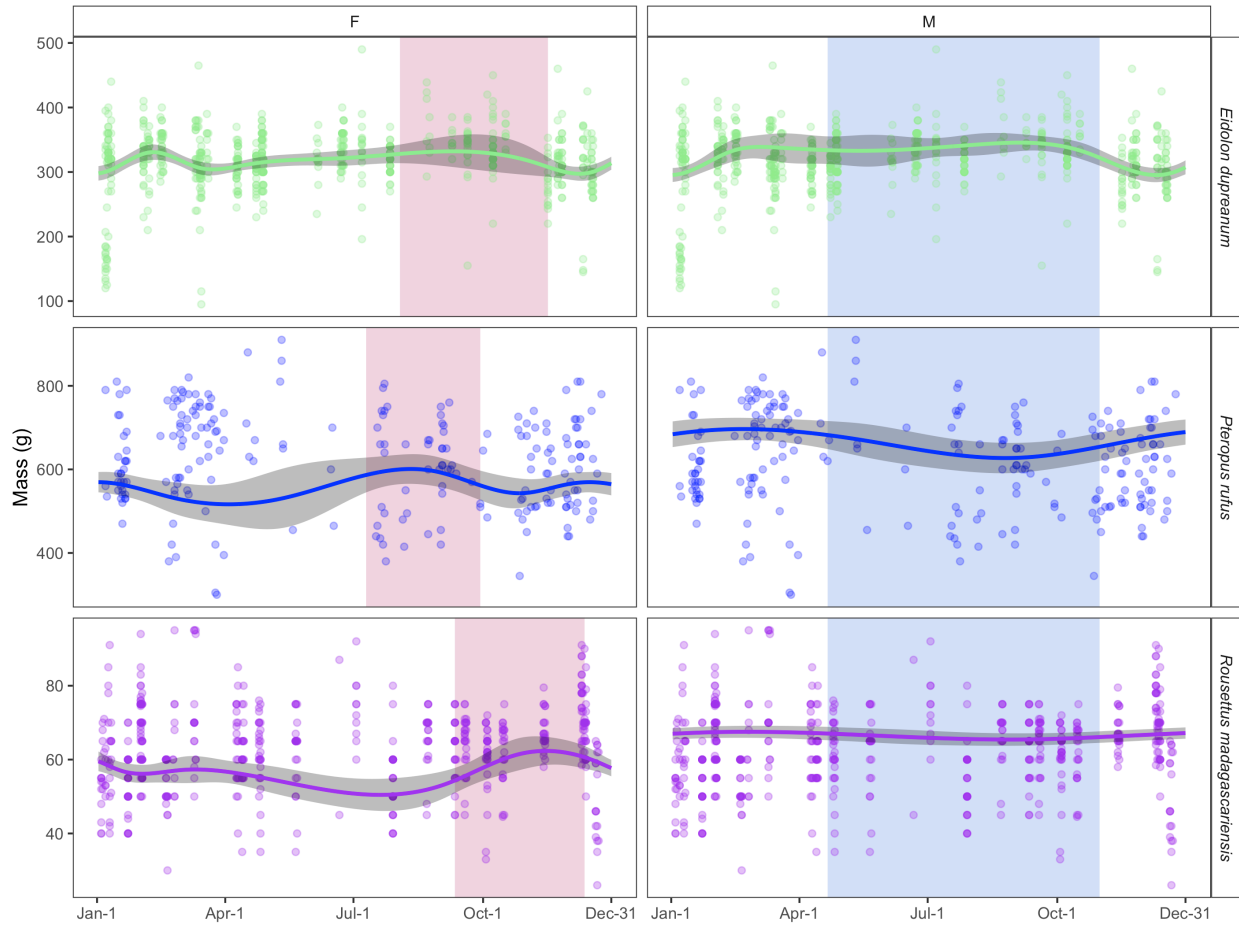
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777 **Fig. S2.** Forearm length (mm) vs. mass (g) relationships for Malagasy fruit bats, separated by
778 sex. Data are depicted as points colored by species. Solid black lines correspond to output from
779 fitted linear regression model of log₁₀ mass predicted by log₁₀ forearm length, incorporating a
780 fixed predictor of species. Residuals depicted in Fig. 3 (main text) were derived by subtracting
781 predictions from data for each individual, as shown here. Model fits are summarized in Table S4.
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807 **Fig. S3.** Figure largely replicates Fig. 3 (main text) but here depicts the output of supplementary
808 GAMs incorporating a direct response variable of bat mass (in g) predicted by day of year (as a
809 cyclic cubic smoothing spline) with a random effect of forearm length. Random effects are
810 silenced here for plotting purposes. As in Fig. 3, raw data are shown as open circles with
811 prediction from fitted GAM model as solid line; 95% confidence intervals by standard error are
812 shown by shading in gray (Table S4). For female plots, pink shading corresponds to the species-
813 specific gestation period; for male plots, blue shading corresponds to the winter dry season in
814 Madagascar.
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