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1 **Can survival analyses detect hunting pressure in a highly connected species?**
2 **Lessons from Straw-coloured fruit bats**

3
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16 **Contributions:**

17 Conceived the research: AJP, DTSH

18 Analysed the data: AJP, DTSH

19 Wrote the manuscript: AJP, DTSH

20 **Highlights**

- 21 • Straw-coloured fruit bat hunting pressure varies across African colonies
- 22 • Estimated annual survival probability in five colonies across Africa was high
- 23 (≥0.64)
- 24 • Social structure affects survival estimates, with male biases increasing estimates
- 25 • Migration and movement may compensate for high local hunting pressure
- 26 • Spatio-temporal studies are vital to assess mobile species conservation status

27 **Keywords:** *Eidolon helvum*, demography, hunting, survival analyses, Bayesian population
28 analyses

29
30 ABSTRACT

31 Animal behaviour, social structure and population dynamics affect community structure,
32 interspecific interactions, and a species' resilience to harvesting. Building on new life history
33 information for the straw-coloured fruit bat (*Eidolon helvum*) from multiple localities across
34 Africa, we used survival analyses based on tooth-cementum annuli data to test alternative
35 hypotheses relating to hunting pressure, demography and population connectivity. The estimated
36 annual survival probability across Africa was high (≥ 0.64), but was greatest in colonies with the
37 highest proportion of males. This difference in sex survival, along with age and sex capture
38 biases and out-of-phase breeding across the species' distribution, leads us to hypothesize that *E.*
39 *helvum* has a complex social structure. We found no evidence for additive mortality in heavily
40 hunted populations, with most colonies having high survival with constant risk of mortality
41 despite different hunting pressure. Given *E. helvum*'s slow life history strategy, similar survival
42 patterns and rate among colonies suggest that local movement and regional migration may
43 compensate for local excess hunting, but these were also not clearly detected. Our study suggests
44 that spatio-temporal data are necessary to appropriately assess the population dynamics and
45 conservation status of this and other species with similar traits.

46
47

48 **1 Introduction**

49 “At Avakubi [Democratic Republic of the Congo], November 19, 1909, a flock of perhaps
50 100 had taken shelter for the day beneath the limb of a large tree, some 60 feet above the
51 ground, where they were shaded by a mass of epiphytic ferns and orchids, and formed one great
52 squirming mass. ... After watching their amusing struggles for a while, we fired both barrels of a
53 gun into their midst. We were standing almost directly beneath and for a few seconds it simply
54 rained bats, dead or wounded. ... Hundreds of them are then slain by the natives, who are fond
55 of eating these bats”

56 Allen J A, Lang H, Chapin J (1917) The American Museum Congo expedition collection
57 of bats. (Referring to *Eidolon helvum*, the Straw-colored fruit bat)

58

59 Demographic processes shape population dynamics and therefore have broad
60 implications, for example on infection dynamics and sustainable harvesting capacity (Keeling &
61 Rohani, 2008, Sandercock et al., 2011). Harvesting itself is hypothesized to shape demographic

62 processes through various mechanisms (Sandercock et al., 2011). Under additive mortality,
63 harvesting mortality has no effect on natural birth or death rates, and is additive to natural
64 mortality in a linear fashion. Under compensatory mortality, density-dependent compensatory
65 mechanisms (such as increased birth rates, decreased natural mortality, or increased movement)
66 are evoked, meaning that harvesting adds no additional mortality to natural mortality rate. It is
67 hypothesized that there should come a threshold at which these compensatory processes can no
68 longer compensate and harvesting losses become additive (Sandercock et al., 2011).
69 Understanding the contribution of compensatory or additive mortality processes is crucial for
70 wildlife management and conservation so that offtake limits can be set to ensure harvesting does
71 not deplete a population. Recent research has shown that fruit bats are a group of mammals that
72 are hunted for food, sport or medicine in greater numbers than previously thought (Epstein et al.,
73 2009, Harrison et al., 2011, Kamins et al., 2011, Mickleburgh et al., 2009). Correspondingly,
74 studies on the sustainability of fruit bat bushmeat hunting are in their infancy compared with
75 other terrestrial species.

76 Underlying demographic processes are often poorly elucidated in bats, even in common
77 species. The straw-coloured fruit bat, *Eidolon helvum*, is one of the most common and widely
78 distributed African bats, but is also widely hunted in parts of Africa (Anti et al., 2015, Carvalho
79 et al., 2015, Kamins et al., 2011, Mickleburgh et al., 2009, Niamien et al., 2015). Demographic
80 processes that affect whether hunting mortality may be additive or compensatory and their
81 relevance for *E. helvum* fruit bats are considered under five different, but non-mutually
82 exclusive, circumstances.

83 First, those species with slow life histories (long-lived with low fecundity, or so called
84 ‘K-selected’ species), such as bats, primates, larger ungulates, and long-lived birds, are expected
85 to suffer from additive mortality because they do not have the capacity to compensate for the
86 additional mortality through reproductive surplus (Hamel et al., 2006, Sedingner et al., 2007,
87 Sedingner, et al., 2010). Hayman et al. (2012) estimated high annual adult survival rates and low
88 fecundity for *E. helvum*, supporting expectations for a slow-life-history species.

89 Second, small or declining populations have limited compensatory capacity and are
90 predicted to suffer from additive mortality (Bartmann et al., 1992). Significant *E. helvum*
91 population declines have occurred in some areas of its sub-Saharan range, possibly because of
92 habitat loss and over-harvesting for food and medicine (Mickleburgh et al., 2010, Mickleburgh et

93 al., 2009, Perpetra & Kityo, 2009, Sodeinde & Soewu, 1999). Smaller, fragmented *E. helvum*
94 populations also exist on a small number of offshore islands, including Pemba, off the Tanzanian
95 coast (Hayman & Hill, 1971) and Príncipe, São Tomé and Annobón in the Gulf of Guinea (Juste
96 & Ibanez, 1994). While Bioko island in the Gulf of Guinea is close enough for bats to mix freely
97 with the continental population, bats on Príncipe, São Tomé and Annobón islands are isolated
98 and genetically distinct from one another (Peel et al., 2013). These smaller island populations
99 may be more likely to suffer additive mortality in response to harvesting.

100 Third, migration and mixing among spatially structured populations can be a
101 compensatory mechanism through demographic rescue (Cooley et al., 2009, Kvasnes et al.,
102 2010). Continental *E. helvum* bats are seasonally migratory (Fahr et al., 2015, Funmilayo, 1979,
103 Hayman et al., 2012, Mutere et al., 1980, Richter & Cumming, 2006, Thomas, 1983), and are
104 capable of travelling >2500 km across international borders and up to 370 km in a single night
105 (Richter & Cumming, 2008). In contrast, the isolated nature of the island populations (or other
106 fragmented populations) might also make them prone to additive effects.

107 Fourth, harvesting during or immediately after periods of natural mortality is more likely
108 to be additive than if conducted before such periods (Boyce et al., 1999, Kokko, 2001,
109 Ratikainen et al., 2008). Hunting pressure is spatially heterogeneous across *E. helvum*'s range
110 (Kamins et al., 2011, Mickleburgh et al., 2009, Peel et al., In press). *E. helvum*'s migratory
111 behaviour includes a tendency to vacate and arrive in roosts *en masse* (Fahr et al., 2015, Hayman
112 et al., 2012, Peel et al., In press, Richter & Cumming, 2006, Thomas, 1983), resulting in the
113 shifting seasonal presence of an apparently abundant resource for hunters along these migration
114 routes.

115 Last, individual susceptibility to harvesting may vary with the type and timing of
116 harvesting; for example, specific hunting methods intentionally or unintentionally target specific
117 age or sex groups (Boyce et al., 1999). A variety of hunting methods have been documented for
118 *E. helvum*, including shooting, slingshotting, capture in nets and hitting individuals that have
119 fallen to the ground (Kamins et al., 2011, Mickleburgh et al., 2009, Peel et al., In press),
120 however, few comprehensive data exist on how roost structure varies with age and sex, and in
121 different locations or different seasons.

122 Empirical investigations to directly estimate the effect of harvesting within a target
123 species or population are complicated by these multifactorial responses. For example,

124 comparison of population counts among populations with differing harvest rates has been used to
125 detect whether harvesting is likely to be additive or compensatory (Bodmer et al., 1997).
126 However, in the case of compensatory mortality, population counts alone cannot separate the
127 contributions of potentially contributing density-dependent processes (e.g. altered birth rates,
128 survival and movement). The necessity to disentangle the various processes that contribute to
129 population size when examining the effects of harvest on survival can be avoided by using mark-
130 recapture techniques and harvest experiments (Bartmann et al., 1992, Cooley et al., 2009, Duriez
131 et al., 2005, Obbard & Howe, 2008, Sandercock et al., 2011, Schaub & Lebreton, 2004, Servanty
132 et al., 2010). These methods allow the effect of hunting to be anticipated by estimated harvesting
133 rates and comparing those to survival rates under different harvesting pressures.

134 Logistical problems can preclude the possibility of using capture-recapture studies in
135 some species, including bats. Instead, life table analyses enable population age structure, growth
136 rate and survivorship patterns to be estimated and can allow for maturation of young and
137 senescent mortality (Fieberg & DelGiudice, 2011, Kraus et al., 2013, Siler, 1979, Stolen &
138 Barlow, 2003), thereby providing insight into the demographic processes of species for which
139 cohort studies are not feasible. The flexible “Siler” model allows us to fit a function that includes
140 maturation and senescence with a constant hazard (exponential) survival pattern as a base. The
141 demographic processes relating to mortality for long-lived species, in which we might expect
142 such maturation and senescence processes, can therefore be inferred in the absence of capture-
143 recapture data.

144 Our expectations for long-lived species such as bats is that harvesting mortality will be
145 additive. However, the highly connected colonies of *E. helvum*, determined through telemetry
146 (Hayman et al., 2012) and inferred through population genetics (Peel et al., 2013), suggest that
147 migration could be a compensatory mechanism that will overwhelm the local hunting pressure.
148 In a companion paper, we provide new information on *E. helvum* colony sizes, hunting pressure,
149 and age and sex structure for multiple colonies across tropical Africa (Peel et al., In Press). Here,
150 we test hypotheses relating to hunting pressure and demography in this long-lived, yet highly
151 mobile, species. First, we hypothesize that different host demographic structures and survival
152 rates exist among regions and test whether this can be associated with different levels of local
153 hunting pressure, or is likely related to other seasonal demographic and migratory processes.
154 Second, we determine if mortality rates differ at different population sizes to make inferences

155 regarding whether mortality through hunting is additive to natural mortality, or alternatively, that
156 local movement and regional migration act as a compensatory mechanism. To test these
157 hypotheses, we estimate harvest pressure and mortality risk across age classes from five different
158 colonies across Africa and its outlying islands.

159

160 **2 Methods**

161

162 We used the background life history and hunting information for a subset of colonies of *E.*
163 *helvum* across tropical Africa (Peel et al., 2016, and deposited in the online data repository,
164 Dryad: doi:10.5061/dryad.2fp34). In particular, we present data from Accra (Ghana), Dar es
165 Salaam (Tanzania), Morogoro (Tanzania), São Tomé (São Tomé and Príncipe), Príncipe (São
166 Tomé and Príncipe), and Bioko (Equatorial Guinea) (Fig. 1). All fieldwork was undertaken under
167 permits granted by national and local authorities (listed in Acknowledgements) and under ethics
168 approval from the Zoological Society of London Ethics Committee (WLE/0489 and WLE/0467),
169 using field protocols which followed ASM guidelines (Sikes et al., 2011).

170

171 Bats were either captured at the roost with mist nets as they departed the roost site at dusk
172 (Ghana, Tanzania, Equatorial Guinea) or returned at dawn (Príncipe), or were shot by local
173 hunters from roost or feeding sites (São Tomé). Morphometric (forearm length and weight) and
174 demographic (age class, sex and reproductive status) data were recorded at the time of capture,
175 and teeth were collected to determine age in years from tooth cementum annuli. Counting the
176 cementum and dentine annuli was done by microscopy following histological preparation of
177 tooth roots by Matson's laboratory, Milltown, Montana (Matson, 1993). Annuli were assumed to
178 be deposited annually, based on other studies and the species strong seasonal migratory
179 behaviour (Divljan et al., 2006, Hayman et al., 2012). Canine teeth were removed from dead bats
180 killed for other purposes, including by hunters for meat, and processed as described elsewhere
181 (Bodkin et al., 1997, Hayman et al., 2012, Matson, 1993, Peel et al., In press). Each age
182 estimation (n=233 bats) was scored with a certainty code: A: highest certainty of reported age
183 (51% of samples), B: histological evidence supported a given age result ± 0.5 –1.5 years (46% of
184 samples), or C: tooth or section quality was too compromised to accurately age (3% of samples).
185 The latter were not used in this study. The specific age structure of each roost was standardized

186 according to the proportion of individuals caught within each age class. For example, in Bioko
187 84/105 (80%) of bats caught were less than 2 months old, but these were not aged through tooth
188 cementum analyses. The proportion of 0-year-old bats was then corrected for in the tooth
189 cementum data accounting for this capture bias.

190 In each location, roost or emergence counts were conducted following established
191 techniques to estimate population sizes. Several methods were used, according to what was most
192 appropriate in each location. The methods were daytime roost counts in Tanzania, Bioko, Ghana
193 (Baranga & Kiregyera, 1982, Fahr et al., 2015, Hayman et al., 2012, Perpetra & Kityo, 2009) and
194 emergence counts in Príncipe and São Tomé (Dallimer et al., 2006). These methods and results
195 are described in detail elsewhere (Peel et al., In press).

196 Data on bat-human interactions were gathered via informal conversations and via
197 questionnaire-based surveys (Table 1 and Appendix) (Peel et al., In press). Hunting pressure was
198 then qualitatively categorised for each colony. Hunting was deemed ‘low’ in Dar es Salaam,
199 Morogoro and Príncipe. Accra was estimated as ‘medium’ based on limited hunting in the
200 immediate area, but high levels of hunting in nearby connected colonies (Kamins et al., 2011).
201 São Tomé was subjectively deemed ‘high’ based on questionnaire responses, anecdotal reports
202 from hunters and local residents and bat roosting behaviour, such as roosting away from human
203 habitation (Peel et al., In press).

204 To estimate annual survival probability from age frequencies, and to test for variation in
205 survival probability with age, we fit life table models to tooth age frequency data as performed
206 elsewhere for mammal populations (Fieberg & DelGiudice, 2011, Kraus et al., 2013, Siler, 1979,
207 Stolen & Barlow, 2003). Population growth rates (λ) cannot be estimated using our approach and
208 so we assumed λ was constant (I) and assumed a stationary age structure (Hayman et al., 2012),
209 but tested the sensitivity to this assumption by re-fitting the models with $\ln(\lambda) = -0.1$ (10%
210 decline). As with the Accra colony data (Hayman et al., 2012), we tested five candidate models
211 (below) based on models proposed by Siler (1979). This modelling approach assumes a constant
212 baseline mortality risk operating throughout life and considers two additional factors, maturation
213 (decreasing risk in early life) and senescence (increasing risk in later life). Annual probability of
214 survival of mature animals at age x under constant baseline risk is given by the exponential
215 model:

$$l_{x,2} = \exp(-a_2x)$$

216

217 and maturation and senescence elements are defined respectively by Gompertz models:

$$l_{x,1} = \exp\left(\left(-a_1/b_1\right)\left(1 - \exp(-b_1x)\right)\right)$$

$$l_{x,3} = \exp\left(\left(a_3/b_3\right)\left(1 - \exp(b_3x)\right)\right)$$

218 where a_i is the initial hazard for each element, b_i is the rate at which the hazard decreases
 219 or increases with age during maturation or senescence respectively, and x denotes age in years.
 220 Subscripts $1-3$ denote, respectively, maturing, constant and senescing elements. Overall
 221 survivorship is then given by the product of desired components, such that the five models tested
 222 were constant risk ($l_x = l_{x,2}$), maturing risk ($l_x = l_{x,1} l_{x,2}$), senescing risk ($l_x = l_{x,2} l_{x,3}$), both maturing
 223 and senescing risks ($l_x = l_{x,1} l_{x,2} l_{x,3}$, aka the ‘Siler’ model) or both maturing and senescing risks
 224 without the constant risk ($l_x = l_{x,1} l_{x,3}$). The inclusion of the latter model is an extension of
 225 previous work (Hayman et al., 2012). The model parameter estimates will allow greater
 226 understanding of the risk of mortality to different aged bats. For example, if younger bats are
 227 most affected by hunting, the initial hazard a_1 will be higher in colonies with high hunting
 228 pressure. If hunting increases juvenile survival due to compensatory mechanisms, $1/b_1$ may be
 229 higher in heavily hunted colonies. If hunting affects all mature bats equally, a_2 will be increased
 230 in those with heavy hunting pressure, and if hunting decreases, the overall age a_3/b_3 will be
 231 reduced as the risk of senescence reduces.
 232

233 In contrast to our previous work using maximum likelihood (Hayman et al., 2012), we
 234 chose to fit these five non-linear models within a Bayesian framework because sample sizes were
 235 small for some colonies. We used a normal error structure with ‘uninformative’ (flat) priors. We
 236 chose normal (N) or uniform (U) distribution priors for the model parameters. Thus our full five-
 237 parameter Siler model for the hazard rates μ was:

$$\mu[i] = a e^{(-a_2 \text{Age}[i])} e^{((-a_3/b_3)(1 - e^{(b_3 \text{Age}[i])})} e^{((-a_1/b_1)(1 - e^{(-b_1 \text{Age}[i])})})}$$

238 Where:

$$P(a, a_1, a_2, a_3, b_1, b_3 | y_i) \propto \prod_{i=1}^n N\left(y_i \mid \mu_i, \frac{1}{\sigma^2}\right)$$

$$U(a | 0, m_a)$$

$$N(a_1 | 0, \sigma_{a_1})$$

$$N(a_2 | 0, \sigma_{a_2})$$

$$N(a_3 | 0, \sigma_{a_3})$$

$$N(b_1|0, \sigma_{b_1})$$

$$N(b_3|0, \sigma_{b_3})$$

$$U(\sigma|0, m_\sigma)$$

239 Prior distribution dispersion parameter subscripts refer to the parameter of interest. We
240 typically used $\sigma = 100$ for the uninformative normal prior distributions. We wrote all the code in
241 R (R Development Core Team, 2013) and used the R2OpenBUGS package (Sturtz et al., 2005)
242 to interface with OpenBUGS (Spiegelhalter et al., 2007). We ran three chains, for 10,000
243 iterations, discarding the first 1000 (10%) as burnin and did not thin the values at all, though we
244 compared values and distributions with (every 10) and without thinning. We used the *nls2*
245 function in the R package ‘nls2: Non-linear regression with brute force’ (Grothendieck, 2013) to
246 help select initial conditions from a grid of parameter values, but chose randomly from values
247 using appropriate distributions once appropriate initial conditions were found (not shown).

248 We estimated age-specific survival (S_x) simply from the fitted risk models such that: $S_x =$
249 $l(x+1)/l(x)$. Results (see below) generally supported the assumption of constant survival with bat
250 age (model 1, $l_x = l_{x,2}$). Mean life expectancy calculated from annual survival probabilities (S)
251 using the formula life expectancy = $-1/\ln(S)$ from the constant risk model $l_x = l_{x,2}$. Colony-
252 specific age-constant survival rates were therefore plotted against colony size estimates and
253 hunting pressure estimates to assess whether any evidence existed for compensatory or additive
254 mortality rates, and against sampling phase and colony sex ratio to assess the impact of seasonal
255 dynamics and migration on survival estimates. The latter were further explored using linear
256 mixed-effects models with age in years as the response variable, sex as a fixed-effect parameter
257 and location and/or phase as a random effect, using the *lmer* function in the *lme4* package (Bates,
258 Maechler et al., 2013) in R. The age data (y) was transformed through a square-root
259 transformation of the data and maximum likelihood used to fit the model to data, such that $y \sim I$
260 $+ Sex + (I|Location)$ and, separately, $y \sim I + Sex + (I|Phase)$. Further details regarding the data
261 for these variables are in our companion paper (Peel et al., In press). For all results for the
262 Bayesian Siler risk-based models 95% credible intervals are given, elsewhere 95% confidence
263 intervals.

264

265 **3 Results**

266 Tooth age data were available from six colonies of straw-coloured fruit bats. We were
267 able to fit the models to data from five colonies: Accra (Ghana); Dar es Salaam (Tanzania),
268 Morogoro (Tanzania) São Tomé (São Tomé and Príncipe) and Príncipe (São Tomé and
269 Príncipe). Data from Bioko (Equatorial Guinea) were highly biased towards very young bats (<2
270 months) and we were unable to fit the models to these data (Peel et al., In press).

271 All Markov chain Monte Carlo (MCMC) chains converged well in the Bayesian analyses
272 once appropriate initial conditions were chosen and the models ran. Example model outputs and
273 all parameter estimates with credible intervals are shown in the Appendix.

274 The constant risk model had the strongest support (lowest DIC values) in all but the
275 Príncipe population (Spiegelhalter et al., 2002) (Table 2). For Príncipe, the
276 maturation/senescence model ($l_x = l_{x,1} l_{x,3}$) was most strongly supported over all other models
277 (Table 2, underlined). However, even when there was support for a better model over the
278 constant model, the effect size was small, with overlapping credible intervals for the predicted
279 age frequencies (Fig. 2). Fits of each model to the data are shown in Fig. 2. Comparison of
280 parameter estimates also provides little support for differing parameters in the Siler model
281 among locations with most maturation and senescence related parameter estimates including zero
282 (Appendix). We also tested the assumption that these populations were at constant population
283 size during the lifetimes of these bats by altering $\ln(\lambda)$ from 0 to -0.1 (i.e. a negative population
284 growth rate). The estimated parameters varied little by including this change (Appendix).
285 Therefore, we used the constant survival rates for further analyses for simplicity and to allow
286 comparison among sites.

287 In all analyses our estimates of survival across age groups support that *E. helvum* is a
288 relatively long-lived species, with a mean life expectancy estimates across the colonies ranging
289 from 2.3 to 6.8 years, as can be seen after converting the model results to annual survival
290 probabilities (Table 3). Using the best model results for the location with the highest survival,
291 Accra in Ghana, and predicting the age distribution, our model predicts that individuals may live
292 up to 30 years of age (Fig. 3), consistent with studies reporting individuals up to 21 years
293 (DeFrees & Wilson, 1988).

294 Analyses determining if harvest mortality was additive or led to compensatory survival
295 were inconclusive. Neither colony size nor hunting was statistically supported as an explanatory
296 covariate for survival. Since compensatory and additive mortality represent density-dependent

297 and density-independent natural mortality, respectively, if mortality is compensatory and in the
298 absence of social facilitation effects, lower survival rates are expected with larger colony sizes
299 (Fig. 4). In comparison, rates are not expected to vary with population size when mortality is
300 additive (Burnham & Anderson, 1984). Here, plotting constant survival rates against population
301 size showed no evidence for density-dependent (compensatory) mortality in *E. helvum* (Fig. 4).
302 The São Tomé population size is likely to be underestimated (Peel et al., In press), but it is not
303 known by how much and if that would strengthen support for additive mortality. In turn, if
304 natural mortality rates cannot compensate for increased harvest, then survival is expected to
305 decline with harvest intensity (Anderson & Burnham, 1976). Alternatively, if compensatory
306 changes in natural mortality can occur, then constant survival rates will be observed in spite of
307 increased harvest rates. Plotting constant survival rates against harvest rates suggested that *E.*
308 *helvum* mortality rates could show compensation for hunting pressure. However, a caveat
309 associated with this plot is that hunting estimates were only qualitatively estimated relative to
310 population size.

311 A significant relationship was observed between colony sex ratios and survival rates (F-
312 statistic 15.65, p 0.029; Fig. 4), however there is no relationship between sampling phase and
313 survival rate (Appendix).

314 **4 Discussion**

315 Studies on the effects of hunting on bat populations are in their infancy. *Eidolon helvum*,
316 like other fruit bats with slow life histories, is poorly adapted to compensate for hunting
317 demographically (Hayman et al., 2012, McIlwee & Martin, 2002). Previous harvest models of
318 fruit bats have assumed additive hunting mortality (Epstein et al., 2009), yet this assumption has
319 not been examined. Here, we explored the factors expected to determine *E. helvum*'s response to
320 harvesting pressure.

321 Survival rates and associated life expectancies calculated here for *E. helvum* bats in
322 Tanzania (Morogoro, 0.65, 0.60-0.69 95% CI, Dar Es Salaam 0.85, 0.76-0.92), São Tomé (0.74,
323 0.67-0.79 95% CI) and Príncipe (0.77, 0.65-0.86 95% CI) were comparable with previous
324 estimates from Accra (0.83, 0.73-0.93 95% CI) (Hayman et al., 2012). The estimate for Accra
325 (0.86, 0.77-0.93 95% CI) was slightly different to that previously estimated (0.83, 0.73-0.93 95%
326 CI), due to stochastic Bayesian modelling and increased sample size, but were within reported
327 confidence limits. Our mean life expectancy estimate across colonies is 4.5 years (range 2.3 –

328 6.7), but our models suggest individuals may live up to approximately 30 years old in the wild
329 (Fig. 3).

330 Data on mechanisms governing natural mortality on fruit bats are limited, but McIlwee &
331 Martin (2002) argued against density-dependence being a major contributor, partly due to
332 reported causes of mortality for flying-foxes not being related to, or dependent on, the size or
333 density of the populations. Our results showed no evidence for density-dependent mortality
334 operating within colonies, irrespective of the presence of hunting (Fig. 4), suggesting the
335 colonies studied here are not at carrying capacity. This is consistent with reports of population
336 declines due to other threatening processes such as habitat loss (Mickleburgh et al., 2009), and
337 thereby greater susceptibility to additive effects of hunting (Bartmann et al., 1992, Sandercock et
338 al., 2011). Exploring our model's sensitivity to changes in population growth rate (λ) does little
339 to help us understand these population dynamics and determine if the colonies are in decline
340 (Fig. S3).

341 *Eidolon helvum*'s mobility might help counteract additive effects of hunting-related
342 mortality. The species moves among colonies within a region (Hayman et al., 2012) and
343 regionally across international borders during migration (Richter & Cumming, 2008), resulting
344 in a panmictic population structure across sub-Saharan Africa (Peel et al., 2013). This daily
345 mobility and migratory capacity allows flexibility to utilize changing availability of food
346 resources, maintenance of a wide and diverse gene pool, and avoidance of threats such as
347 hunting. Individual animal movements within the panmictic continental population likely
348 compensates for localised hunting-related mortality.

349 Conversely, smaller island populations with less migratory and rescue capabilities may be
350 more likely to experience additive effects of hunting. Similar physical environments in the paired
351 island system of São Tomé and Príncipe would be expected to result in little difference in natural
352 survival between the two islands. However, differences in hunting pressure exist and while
353 constant survival rates were similar, the Príncipe colony showed evidence for both maturation
354 and senescence (Table 3). With an absence of migration and heavy hunting pressure, Príncipe
355 may be the most natural system in our data set. Given this, it would suggest harvesting may
356 remove maturation and senescence signals by altering demographic structure, leading to more
357 constant risk across age classes. Alternatively, results could differ between the two islands due to
358 sampling biases. The breeding seasons of *E. helvum* are out of phase on the islands, and sample

359 collection was conducted via hunting at dispersed, small day-roosts soon after the beginning of
360 the birth pulse in São Tomé versus via overnight mist-netting outside of breeding and mating
361 seasons in a large colony in Príncipe (Peel et al., In press). Follow-up studies in these two island
362 systems would be valuable in providing insight into what age structure of long-lived bats should
363 look like, and the conservation implications of the heavy hunting currently being experienced in
364 São Tomé. Studies of declining and smaller isolated populations may also be used to determine if
365 social facilitation through Allee effects exist, thus leading to intermediate colony sizes having
366 highest survival through the positive Allee effects and lack of inhibitory mortality when at
367 carrying capacity.

368 Heterogeneity among individuals in their susceptibility to harvest may affect the overall
369 population response. Here, a greater proportion of males predicted greater survival probability.
370 We speculate that rather than males being longer lived, this might reflect seasonal variation in
371 social structures via non-random roosting and migration, resulting in unmeasured colony ‘types’
372 within sampled populations (Peel et al., In press). During periods where the majority of
373 individuals in a colony undertake seasonal migration, the two colonies here with highest
374 proportions of males and survival rates (Accra and Dar es Salaam) maintain ‘resident’ male
375 colonies where perhaps older, more dominant males are able to remain in the colony and
376 maintain their roosting territory. In Ghana, females migrated prior to males and more males
377 remained resident (Hayman et al., 2012) and male biases were observed in small roosts in São
378 Tomé (Peel et al., In press), however sample sizes were insufficient to support separate analyses
379 by colony type. Greater male survival has been reported in North American little brown bats,
380 *Myotis lucifugus*, however other studies report greater female survival being greater, with non-
381 random bat roosting noted as a confounding factor (Keen & Hitchcock, 1980). Other robust bat
382 survival studies including large capture-recapture studies (e.g. Sendor & Simon, 2003, Hayman
383 et al., 2012) have not found differences in survival between sexes.

384 Hunting methods such as netting and shotguns at roosts are presumed to be random
385 (Epstein et al., 2009), though only if the targeted colony is an unbiased representation of the total
386 population. With the heterogeneity in colony types observed here, the effect of even ‘random’
387 hunting methods is likely to vary according to the location and timing of hunting (Peel et al., In
388 press). A particular region where hunting occurs may only ever see migrating populations with a
389 female- and younger-age class bias. Alternatively, some hunting methods may be truly biased.

390 Hunting using wire-mesh fruit traps during the mating season in São Tomé and Príncipe results
391 in a male-biased capture if a female is caught first (Peel et al., In press).

392 Heterogeneity in survival and vulnerability to harvest can mimic compensation and mask
393 detection of additive mortality (Sandercock et al., 2011). Heterogeneity in colony structure and
394 susceptibility to hunting is an important factor to control for, and further characterisation of the
395 relationship between age and sex biases and hunting pressures should be a focus for future
396 studies. Relative seasonality of natural mortality and harvesting can change the way the
397 harvesting mortality affects a species' population dynamics (Boyce et al., 1999). No data exist on
398 seasonality in natural mortality in *E. helvum*. Migration is typically assumed to be costly, with
399 cost positively associated with migration distance (Lok et al., 2015), so higher natural mortality
400 of *E. helvum* peaks could be expected during and soon after migration. Overlap of hunting with
401 migration might therefore result in additive mortality. Strong seasonality of bat hunting has been
402 reported in other species (Brooke & Tschapka, 2002, Epstein et al., 2009, Struebig et al., 2007),
403 coinciding with seasonal peaks in abundance due to migration. Kamins et al. (2011) reported
404 strong hunting seasonality (November to March) in Ghana, coinciding with the beginning of the
405 gestation period through to the beginning of the birthing period and northerly migration in the
406 region (Hayman et al., 2012, Thomas, 1983), so peaks in hunting naturally coincide with
407 migratory influxes.

408 A caveat in our analyses is we standardize the age count data of each colony to account
409 for tooth analyses being conducted on a subset of individuals caught (Peel et al., In press). The
410 standardisation may smooth over the subtler effects of maturation and senescence, though we
411 feel this is unlikely to be a major effect as the Príncipe data still showed maturation and
412 senescence (Table 2). An alternative explanation for the finding that there is constant risk and
413 relatively high survival rates across locations may be because life table analyses can be biased if
414 there is not a stable age distribution (Williams et al., 2002). Changes in hunting pressures and
415 methods may affect inferences from life table analyses, depending on whether the populations
416 are in decline, hunting is more or less random, or if it is variable in intensity. In rapidly declining
417 populations, an analysis of age structure may fail to detect the decline, especially if harvesting
418 affects all age classes. Our analyses were relatively insensitive to changes in population growth
419 rate (λ , Fig. S3), highlighting the need for longitudinal studies.

420 Despite observations and analyses presented here involving considerable effort and
421 contributing to sparse and patchy data published on this species, we were unable to test all our
422 hypotheses. Sex was the strongest predictor of survival, though we propose this is likely to be a
423 function of colony ‘type’ rather than inherently longer survival of males. The lack of knowledge
424 of social structure, roost location and colony sizes of *E. helvum*, and other harvested bat species,
425 limits the capability to determine the risk from over-hunting and warrants further studies across
426 large spatial scales.

427 Based on all the contributing factors discussed, we hypothesize natural mortality in *E.*
428 *helvum* includes maturation with reduced mortality risk and senescence, as observed in the least
429 hunted colony from Príncipe. Our study failed to find substantial differences in survival rates
430 among sites with different hunting and migration rates. However, we hypothesize that hunting is
431 largely additive to natural mortality in *E. helvum*. but that the large continental distribution with
432 regional variation in hunting pressure and migration among source and sink colonies may allow
433 some compensation. Local movement and regional migration and compensation they may
434 provide highlights the conservation benefit for maintaining habitat continuity in migratory
435 species.

436 Our inability to detect the impact of hunting through life table methods raises an
437 important issue for conservationists, because *E. helvum* is extremely mobile, long-lived, and
438 highly hunted. *Eidolon helvum* was listed as Near Threatened in 2008 due to significant
439 population declines (Mickleburgh et al., 2010). The potential implications for ecosystem
440 functioning through pollination and seed dispersal resulting from even small declines of a
441 common and widespread species like *E. helvum* are substantial (Gaston & Fuller, 2008). Our
442 studies suggest that robust longitudinal, multi-site and indeed multi-national studies are required
443 to determine if this species is being over-harvested. In the absence of such studies, *E. helvum* and
444 other similar species may be driven into decline without us knowing it.

445

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466

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624

625

Figures and Tables626 **Table 1**

627 Hunting and population size details for colonies used in survival analyses, sorted by hunting
 628 pressure. * Likely substantially underestimated (Peel et al., In press). ** Range from 4,000 to
 629 1,000,000 (Hayman et al., 2012)

Location	Estimated hunting pressure	Number of bats caught	Proportion male	Estimated population size
São Tomé, São Tomé and Príncipe	High	102	0.91	9,000*
Accra, Ghana	Medium	1518	0.39	100,000**
Dar es Salaam, Tanzania	Low	130	0.74	5,000
Príncipe, São Tomé and Príncipe	Low	61	0.46	24,000
Morogoro, Tanzania	Low	101	0.53	10,000

630

631

632 **Table 2**

633 Deviance information criterion (DIC) values for each model for each data set analysed. Support
 634 for models with greater than two DIC units are indicated by bold text. For Príncipe, the ‘Both’
 635 model with maturation and senescence only was better than all other models (underlined).
 636 Lowest DIC values are in italics.

	Dar es Salaam	Morogoro	Accra	São Tomé	Príncipe
Constant	<i>93.88</i>	55.53	<i>176.90</i>	66.10	77.32
Maturation	94.81	57.93	177.59	68.46	79.10
Senescence	94.81	57.53	177.59	68.63	79.09
Maturation-Senescence	94.88	58.15	178.11	69.13	<u>76.93</u>
Siler	95.29	58.12	178.18	68.53	78.06

637

638

639 **Table 3**

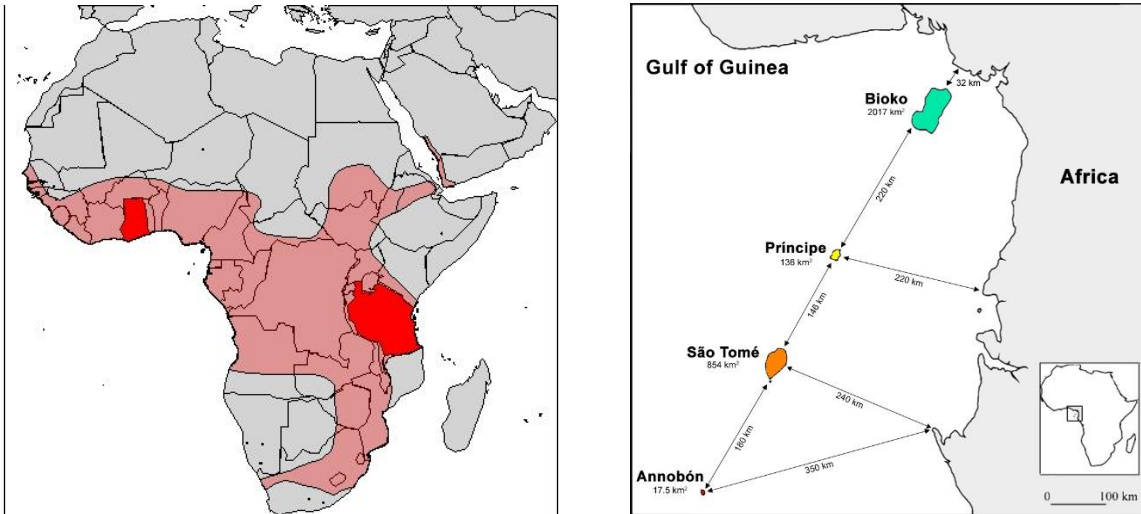
640 Mean life expectancy calculated from annual survival probabilities (S) using the formula life
641 expectancy = $-1/\ln(S)$, where S was estimated from the constant risk model $l_x = l_{x,2}$ (see methods).

Location	Mean annual survival probability (S)	Mean life expectancy (years)
Dar es Salaam	0.86 (0.76-0.92)	6.71
Morogoro	0.65 (0.60-0.69)	2.32
Accra	0.86 (0.77-0.93)	6.71
São Tomé	0.74 (0.67-0.79)	3.26
Príncipe	0.77 (0.65-0.86)	3.87

642

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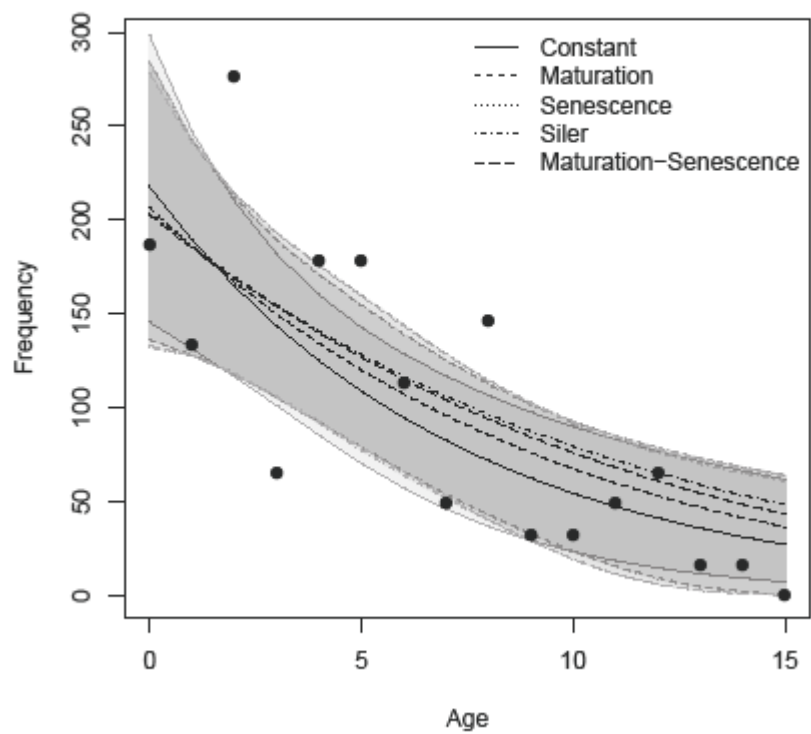
644 FIGURES



645
646 **Fig. 1.** The distribution of the Straw-coloured fruit bat, *Eidolon helvum*, red shading, with the
647 continental sampling locations shown (red, left map). Distribution data were from the IUCN Red
648 List (<http://www.iucnredlist.org/>) and maps from rworldmap (South, 2011). The Gulf of Guinea
649 island sampling locations with the distances to the mainland (right map).

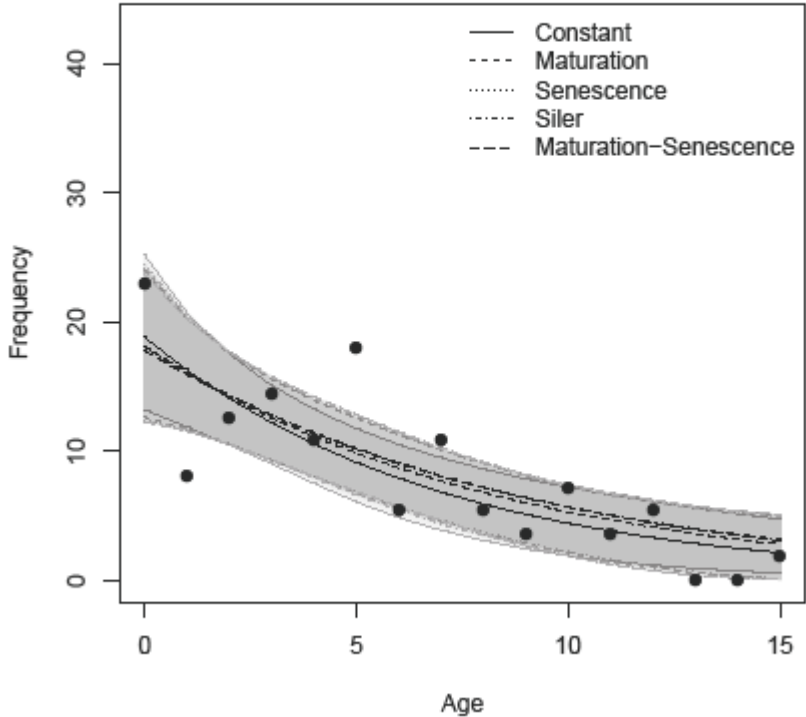
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Accra



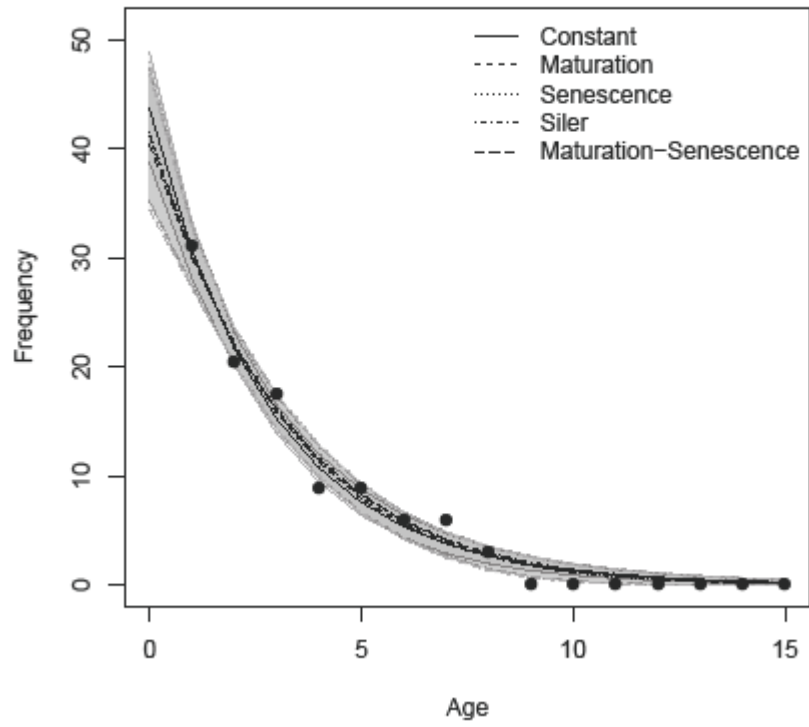
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DarEsSalaam



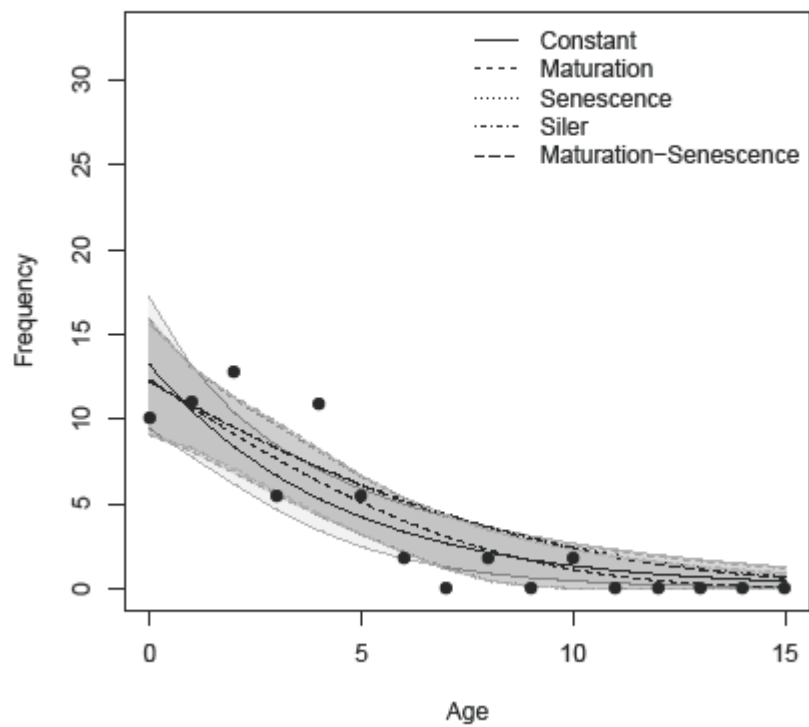
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Morogoro

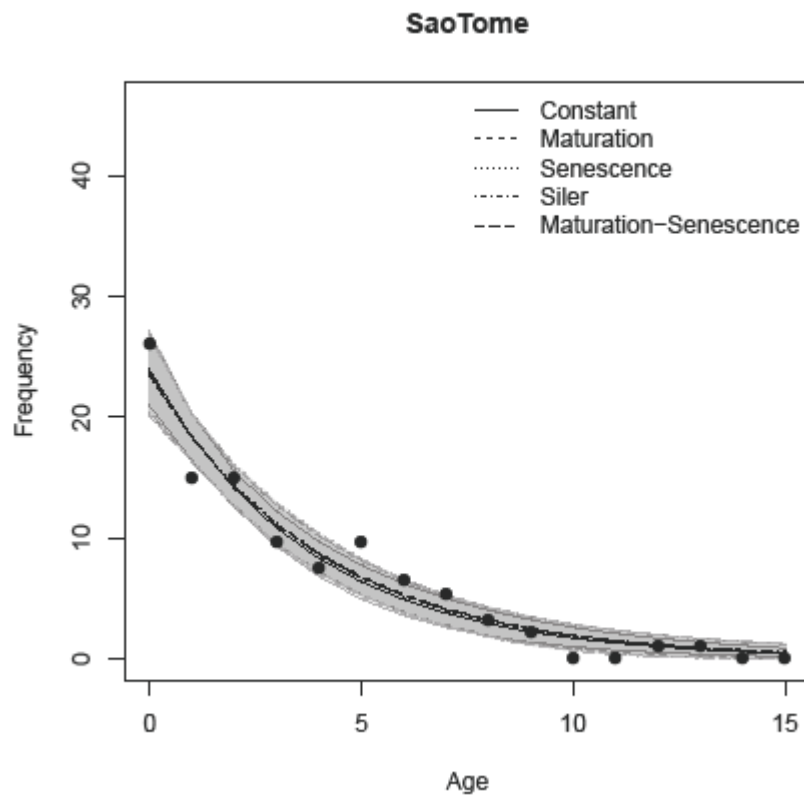


654

Principe



655



656

657 **Fig. 2.** The hazard model fits to the standardised tooth cementum annuli data for each colony.

658 Overall survivorship is constant risk ($l_x = l_{x,2}$, solid line), maturing risk ($l_x = l_{x,1} l_{x,2}$, dashed line),

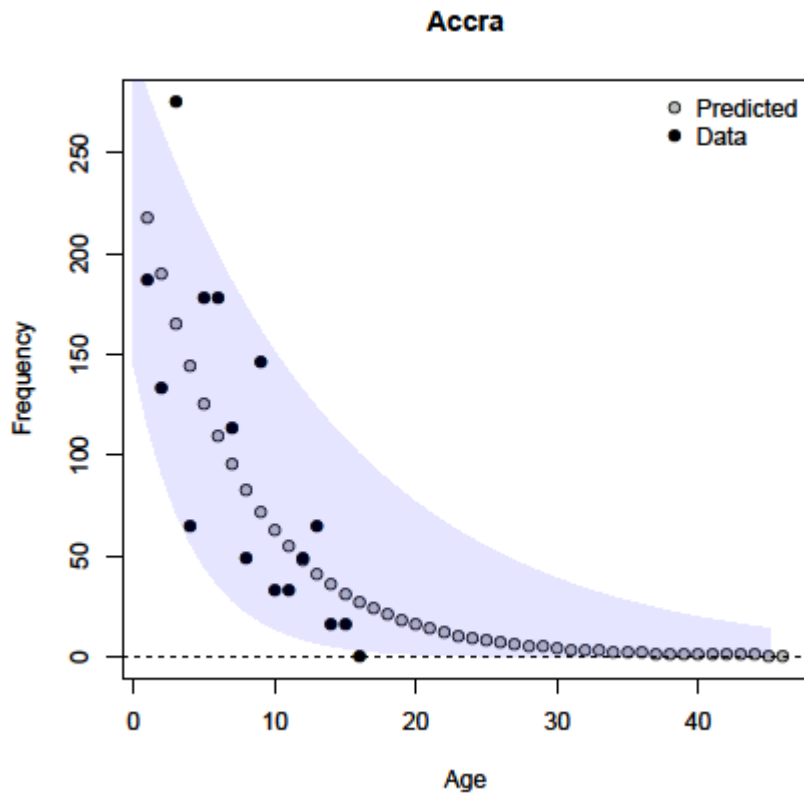
659 senescing risk ($l_x = l_{x,2} l_{x,3}$, dotted line), and constant, maturing and senescing risks ($l_x = l_{x,1} l_{x,2}$

660 $l_{x,3}$, dot-dashed line) and maturing and senescing risks only ($l_x = l_{x,1} l_{x,3}$, long-dashed line). 95%

661 credible intervals are shown in grey.

662

663



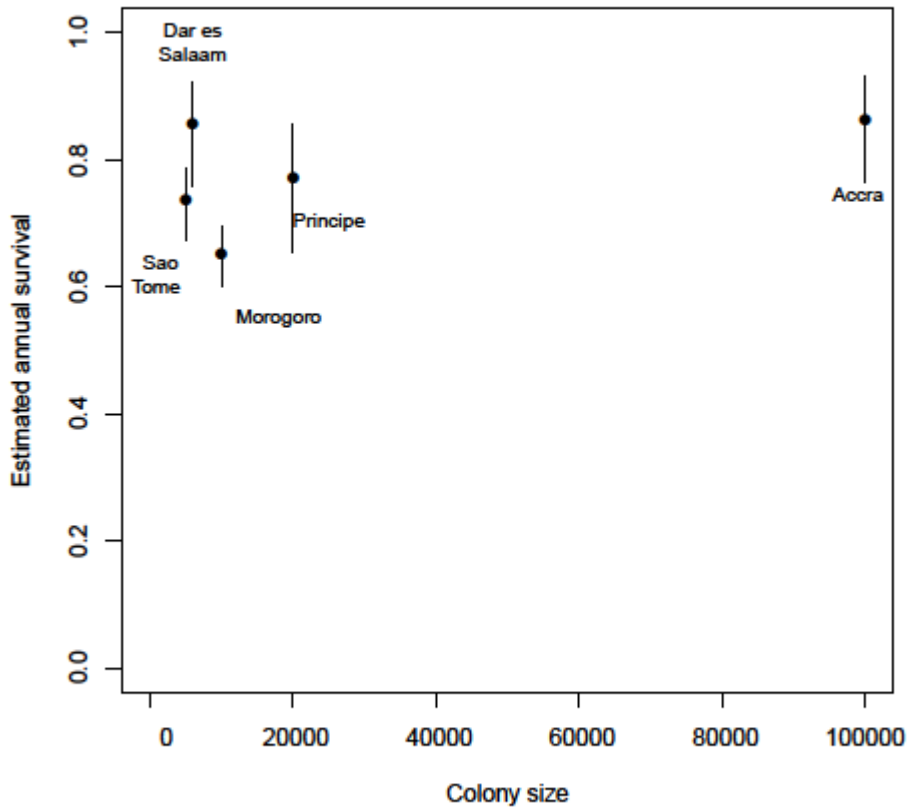
664

665 **Fig. 3** Predicted age frequencies for the Accra, Ghana colony using the constant survival rates

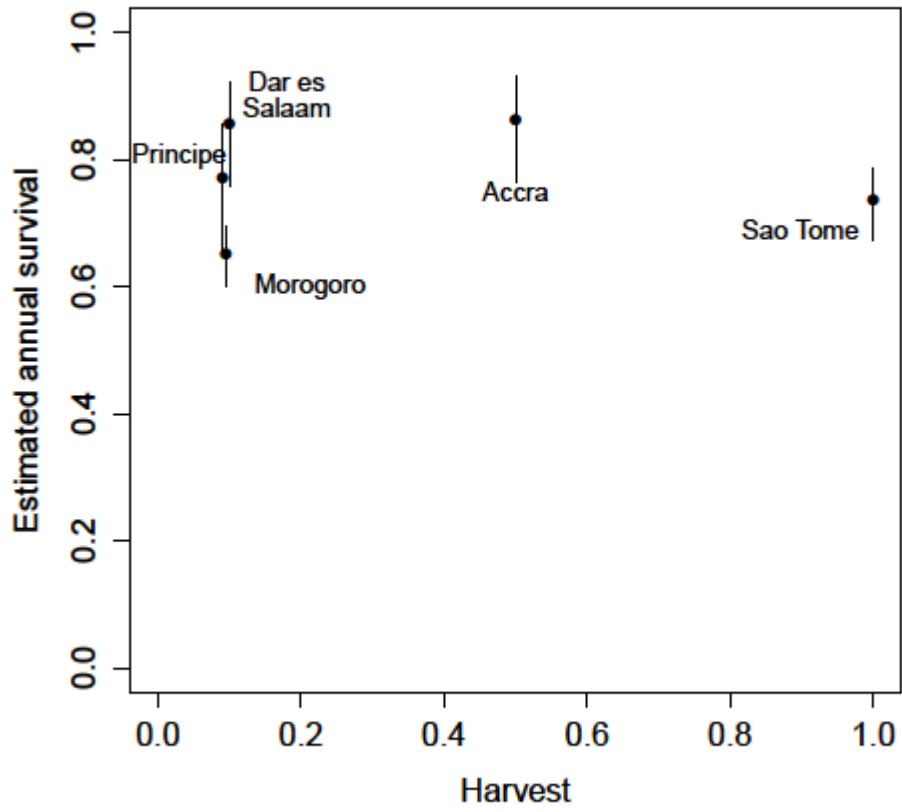
666 estimated for *Eidolon helvum*. 95% confidence intervals are shown.

667

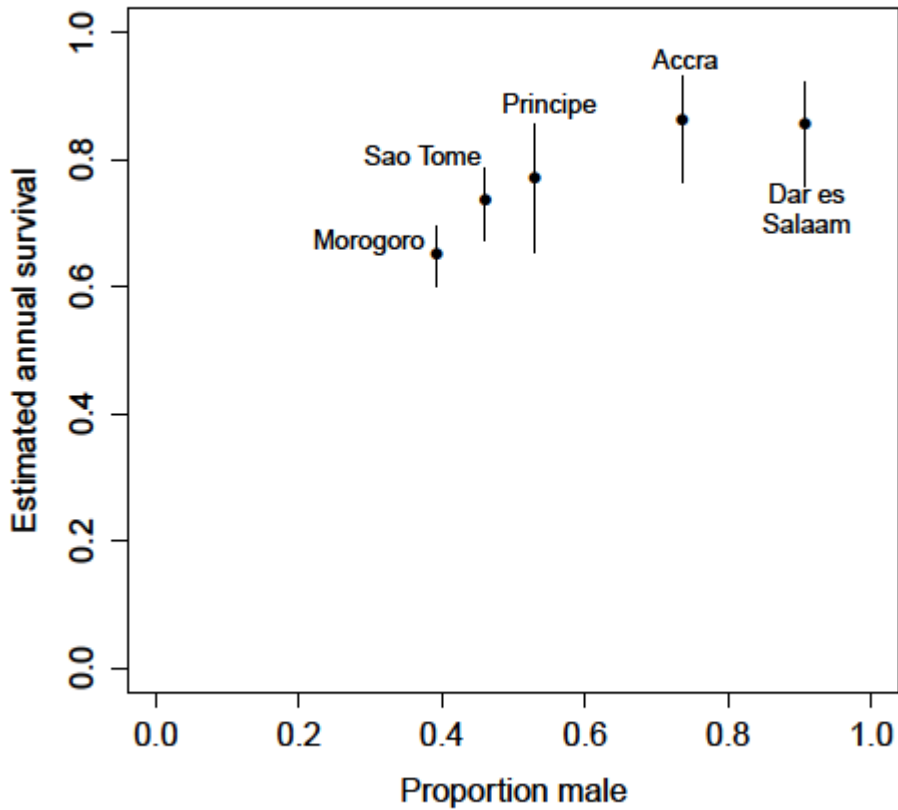
668



669 A)



670 B)



671 C)

672 **Fig. 4** Constant survival rates estimated for *Eidolon helvum* from five different locations with
 673 differing colony size (A) harvest rates (B, ranked 0 to 1 subjectively on hunting pressure, Peel et
 674 al., In press), and proportion of males (C). Constant survival rate estimates and proportion male
 675 across five colonies were correlated (F-statistic 15.28, $p < 0.05$). Mean estimates with 95%
 676 credible intervals are shown for each colony.

677

678