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Effects of climate variability on the demography of wild geladas

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25 **Keywords:** climate change, demographic buffering, environmental stochasticity, primates, vital
26 rates

27 **Abstract**

28 Nonhuman primates are an essential part of tropical biodiversity and play key roles in
29 many ecosystem functions, processes, and services. However, the impact of climate variability
30 on nonhuman primates, whether anthropogenic or otherwise, remains poorly understood. In this
31 study, we utilized age-structured matrix population models to assess the population viability and
32 demographic variability of a population of geladas (*Theropithecus gelada*) in the Simien
33 Mountains, Ethiopia with the aim of revealing any underlying climatic influences. Using data
34 from 2008-2019 we calculated annual, time-averaged, and stochastic population growth rates (λ)
35 and investigated relationships between vital rate variability and monthly cumulative rainfall and
36 mean temperature. Our results showed that under the prevailing environmental conditions, the
37 population will increase ($\lambda_s = 1.021$). Significant effects from rainfall and/or temperature
38 variability were widely detected across vital rates; only the first year of infant survival and the
39 individual years of juvenile survival were definitively unaffected. Generally, higher temperature
40 in the hot-dry season led to lower survival and higher fecundity, while higher rainfall in the hot-
41 dry season led to increased survival and fecundity. Overall, these results provide evidence of
42 greater effects of climate variability across a wider range of vital rates than those found in
43 previous primate demography studies. This highlights that although primates have often shown
44 substantial resilience to the direct effects of climate change, their vulnerability may vary with
45 habitat type and across populations.

47 **Introduction**

48 Atmospheric concentrations of greenhouse gases are approaching levels unseen in the
49 past 20 million years, critically altering the atmosphere, oceans, and freshwaters (Beerling &
50 Royer, 2014). Concomitantly, temperature and precipitation regimes have become more variable
51 and extreme and will likely continue to intensify globally (IPCC, 2021). Although the body of

52 literature regarding the effects of climate variability on animal demography and population
53 dynamics continues to grow, the complexity of the underlying mechanisms demands further
54 advances in research and methodology (Blois *et al.*, 2013; Boyce *et al.*, 2006). Climate changes
55 will not, however, exert equivalent effects on all taxa, requiring detailed study to ensure that
56 conservation challenges are met with a tailored approach (Moritz & Agudo, 2013). Nonhuman
57 primates are among the most highly studied and most vulnerable mammal clades, with ~66.5%
58 of species at risk of extinction (IUCN, 2021), but relatively few studies have investigated the
59 effects of climate variability on their demography (Estrada *et al.*, 2017). Although their frequent
60 occurrence in forested habitats and small group sizes often present logistical and statistical
61 obstacles to robust data collection and analysis, even scant demographic data have been shown to
62 provide useful insight into the conservation needs of primate populations (Blomquist,
63 Kowalewski & Leigh, 2009). Particularly in the current era of climate change, detailed
64 demographic research can help disentangle the complex interactions between environmental
65 factors and population shifts.

66 Previous studies have already indicated that climate can have pronounced effects on the
67 demography of primates. For example, severe climatic events such as El Niño have been shown
68 to greatly increase extinction risk in Milne Edward's sifaka (*Propithecus edwardsi*) populations
69 already under pressure from hunting and deforestation (Dunham *et al.*, 2008). Clear local climate
70 effects on demography have also been found in Verreaux's sifakas (*Propithecus verreauxi*)
71 (Lawler *et al.*, 2009). Although studies such as these raise serious concerns given predicted
72 increases in local climate extremes (Orlowsky & Seneviratne, 2012) and higher temperature and
73 precipitation variance (Watterson, 2005) due to climate change, others have suggested
74 substantial resilience of vital rates (which measure demographic rates such as survival,
75 reproduction, and death) across a variety of species (Morris *et al.*, 2011; Campos *et al.*, 2017).

76 A study of seven primate species showed that populations tend to exhibit low temporal
77 demographic variability compared to other vertebrate taxa and that this variability had little
78 effect on long-term fitness, suggesting that traits such as dietary flexibility, sociality, and highly
79 developed cognition may buffer against the detrimental effects of environmental stochasticity
80 (Morris *et al.*, 2011). More comprehensive analyses of the same primate populations found
81 relationships between local and/or larger-scale climate variability and fecundity in three species,
82 but little evidence for climate influences on survival (Campos *et al.*, 2017). Notably, none of the

83 vital rates for which climate variation was a strong predictor had large impacts on population
84 growth rate as a whole.

85 In this study, we used demographic and life history data to assess the viability and
86 demographic variability of a gelada (*Theropithecus gelada*) study population with respect to
87 underlying climate influences. Geladas aggregate into the largest groups of any non-human
88 primate and are easily observed upon the Afro-alpine grasslands they inhabit, which facilitates
89 extensive data collection. Yet, their high altitude habitat and narrow, granivorous diet may also
90 make them particularly sensitive to climatic change and synergistic anthropogenic factors,
91 though seasonal reliance on belowground plant organs during the dry season may buffer some of
92 these effects (Fashing *et al.*, 2014). Preliminary climate models have suggested that for every
93 2°C increase in mean global temperature, the lower altitudinal limit of gelada habitat will rise by
94 500m and approximately halve suitable habitat area (Dunbar, 1998). This pressure is likely to be
95 exacerbated by the concurrent expansion of arable land. Sustained agricultural encroachment in
96 protected areas has already led to severe erosion and significant loss of the aboveground biomass
97 upon which geladas rely (Hunter, 2001). These pressures are corroborated by worsening trends
98 of crop-raiding and intensifying human-gelada conflict (Yihune, Bekele & Tefera, 2009).
99 Furthermore, mounting research comparing study sites with different levels of anthropogenic
100 disturbance supports the notion that these activities can significantly alter gelada feeding ecology
101 and behavior (Fashing *et al.*, 2014; Woldegeorgis & Bekele, 2015). These studies suggest that
102 geladas may be under increasing threats, but detailed demographic analyses supporting these
103 findings are currently lacking. In this study, we focused identifying any significant effects of
104 climate variability on vital rates by modelling vital rate responses to precipitation and
105 temperature as well as assessing the viability of the study population, thus granting more detailed
106 insight into how climate influences demographic change.

107

108

109 **Materials & Methods**

110 *Study Species*

111 Geladas are the lone extant species of the formerly widespread genus *Theropithecus*
112 (Delson, 1993) and are endemic to the highlands of Ethiopia (Dunbar, 1993). Their range is often

113 discontinuous as they only inhabit elevations from 1500-4500m in which the rugged landscape is
114 dominated by largely treeless plateaus of Afroalpine grassland fragmented by sheer escarpments
115 (Iwamoto & Dunbar, 1983; Iwamoto, 1993). As the only gramnivororous primate species, the
116 gelada diet consists primarily of graminoid (grass-like) leaves (Hunter, 2001, Fashing *et al.*,
117 2014). Yet unlike other grazers, geladas organize into a complex, multi-level social system of
118 basic reproductive units of typically one male with 1-12 adult females and their offspring, bands
119 of frequently associating units, and herds of converging bands reaching up to 1200 individuals
120 (Kawai *et al.*, 1983; Snyder-Mackler, Beehner & Bergman, 2012). Geladas have been classified
121 as moderately seasonal breeders (van Schaik *et al.*, 1999) with an ecological birth peak occurring
122 during maximum green grass availability in the late cold-wet season; however, a larger social
123 birth peak driven by seasonal male unit takeovers occurs in the cold-dry season (Tinsley Johnson
124 *et al.*, 2018). Their uniquely compartmentalized social structure and terrestrial lifestyle facilitates
125 demographic data collection despite very large group sizes. In addition, geladas have a dispersal
126 pattern in which females remain with their natal unit through life while males emigrate to all-
127 male bachelor groups as subadults or even juveniles (Le Roux *et al.*, 2011; Snyder-Mackler *et*
128 *al.*, 2014). This dispersal system ensures a negligible amount of immigration and emigration by
129 females which form the foundations of many demographic analyses.

130 At present, geladas are designated as Least Concern by the IUCN Red List as they are
131 abundant within their range and no evidence suggests dramatic range-wide decline (Gippoliti *et*
132 *al.*, 2019). Nonetheless, the species is protected under the Endangered Species Act and, like most
133 primates, listed in Appendix II under the CITES treaty, which prohibits its trade for commercial
134 purposes. Extrapolations from surveys in 1973 yielded a maximum range-wide population
135 estimate of 250,000 individuals (Dunbar, 1998), whereas the most recent surveys estimate a
136 number closer to 50,000-60,000 individuals (Beehner & Bergman, unpublished data). With the
137 global population in decline (Gippoliti *et al.*, 2019) and all wild populations restricted to the
138 Ethiopian plateau (Mori & Belay, 1990; Oates, 1996), these specialized primates are in a
139 precarious position despite their relative stability.

140

141 *Study Site*

142 This study was conducted as part of the Simien Mountains Gelada Research Project in the
143 Simien Mountains National Park in North Gondar, Ethiopia (Fig. 1), which contains one of the

144 largest populations of geladas (Beehner *et al.*, 2007) and is the only area in which they are
145 explicitly protected (Dunbar, 1993). In 2007, the Simien Mountains area was estimated to
146 contain 4260-4560 geladas (Beehner *et al.*, 2007); however, a more recent and comprehensive
147 survey estimated this number at closer to 7500 individuals (Beehner & Bergman, unpublished
148 data). The study population inhabits the Sankaber region, which ranges from 13°12'40" -
149 13°14'10" N and 38°00'47" - 38°02'00" E with elevation from 3000-3300m.

150 Sankaber and the Simien Mountains are identified as an Afroalpine grassland ecosystem
151 (Puff & Nemomissa, 2005) characterized by dramatic escarpments topped with grassland and
152 scrubland with sparse trees. Seasons are delineated by temperature and precipitation with the hot-
153 dry season running approximately from February to May, the cold-wet season from June to
154 September, and the cold-dry season from October to January (Tinsley Johnson *et al.*, 2018). Cold
155 nights (< 8.5°C) occur throughout the year, but daytime temperatures vary from average highs of
156 ~16°C in the cold-wet and cold-dry seasons, to ~20.5°C in the hot-dry season. Rainfall varies
157 more dramatically throughout the year with a sharp peak during the cold-wet season.

158 Despite its designation as a National Park in 1969, the Simien Mountains have
159 historically suffered from a high amount of disturbance from agriculture (Dunbar, 1977;
160 Iwamoto, 1979), and encroachment on protected land remains a prominent issue (Ejigu &
161 Bekele, 2014; Woldegeorgis & Bekele, 2015). Levels of disturbance vary across Sankaber with
162 human activity nominally prohibited on the plateau itself and increasing with proximity to the
163 village of Michiby (also located within the park). Livestock encroachment was widespread prior
164 to 2015 when new grazing restrictions went into place. In addition, a dirt and gravel road cuts
165 through the study area and is often used to transport goods and people.

166

167 *Data Collection*

168 Data were collected over 11 years between December 31, 2008 and December 31, 2019
169 from the Sankaber gelada population, using all female individuals from the units observed for the
170 entire study duration. This included 281 total females and 128 females of reproductive age for
171 estimating survival and fecundity rates, respectively. Behavioral, demographic, genetic, and
172 hormonal data have been systematically collected by the project since 2006, but routine
173 recording of all demographic events for a core set of gelada reproductive units was not fully

174 established until 2008. The dates for births, deaths, immigrations, emigrations, and
175 developmental transitions were recorded as the first day the event was observed. If more than
176 two days passed between observations of the corresponding group (and in the absence of other
177 information such as a wet infant or an umbilical cord for births), we assigned the midpoint of the
178 missing period as the event date. Deaths were assigned to females on the first day they were no
179 longer observed with their reproductive unit. For females, this is appropriate because female
180 geladas generally remain within their natal units throughout their lives. Similarly, we assumed
181 that the disappearance of any infant prior to weaning was a case of mortality.

182 Daily weather data including cumulative rainfall (mm), minimum and maximum
183 temperature (°C), and humidity were collected across the duration of the study period. This was
184 respectively done using a rain gauge and a shaded La Crosse WS-2315 U weather station (La
185 Crosse Technology; La Crosse, WA, USA). Nearly four months of data were not collected in
186 2016 due to field site evacuation. While we could not interpolate these data, all other sporadic
187 missing data over the study duration (due to occasional equipment failure or human error) were
188 interpolated with a classification and regression tree (CART) machine learning algorithm using
189 the *imputation* R package (van der Loo, 2021). CART algorithms use predictor values and cut
190 points to split the sample into homogeneous subsamples, and form binary decision trees through
191 this repeated process to impute the best values (Breiman *et al.*, 1984).

192
193 *Data Analysis*

194 ***Population Growth Rates***

195 The raw dataset contained comprehensive demographic and life history data from the
196 study population, yielding 11 years of data to be split into separate 1-year censuses taken on
197 December 31 of each year. These were then transformed into corresponding projection matrices
198 (**A**) populated with vital rates. Based on the minimum age at first reproduction of 4.9 years from
199 a range of 4.9 to 7.6 years with a median of 6.1 (Roberts *et al.*, 2017), there were five age classes
200 before reaching adulthood (see Fig. S1 in the Appendix). We chose to use minimum age at first
201 reproduction rather than alternatives such as median age as this more accurately reflected the
202 gelada life cycle as well as numbers of adults and juveniles in each census.

203 As shown in the matrix below, S_n , S_j , and S_a represented the probability of survival from
 204 one census to the next for infants, juveniles, and adult females, respectively (i.e., the number of
 205 individuals in the age class at $t + 1$ divided by the number of individuals in the preceding age
 206 class at t). Fecundity (F_a) was defined as the mean number of female offspring produced by all
 207 adult females across each intercensus interval with each adult capable of producing either 0 or 1
 208 offspring. To determine the number of individuals that survived to the first age class in each
 209 year, fecundity (F_a) was multiplied by the first infant survival rate (S_{n1}), defined as the proportion
 210 of infants born in an intercensus interval that survived to the first census after their birth.
 211 Because these individuals were born at any time during the interval, they ranged from 1 day (if
 212 born on December 30th) to nearly 1 year (if born on January 1st) of age at the time of entering the
 213 first age class. The proportion of infants in the first age class that survived to become juveniles in
 214 the second age class was subsequently designated as the second infant survival rate (S_{n2}). This
 215 transition (S_{n2}) of infants to the juvenile stage emulated the median weaning age of 1.5 years
 216 with a range of approximately 1 to 2 years. Individuals then proceeded in an annual stepwise
 217 fashion through the four juvenile age classes before transitioning to the adult stage (S_{j4}) at 5 to 6
 218 years of age. The adult stage was not age-stratified, so the matrix contained only one adult
 219 survival rate (S_a) rather than proceeding through additional age classes. Please see the life cycle
 220 graph (Fig. S1) in the Appendix for a full visualization and further explanation.

$$221 \quad \mathbf{A} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & S_{n1} \times F_a \\ S_{n2} & 0 & 0 & 0 & 0 & 0 \\ 0 & S_{j1} & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{j2} & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{j3} & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{j4} & S_a \end{bmatrix}$$

222 For each annual matrix, we calculated the dominant eigenvalue (λ) to assess the
 223 population growth rate as the population was close to stable stage structure in each year. This
 224 was verified using Keyfitz' Δ to compare the observed stage distribution of each annual matrix
 225 with the corresponding stable stage distribution (Keyfitz, 1968). These values ranged from 0.098
 226 to 0.175, indicating that the study population remained close to stable stage structure throughout
 227 the sampling period. In addition, we calculated the average deterministic growth rate and used
 228 numerical simulations to calculate the stochastic population growth rate (λ_s) with 95%

229 confidence intervals using the *stoch.growth.rate()* function with 50000 iterations from the *popbio*
230 package (Stubben & Milligan, 2007) in R (R Core Team, 2017).

231 In addition, sensitivities were calculated to determine the extent to which an absolute
232 change in each vital rate leads to a change in λ . The relevant matrix elements were summed to
233 acquire the cumulative sensitivities of infant and juvenile survival, while the chain rule was used
234 to separate the sensitivity of the fecundity term from that of the first infant age class survival rate
235 (Caswell, 2001).

236

237 *Climate Analysis*

238 Rainfall and temperature have long been established as important predictors of net
239 primary productivity (NPP), which further correlates to plant biomass (Chu *et al.*, 2016). By
240 extension, they are likely a reasonable metric for food availability, which inevitably affects vital
241 rates. Prior research on gelada feeding ecology in the Simien Mountains has also found that
242 aboveground food availability strongly positively correlated with rainfall across the previous 30,
243 60, and 90 days (Jarvey *et al.*, 2018). To be conservative, we tested both cumulative monthly
244 rainfall and mean monthly temperature for their relationships to vital rates.

245 This was accomplished with a moving window approach using the *climwin* package
246 (Bailey & van de Pol, 2016) to assess the effects of climate on gelada vital rates across every
247 possible combination of consecutive time windows within the 24 months preceding each census
248 on December 31. In keeping with Campos *et al.* (2017), a 24 month timeframe was chosen to
249 accommodate the lagged environmental effects on demography that have been shown to occur in
250 primates (Wiederholt & Post, 2011) and other animals (Hansen *et al.*, 2013). This method did,
251 however, exclude the 2016 and 2017 censuses due to missing data. We then converted each vital
252 rate into a binary list in which each relevant individual was assigned either a 1 if they survived to
253 the next census or gave birth in the intercensus interval or a 0 otherwise. These were then
254 modelled in generalized linear mixed models (GLMMs) with binomial error distributions and a
255 yearly random effect on the mean vital rate to investigate potential relationships between vital
256 rates and variability in either cumulative monthly rainfall or average monthly temperature.
257 Collinearity was avoided by the inclusion of only one climate variable per model.

258 For each combination of vital rates and climate variables, models of each time window
259 were ranked by sample size-corrected Akaike's information criterion (AIC_C; Burnham &

260 Anderson, 2002) against a null model with no climate variable. The moving window approach
261 suffers from a relatively high risk of false positives due to the sheer number of models involved.
262 Subsequently, P_C statistics have been shown to effectively discriminate Type I and Type II error
263 from true climate signals in as few as five iterations (van de Pol *et al.*, 2016). These values were
264 determined by comparing the number of models from observed versus randomized data falling
265 into the 95% confidence set over 100 iterations (van de Pol *et al.*, 2016). Each $P_C < 0.5$ was then
266 subjected to k -fold cross-validation to further evaluate model validity. k should ideally be a
267 whole number divisor of the number of trials, so with nine years of data, $k = 3$ was chosen.
268 Model reliabilities were further tested by evaluating the quantity of model weights falling within
269 the 95% confidence set where a lower percentage indicates higher confidence in a true signal
270 (Bailey & van de Pol, 2016). The strength of the relationship between a given climate variable
271 and vital rate was represented by β , which signifies the degree to which change in the climate
272 variable corresponds to change in the vital rate.

273 Because our dataset does not have the necessary level of sampling variability, we did not
274 estimate annual vital rates based on GLMMs with the random effect of year to reduce sampling
275 error. Other studies that have done so had some level of sampling variability inherent to their
276 methodology. For example, Altwegg *et al.* (2007) acquired survival data on barn owls (*Tyto*
277 *alba*) through a mark-recapture method, and Morris *et al.* (2011) used both males and females to
278 calculate survival rates, thus introducing sampling variability due to the conflation of dispersal
279 and mortality for either males or females. To the contrary, geladas have a matrilineal social
280 system (i.e., females do not disperse) and we exclusively used data collected through direct
281 observation of female individuals. Disappearances could therefore always be considered
282 mortality, particularly as they were almost always preceded by injury or disease.

283

284

285 **Results**

286 *Descriptive Statistics, Population Growth Rates, and Other Life History Statistics*

287 The sample population of females consisted of 281 unique individuals. Of 331 births, 157
288 were females, 174 were males, and 3 were unsexed, which yields an even sex ratio of 47%

289 females to 53% males. Deaths included three unsexed infants, 10 female infants, 53 juvenile
 290 females, and 56 adult females.

291 Deterministic population growth rates varied between 0.9427 and 1.0607 (Table 1) with
 292 an average of 1.0218. The corresponding stochastic growth rate (λ_s) was 1.0208. A time-
 293 averaged matrix was also used to compute net reproductive rate (1.43 individuals) and female
 294 lifespan conditional upon survival to adulthood (17.8 years). Net reproductive rate is defined as
 295 the average number of female offspring born to each female during her lifespan. Population
 296 growth rate was consistently most sensitive to adult survival, moderately sensitive to fecundity
 297 and juvenile survival, and least sensitive to infant survival (Fig. 2). In addition, it was
 298 comparably sensitive to each individual age class of both infant and juvenile survival.

299

300 *Table 1. Population growth rate (λ) and sample sizes in each annual census period and the aggregated*
 301 *stochastic growth rate (λ_s). λ ranged between 0.9427 in 2017 to 2018 and 1.0607 in 2013 to 2014.*

Population Growth Rates (λ)												
Year	08.09	09.10	10.11	11.12	12.13	13.14	14.15	15.16	16.17	17.18	18.19	stoch
λ	0.9787	0.9902	1.0391	1.0132	1.0091	1.0607	1.0584	1.0043	1.0389	0.9427	1.0540	1.0208
N	125	127	124	124	133	138	144	150	164	156	149	N/A

302

303 *Climate Analysis*

304 Moving window climate analysis showed fecundity to have significant positive
 305 relationships with both rainfall ($P_C = 0.460$) and temperature ($P_C = 0.445$). In the best models, the
 306 rainfall from February to April (hot-dry season) of the census year ($\Delta AIC_C = -4.181$, Fig. 3) and
 307 the temperature in February of the census year ($\Delta AIC_C = -3.804$, Fig. 3) had positive effects on
 308 fecundity ($\beta = 0.346$ and 0.439 , respectively).

309 Of the four juvenile survival rates, none were significantly affected by climate influences;
 310 however, when aggregated into a single vital rate to evaluate the unified juvenile life stage and
 311 account for low sample sizes, there was a significant relationship with temperature ($P_C = 0.064$).
 312 The best model included January to May of the year prior to the census year ($\Delta AIC_C = -9.847$,
 313 Fig. 4), indicating that higher temperature in the hot-dry season of the previous year may
 314 decrease survival in the subsequent year ($\beta = -3.230$).

315 Adult survival had significant relationships with both temperature ($P_C = 0.429$) and
316 rainfall ($P_C = 0.495$). In the best models, the temperature in April of the previous year ($\Delta AIC_C = -$
317 3.554 , Fig. 4) and the rainfall in March of the previous year ($\Delta AIC_C = -3.715$, Fig. 5) had
318 negative relationships to adult survival ($\beta = -0.523$, $\beta = -0.607$). These results indicate that higher
319 temperature and rainfall in the hot-dry season may decrease survival in the following year.
320 Conversely, the second infant survival rate (S_{n2}) had a significant positive relationship with
321 rainfall ($P_C = 0.450$) with the best model including March to July of the census year ($\Delta AIC_C = -$
322 5.378 , Fig. 5), which suggests that higher rainfall in the hot-dry season and early cold-wet may
323 lead to higher infant survival ($\beta = 0.896$). For the top models of all combinations of vital rates
324 and climate variables with corresponding statistics, see Table S1 in the Appendix.

325

326

327 Discussion

328 *Population Growth Rates*

329 Although the results indicate that the average population growth rate of the Sankaber
330 gelada population was > 1 , the annual growth rates varied greatly over the study period from
331 0.9427 to 1.0607 . The sensitivity analysis showed that adult survival had the greatest influence
332 on population growth rate, while infant survival had the least influence (Fig. 2). The population
333 growth rate was moderately sensitive to fecundity and, slightly less so, to juvenile survival. This
334 largely corroborates the generally held expectations for long-lived vertebrates (Eberhardt, 2002)
335 including primates (Lawler, 2011; Morris *et al.*, 2011). Furthermore, Pfister's (1998) hypothesis
336 proposes that vital rates which strongly influence fitness should vary less over time. This is based
337 on the prediction that increasing vital rate variation decreases long-term fitness; therefore,
338 natural selection should act to reduce variability in vital rates with the greatest influence on
339 population growth rate (Hilde *et al.*, 2020). Visual comparisons of sensitivities to variance
340 largely aligned with this predicted pattern (see Fig. S2 in the Appendix).

341 With a demographic stochastic growth rate of 1.0208 ± 0.0003 , one would expect
342 increasing population size over time; however, considering this calculation within a broader
343 spatiotemporal scope may grant some insight into the dynamics of the greater Simien Mountains
344 metapopulation. Censuses over an approximately 30-year period have shown that the population

345 at Sankaber as well as those at two other sites (Michibi and Gich) have remained stable across
346 this period (Dunbar, 1975; Ohsawa, 1979; Beehner *et al.*, 2007). These areas are fully within the
347 national park boundaries and are more heavily monitored than external areas. Though there has
348 been little systematic research on the protective influence of active scientific field stations,
349 research presence may provide some buffering against human encroachment (Laurance, 2013).
350 These routinely monitored populations could therefore be more insulated against anthropogenic
351 disturbance than other less protected areas within and outside the park boundaries. Especially
352 given evidence for worsening anthropogenic threats such as erosion and loss of aboveground
353 biomass due to agricultural activity (Hunter, 2001) and increased rates of crop raiding (Yihune,
354 Bekele & Tefara, 2009), stable population size in certain insulated areas fits neatly into a
355 framework of source-sink dynamics (Dunning, Danielson & Pulliam, 1992; Gundersen *et al.*,
356 2001).

357

358 *Demographic Variability vs. Climate Variability*

359 The moving window analyses detected effects of rainfall and temperature in many vital
360 rates in the Sankaber gelada population, including fecundity and adult, combined juvenile, and
361 second infant survival rates. The latter had a positive relationship to rainfall, indicating that
362 higher rainfall in the hot-dry season and early cold-wet season was linked to increased survival
363 in the second infant age class ($\beta = 0.896$). Peak green grass availability typically ends in the
364 cold-dry season, with worsening food scarcity persisting through the hot-dry season until rainfall
365 begins to increase during the cold-wet season of the following year. During this time, geladas
366 increasingly rely on subterranean foods such as roots, corms, and tubers (Fashing *et al.*, 2014;
367 Iwamoto, 1979) whose energetic returns on investment may be limited by the time and effort of
368 their harvest (Hunter, 2001). Perhaps if young geladas at the weaning transition do not access
369 underground foods with the same efficiency as adults, the more rapid return to green grass
370 availability due to dry-season rains increases their ability to survive the dry season.

371 Juveniles across several primate taxa have been shown to exhibit lower foraging
372 efficiency and, in some cases, higher mortality in times of food scarcity (Janson & van Schaik,
373 2002). Furthermore, these effects typically diminish rapidly with age (Janson & van Schaik,
374 2002), supporting the premise that such impacts would be particularly salient in young
375 individuals experiencing their first trials of independently foraging subterranean foods. This prior

376 research is supported by the disappearance of associated climate effects in the survival rates of
377 all subsequent juvenile age classes. Similar patterns of vulnerability to rainfall-linked
378 environmental factors in recently independent individuals have also been substantiated by prior
379 demographic studies on Verreaux's sifaka (Lawler *et al.*, 2009; Richard *et al.*, 2000) and rhesus
380 macaques (*Macaca mulatta*) (Blomquist, 2013).

381 While effects of rainfall were detected in the second infant survival rate, the first infant
382 survival rate corresponded to no detectable climate effects. In addition, first infant and adult
383 survival rates had moderate covariance (0.473), whereas no such relationship occurred between
384 second infant and adult survival rates. This aligns with infant development patterns in which
385 older infants will have started to become increasingly independent from their mothers and more
386 reliant on foraged foods due to the intensification and completion of the weaning process during
387 this period. Conversely, the covariance between first infant and adult survival corroborates prior
388 research that maternal disappearance or death comprised a major source of infant mortality in
389 geladas (Beehner & Bergman, 2008). Furthermore, in the Sankaber population, infants and
390 lactating mothers suffered significantly higher rates of injury during the three months following a
391 takeover (Schneider-Crease *et al.*, 2020). Nearly 60% of all infant mortality was attributed to
392 infanticide and likelihood of death was 32 times higher in the four months following a unit
393 takeover than in periods without takeovers (Beehner & Bergman, 2008). These data suggest that
394 the demographic upheaval brought about by dramatic social events such as male takeovers can
395 overshadow any effects of climate variability in certain vital rates.

396 With that said, effects of climate variability during the dry season were prevalent.
397 Fecundity showed a positive relationship to rainfall during the hot-dry season ($\beta = 0.346$).
398 Although prior research did not find any links between green grass availability and fecundity, an
399 energetic benefit from earlier or greater green grass availability nonetheless seems intuitively
400 probable (Tinsley Johnson *et al.*, 2018). In addition, higher fecundity most strongly correlated
401 with higher temperatures in the early dry-season of the census year ($\beta = 0.439$). This aligns with
402 known correlations linking higher temperatures to lower glucocorticoid levels and returns to
403 reproductive cycling (Tinsley Johnson *et al.*, 2018), which were particularly prevalent in the hot-
404 dry season. Furthermore, the strongest model window fell within the takeover season during
405 which the majority of all such events occur (Pappano & Beehner, 2014) and returns to cycling
406 would be most expected (Tinsley Johnson *et al.*, 2018).

407 Combined juvenile survival had clear evidence of climate signals, indicating that higher
408 hot-dry season temperature in the preceding year was linked to lower survival ($\beta = -3.230$). No
409 climate signals were detected in the survival rates of the individual juvenile age classes, but their
410 much smaller sample sizes in each year may have contributed to this absence. A similar, albeit
411 much weaker, relationship was also found in adult survival ($\beta = -0.523$). These relationships
412 could be related to heat stress, but prior research suggests that thermoregulatory stressors in
413 geladas are typically associated with cold temperatures (Dunbar, 1980, Tinsley Johnson *et al.*,
414 2018). However, there may also be more opaque, indirect explanations for these lagged effects.
415 Although 1-year lagged effects have only been shown in primates due to rainfall and the El Niño
416 climate oscillation (*Brachyteles hypoxanthus* and *Lagothrix lagothricha*: Wiederholt & Post,
417 2011), lagged effects from temperature have been found in a variety of montane and grassland
418 mammals including on population growth in American bison (*Bison bison*: Koons *et al.*, 2015)
419 and adult female survival and juvenile recruitment in woodland caribou (*Rangifer tarandus*
420 *caribou*: DeMars *et al.*, 2021). Willisch *et al.* (2013) found that higher winter air temperatures
421 corresponded to decreased survival in adult males and yearlings in alpine chamois (*Rupicapra*
422 *rupicapra*). Counterintuitive results such as these and the relationship between temperature and
423 juvenile and adult survival in our study suggest that such effects likely arise from indirect and
424 density-dependent factors such as competition and community-level interactions. For example,
425 the demonstrated temperature-induced increases in fecundity may increase competition for
426 resources in the following year. Density-dependent factors could also be of particular importance
427 given that resource availability, and therefore competition, undergoes dramatic seasonal variation
428 compared to tropical environments. While we do not yet understand how long-term climatic
429 cycles affect the availability of grass and other resources in Afroalpine grasslands, warmer
430 temperatures have been shown to exert negative effects on the phenology of numerous grassland
431 plant species in the year after they occur in American tallgrass prairie (Sherry *et al.*, 2011).
432 Should such lagged phenological effects occur, research on female olive baboons (*Papio anubis*)
433 has shown that the intensity of intragroup feeding competition increased during times of lower
434 food availability and higher reliance on fallback foods (Barton & Whiten, 1993; Johnson, 1989),
435 potentially influencing survival. Although this study cannot explain the complex underlying
436 mechanisms by which climate variability influences demographic rates, it nonetheless highlights
437 the risks geladas face as trends in climate change continue to worsen.

438 Lastly, higher rainfall in the hot-dry season of the previous year correlated to lower adult
439 survival ($\beta = -0.196$). No suitable explanation could be found for this relationship and given the
440 strong links between rainfall and NPP, it seems unlikely that higher rainfall during a period of
441 food scarcity would cause a decrease in survival rate. Furthermore, the very weak and
442 inconsistent model weight distribution of this relationship gives reason for skepticism.

443

444

445 *Comparison to Other Primates*

446 Mean vital rates from the Sankaber gelada population largely corroborate the analyses of
447 seven other primate species (Morris *et al.*, 2011). Nearly all of the species, including geladas,
448 were characterized by high survivorship throughout all life stages and relatively low fecundity as
449 expected from the typical reproductive strategy of primates. However, widespread evidence for
450 climate effects across vital rates distinguished geladas from other primates in which similar
451 research has been done. Of seven other primate species previously analyzed using similar
452 modelling techniques, four showed evidence of climate influences upon vital rates, but among
453 these only Verreaux's sifaka did so for more than one vital rate (Campos *et al.*, 2017). In
454 addition, the strongest effects were seen in the three most highly seasonal breeders: Verreaux's
455 sifaka, blue monkeys (*Cercopithecus mitis*), and northern muriquis (*Brachyteles hypoxanthus*).
456 Geladas are moderately seasonal breeders (van Schaik *et al.*, 1999); however, the larger of two
457 distinct birth peaks occurs in accordance with social rather than environmental drivers (Tinsley
458 Johnson *et al.*, 2018). The aforementioned study found no evidence of climate effects in the
459 moderately seasonal white-faced capuchins (*Cebus capucinus*) or yellow baboons (*Papio*
460 *cynocephalus*) (Campos *et al.*, 2017), indicating that this level of reproductive seasonality alone
461 may be insufficient to cause salient relationships between climate and vital rates. Nonetheless,
462 our study did provide evidence for influences of temperature variability on fecundity, suggesting
463 that although reproductive seasonality is predominantly dictated by social factors such as unit
464 takeovers, there may be environmental interactions.

465 Why then might geladas have greater evidence of climate influences across a wider range
466 of vital rates compared to these previously studied primates? The vast majority of primates
467 inhabit tropical ecosystems characterized by highly variable intra- and interannual rainfall

468 patterns (Feng, Porporato & Rodriguez-Iturbe, 2013), whereas geladas and the small number of
469 temperate species, including snub-nosed monkeys (*Rhinopithecus* spp.) and Japanese macaques,
470 further experience substantial daily and seasonal variation in temperature which impose
471 additional thermoregulatory and energetic constraints. Cold temperatures have been shown to
472 present obstacles to female reproduction in geladas (Tinsley Johnson *et al.*, 2018) and other
473 primates (*Aotus azarai*: Fernandez-Duque, Rotundo & Ramirez-Llorens, 2002; *Cercopithecus*
474 *mitis*: Foerster, Cords & Monfort, 2012; *Rhinopithecus bieti*: Xiang & Sayers, 2009), as well as
475 increased mortality in both geladas (Dunbar, 1980) and Japanese macaques (Enari, 2014).
476 Temperature extremes likely also increase the importance of accessibility and quality of fallback
477 foods as previously shown in both Japanese macaques (Hanya *et al.*, 2006) and black and white
478 snub-nosed monkeys (Grueter *et al.*, 2009). Although we did not reveal these specific
479 relationships, these examples illustrate that temperature extremes greatly influence the life
480 history events of primates inhabiting such ecosystems and support the particular importance of
481 temperature as shown by the salient effects on fecundity and adult and juvenile survival found in
482 this study. Given the demonstrated responses of gelada vital rates and the general sensitivity of
483 montane environments to climate change, elucidating the causal relationships between these
484 unique environmental conditions and demography will only become increasingly pertinent.
485 Nonetheless, deeper understanding will require additional research on geladas and other cold-
486 weather primates.

487

488 *Conclusions and Future Directions*

489 This study revealed more extensive climate influences across vital rates in geladas
490 compared to prior primate studies. Although the results painted a tentatively positive picture of a
491 healthy and stable study population, it also revealed the need for more thorough assessment of
492 the broader Simien Mountains metapopulation and geladas as a whole. This is particularly
493 pertinent given evidence for the sensitivity of geladas to climate change due to the environmental
494 extremes of their habitat and the apparent strong responses of their vital rates to changes in
495 climatic conditions. The study also highlighted a continued mismatch between demographic
496 studies suggesting resilience to climatic change (Campos *et al.*, 2017) and the grimmer
497 conclusions of studies investigating phenomena such as extreme climate events and broad-scale
498 climate change (Korstjens & Hillyer, 2016; Estrada *et al.*, 2017; Zhang *et al.*, 2019).

499 This study did not investigate social factors, but prior research has widely demonstrated
500 their great importance. In particular, takeovers have been shown to significantly influence
501 conceptions and births (Tinsley Johnson *et al.*, 2017) and adult female and infant mortality
502 (Schneider-Crease *et al.*, 2020). Future research should therefore explore the impact of such
503 events to provide a more complete understanding of gelada demographic variation. An
504 understanding of how environmental variability affects takeover frequency and timing would
505 improve not only an understanding of the mechanistic drivers of these social shifts, but also the
506 ability to predict their frequency and the demographic changes that follow. These social
507 dynamics may also be more broadly linked to density-dependent factors such as resource
508 competition that result from climate variability and other environmental factors.

509 In conclusion, further research should aim to disentangle the network of influences from
510 direct climate variability, indirect climate change synergies resulting in range loss, stochastic
511 severe weather events, and indirect climate effects acting through social dynamics. This
512 information will benefit not only geladas, but also the greater primate order and other organisms
513 with similar life history strategies, particularly in the current era of accelerating climate change.

514

515

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527

528 **Conflicts of Interest**

529 The authors declare no conflicts of interest.

530

531 **Author's Contributions**

532 ES conceived of the research idea and led the writing of the manuscript; ES and HJ
533 designed the methods and analyzed the data. ES, JB, TB, AL, and NSM contributed to funding
534 for the long-term project and long-term data collection. All authors provided valuable
535 contributions to the drafts and gave final approval for publication.

536

537 **Data Availability**

538 Data and R scripts are available through the Simien Mountains Gelada Research Project
539 GitHub repository:

540 https://github.com/GeladaResearchProject/Sloan_et_al_2022-climate-demography

541

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827 828 **Figures and Tables**

829 **Fig. 1** Location of Simien Mountains National Park and gelada populations throughout Ethiopia.
830 Map sources: ESRI, Inc. 2016, Redlands, CA; Ethiopian Wildlife Conservation Authority.
831

832 **Fig. 2** Time-averaged sensitivities of population growth rate (λ) to each vital rate wherein higher
 833 values represent greater influence upon λ . S_n , S_j , and S_a are respectively infant, juvenile, and
 834 adult survival. S_n and S_j are further split into their respective age classes. F_a is adult fecundity.

835

836 **Fig. 3** Moving window analysis of $\Delta AICc$ for the effect of cumulative monthly rainfall and
 837 monthly mean temperature on adult fecundity. Each grid cell corresponds to a time window
 838 which opens and closes between 0 and 24 months before the annual census as indicated on the
 839 axes. Deeper purple cells indicate more informative models relative to a null model without
 840 climate variables.

841

842 **Fig. 4** Moving window analysis of $\Delta AICc$ for the effect of mean monthly temperature on
 843 survival of juveniles and adults. Each grid cell corresponds to a time window which opens and
 844 closes between 0 and 24 months before the annual census as indicated on the axes. Deeper purple
 845 cells indicate more informative models relative to a null model without climate variables.

846

847 **Fig. 5** Moving window analysis of $\Delta AICc$ for the effect of cumulative monthly rainfall on
 848 survival of the second infant age class and adults. Each grid cell corresponds to a time window
 849 which opens and closes between 0 and 24 months before the annual census as indicated on the
 850 axes. Deeper purple cells indicate more informative models relative to a null model without
 851 climate variables.

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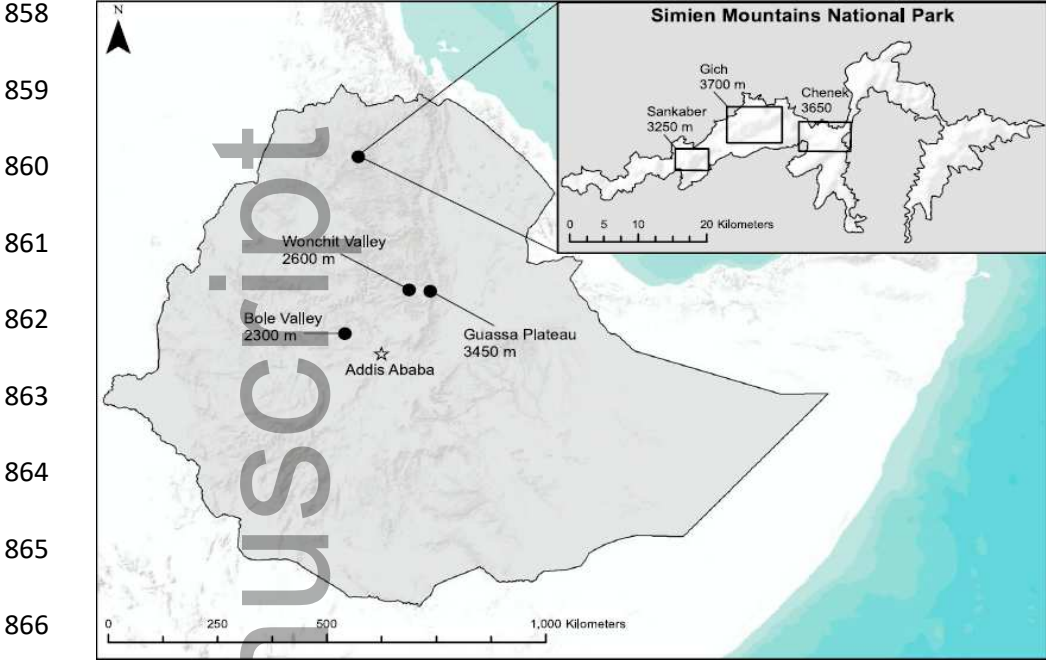
853 *Table 1. Population growth rate (λ) in each annual census period and the aggregated stochastic growth*
 854 *rate (λ_s). λ ranged between 0.9424 in 2017 to 2018 and 1.0823 in 2013 to 2014.*

855

Population Growth Rates (λ)												
Year	08.09	09.10	10.11	11.12	12.13	13.14	14.15	15.16	16.17	17.18	18.19	stoch
λ	0.9751	0.9923	1.0382	1.0141	1.0254	1.0695	1.0823	1.0069	1.0231	0.9424	1.0577	1.0227

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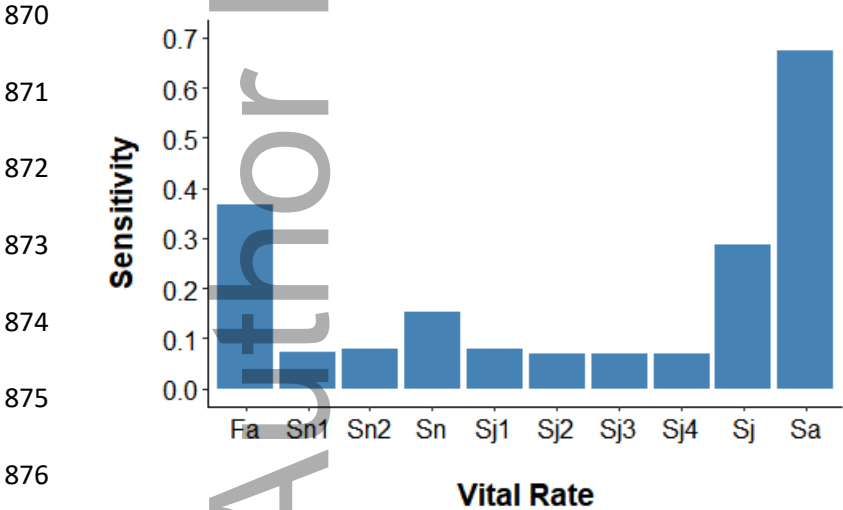
857 **Fig. 1**



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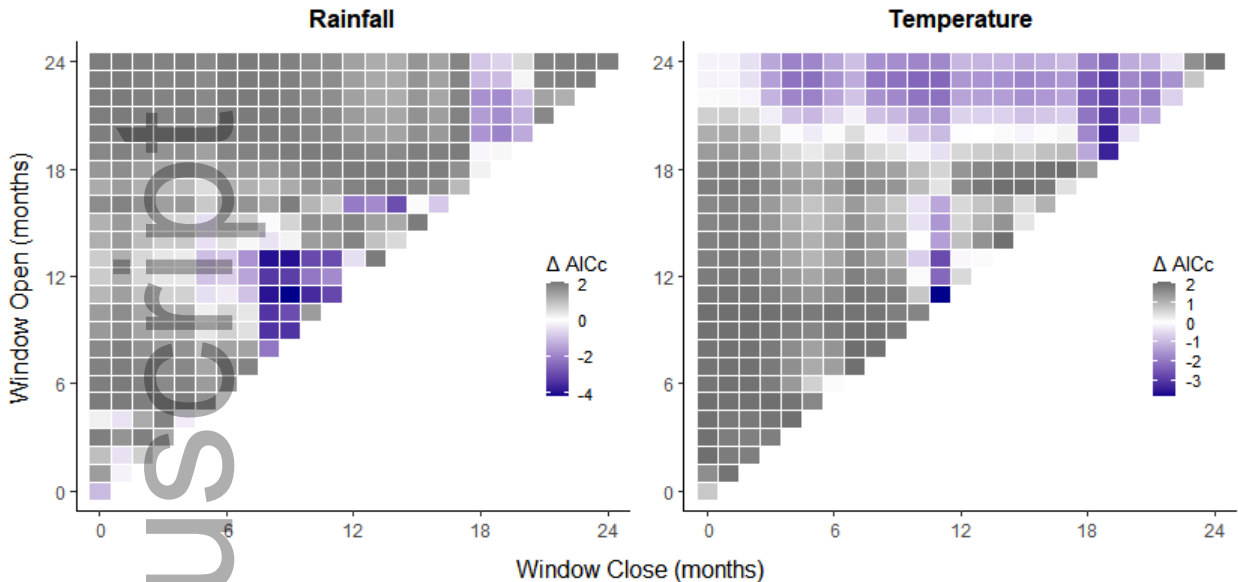
869 **Fig. 2**



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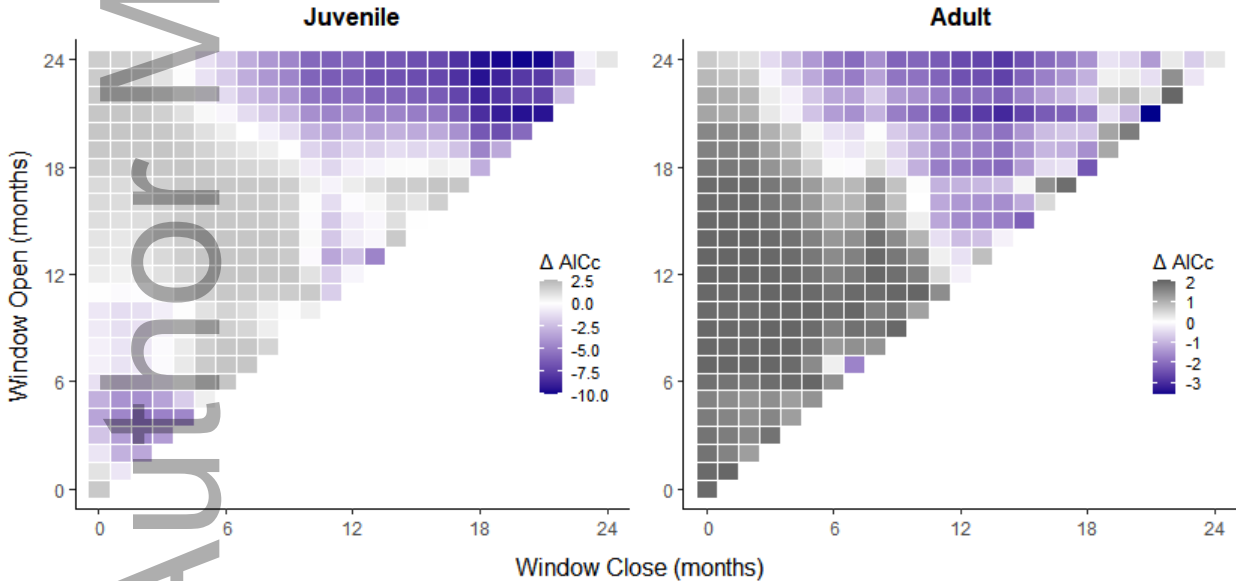
879 **Fig. 3**



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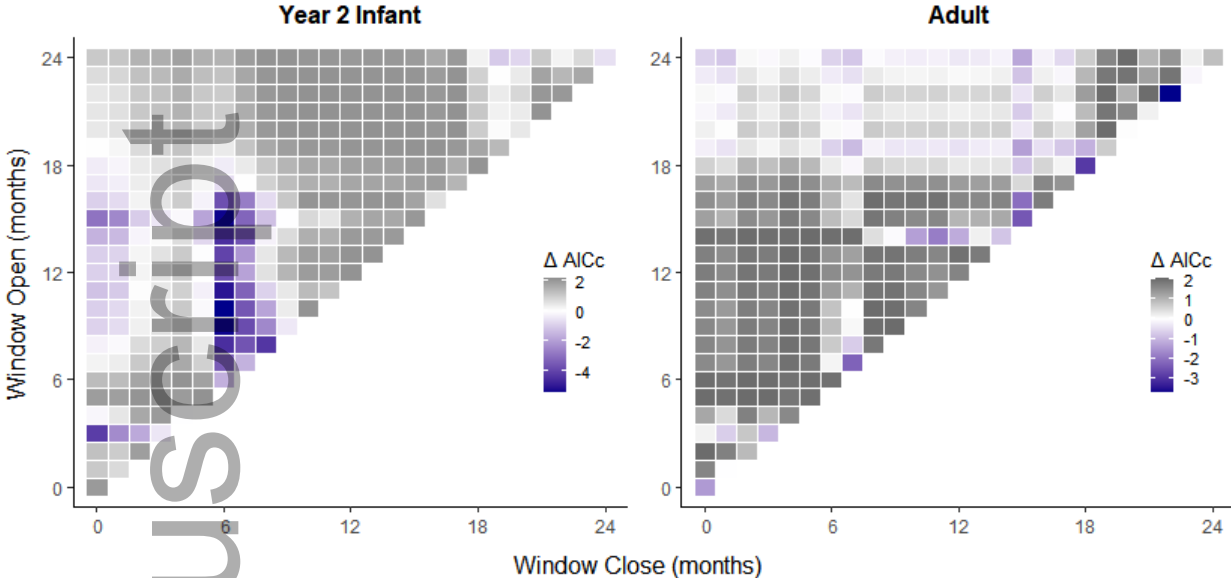
882 **Fig. 4**



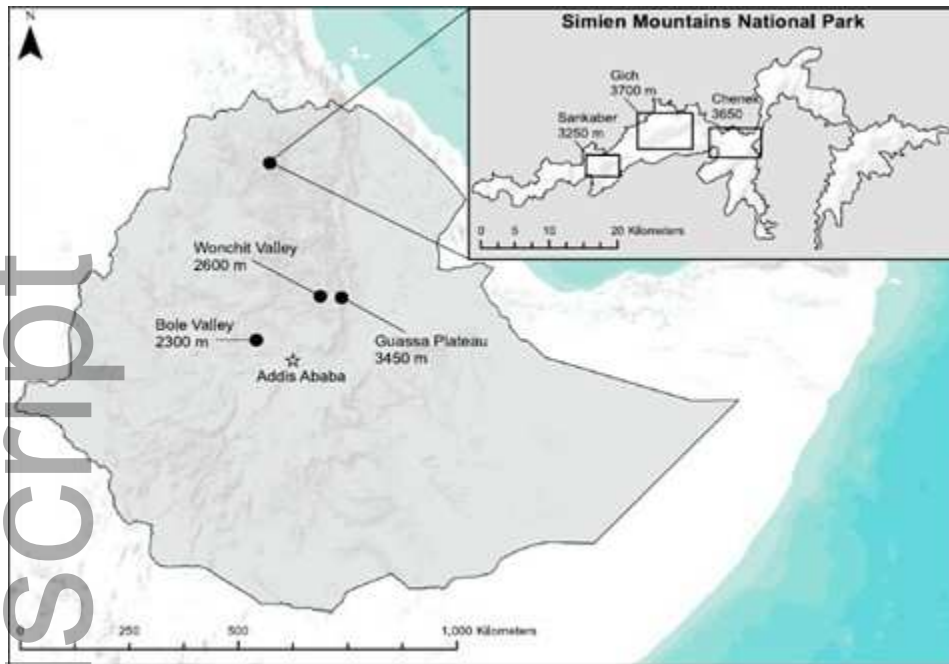
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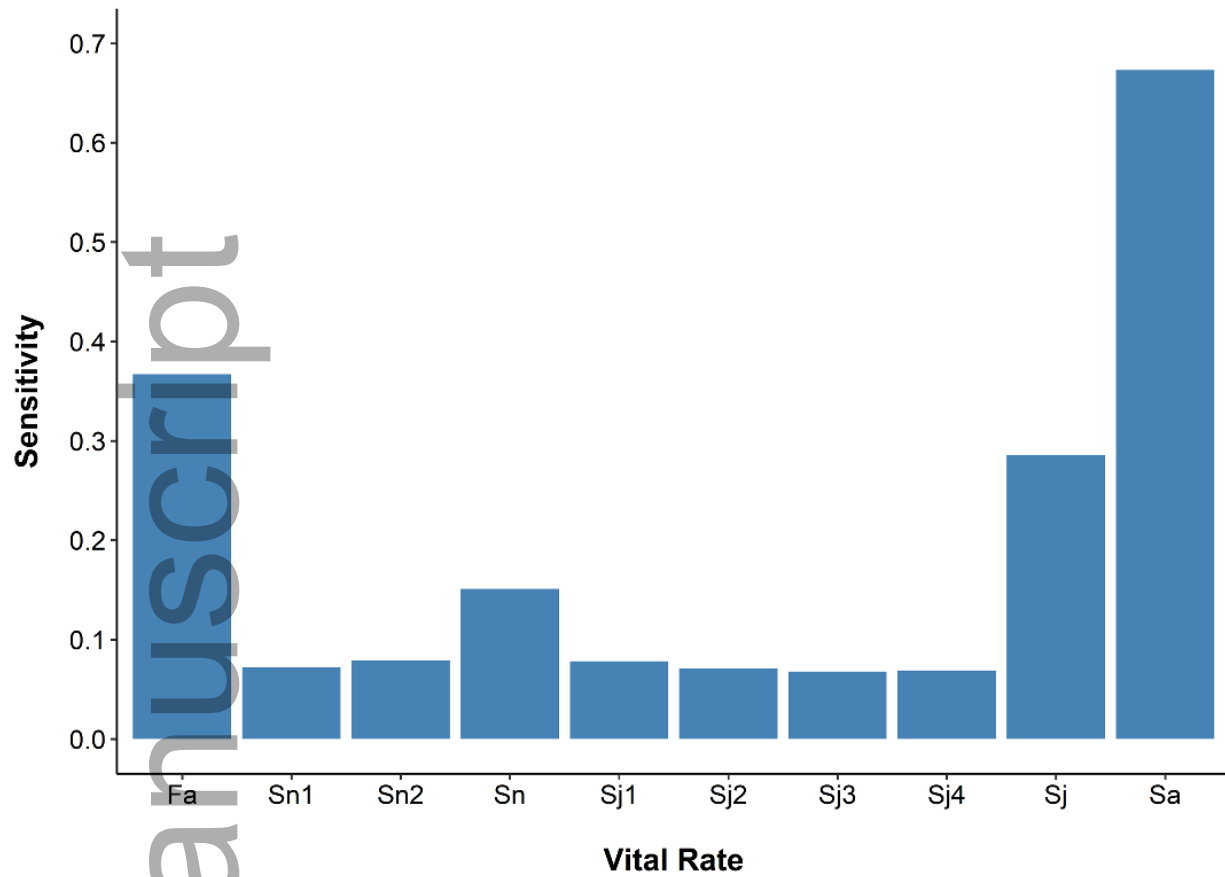
885 Fig. 5



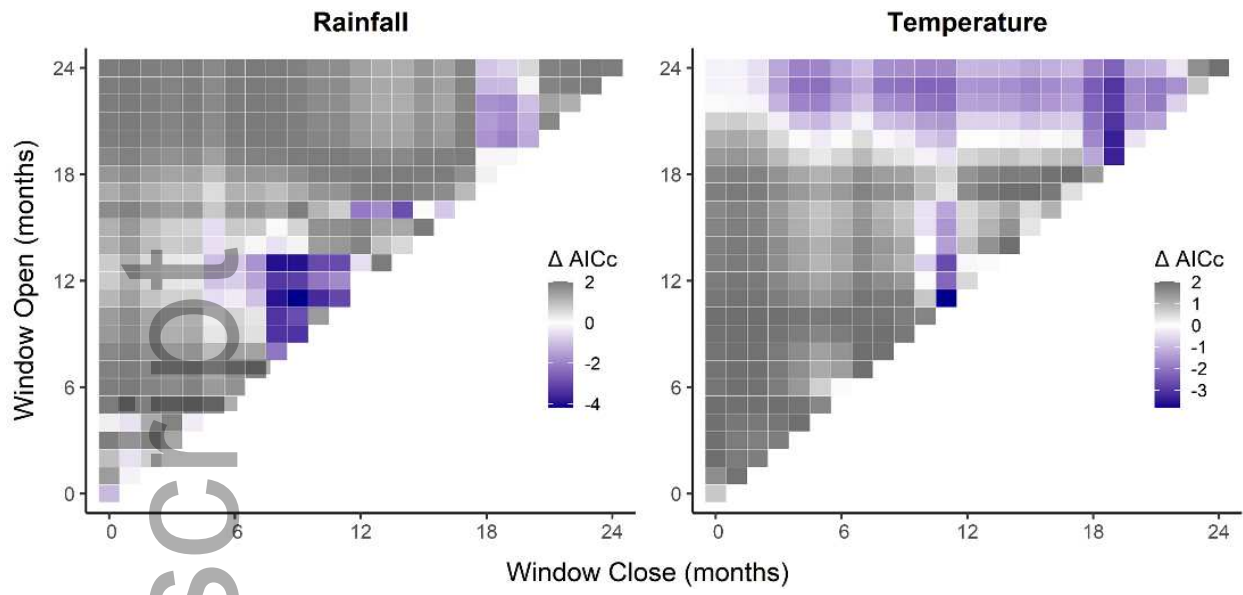
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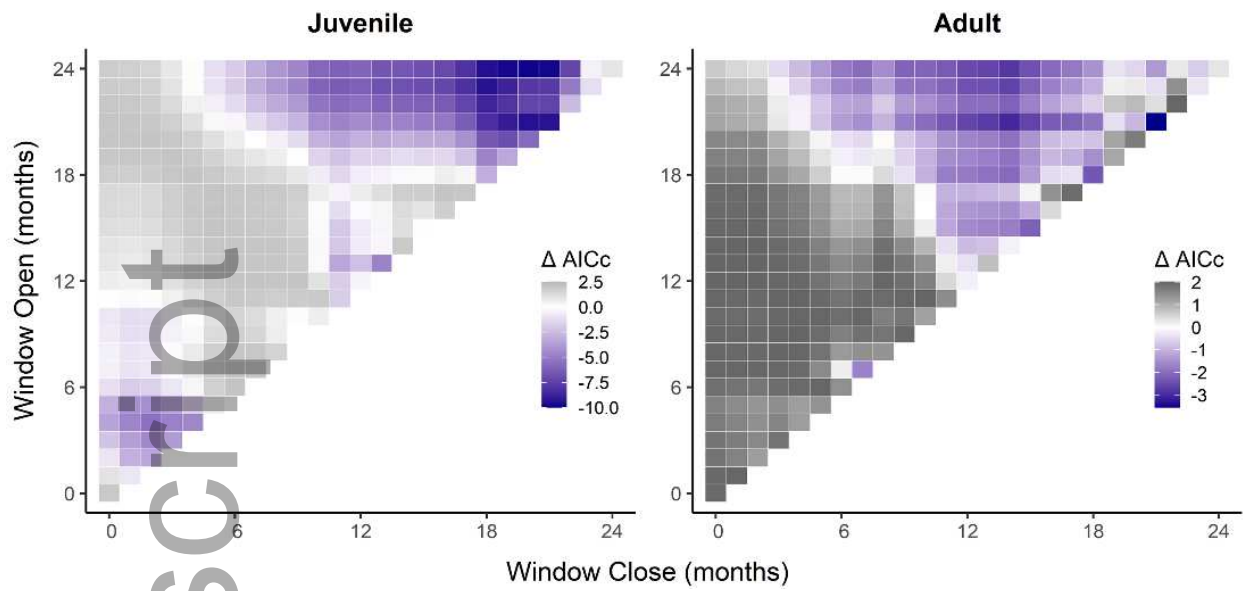


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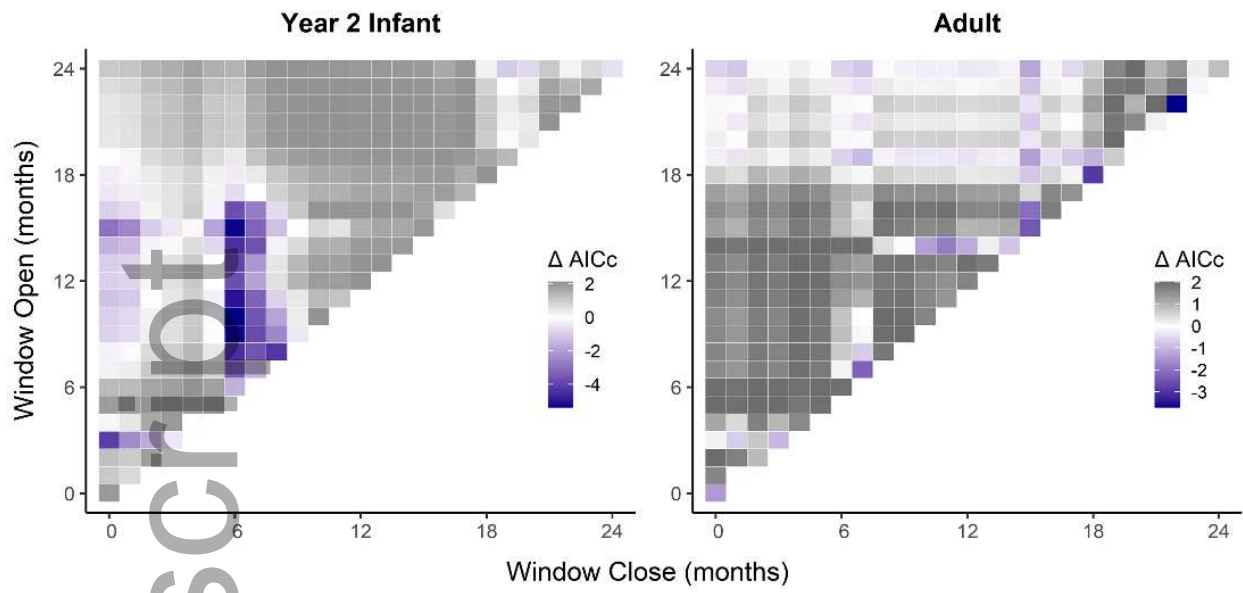


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