

Individual fitness in a small desert mammal predicted by remotely sensed environmental measurements

Avril Harder¹, Mekala Sundaram², Lana Narine¹, and Janna Willoughby¹

¹Auburn University

²Oklahoma State University

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1 **Remotely sensed environmental measurements detect decoupled processes driving**
2 **population dynamics at contrasting scales**

3 Avril M. Harder^{1*}, Mekala Sundaram², Lana L. Narine¹, Janna R. Willoughby¹

4 1. College of Forestry, Wildlife and Environment, Auburn University, Auburn, Alabama, USA

5 2. Department of Integrative Biology, Oklahoma State University, Stillwater, Oklahoma, USA

6 *Author for correspondence:

7 Avril Harder

8 College of Forestry, Wildlife and Environment, Auburn University

9 602 Duncan Drive, Auburn, Alabama, USA, 36849

10 (773) 688-8564, avrilharder@gmail.com

11 **Abstract**

12 The increasing availability of satellite imagery has supported a rapid expansion in forward-
13 looking studies seeking to track and predict how climate change will influence wild population
14 dynamics. However, these data can also be used in retrospect to provide additional context for
15 historical data in the absence of contemporaneous environmental measurements. We used 167
16 Landsat-5 Thematic Mapper (TM) images spanning 13 years to identify environmental drivers of
17 fitness and population size in a well-characterized population of banner-tailed kangaroo rats
18 (*Dipodomys spectabilis*) in the southwestern United States. We found evidence of two decoupled
19 processes that may be driving population dynamics in opposing directions over distinct time
20 frames. Specifically, increasing mean surface temperature corresponded to increased individual
21 fitness, where fitness is defined as the number of offspring produced by a single individual. This
22 result contrasts with our findings for population size, where increasing surface temperature led to
23 decreased numbers of active mounds. These relationships between surface temperature and (i)
24 individual fitness and (ii) population size would not have been identified in the absence of
25 remotely sensed data, indicating that such information can be used to test existing hypotheses
26 and generate new ecological predictions regarding fitness at multiple spatial scales and degrees
27 of sampling effort. To our knowledge, this study is the first to directly link remotely sensed
28 environmental data to individual fitness in a nearly exhaustively sampled population, opening a
29 new avenue for incorporating remote sensing data into eco-evolutionary studies.

30 **Key words:** Landsat, population dynamics, monitoring, fitness

31 **Introduction**

32 Understanding the environmental drivers of population stability and fluctuations is critical for
33 effective natural resource management. However, developing this understanding can require
34 information about ecosystems and land cover at scales and sampling frequencies that are
35 impractical to collect from field efforts alone. Beginning with the launch of the Landsat 1
36 satellite in July 1972, the National Aeronautics and Space Administration/U.S. Geological
37 Survey Landsat Program has consistently provided medium spatial resolution satellite imagery of
38 Earth's surface, with free and open access since 2008 (Wulder et al., 2022). Its data products
39 have contributed to a rapid expansion of interdisciplinary research that relies on ecological
40 knowledge and remote sensing data to describe a variety of patterns, including tracking loss of
41 wetland habitat, detecting shifts in forest canopy composition, and monitoring shifts in
42 phenological cycles (Vogelmann et al., 2016). Much of this work is forward-looking, seeking to
43 describe how natural systems evolve as climate change progresses and to construct relevant
44 projections, but historical remote sensing data can also be used to add new dimensions to
45 datasets lacking contemporaneous environmental measurements (e.g., Boulton et al., 2018; Ndegwa
46 Mundia & Murayama, 2009; Rossi & Leiner, 2022). Herein, we combine remote sensing and
47 weather modeling data with previously collected demographic data to describe environmental
48 factors influencing various components of population dynamics.

49 Our focal population of banner-tailed kangaroo rats (*Dipodomys spectabilis*) has been the
50 subject of myriad studies, including investigations of mate choice patterns, genetic adaptation to
51 arid environments, philopatry and dispersal, and many other eco-evolutionary dynamics (Busch
52 et al., 2009; Jones et al., 1988; Marra et al., 2012; Waser & DeWoody, 2006). These studies
53 were largely based on detailed demographic and genetic sampling, including precise home

54 mound locations for nearly all individuals in the population and a nearly complete pedigree
55 linking parents and offspring (Waser & Hadfield, 2011; Willoughby et al., 2019). Analysis of
56 this pedigree has previously shown that genetic variables, including degree of individual
57 inbreeding or relatedness between mates, explain a portion of individual fitness, but individual
58 birth year (*i.e.*, non-genetic or environmental factors) accounted for a relatively larger proportion
59 of variation in individual fitness (Willoughby et al., 2019).

60 To test which environmental characteristics contribute to these interannual differences in
61 fitness, we used Landsat 5 Thematic Mapper (TM) images to obtain surface temperature data and
62 three other descriptive indices via the Tasseled Cap Transformation (Tasseled Cap brightness,
63 greenness, and wetness) (Kauth & Thomas, 1976). Tasseled Cap values can be used to describe
64 variation in soil moisture content, ground cover type, and plant communities, with previous
65 practical applications including assessing impacts of natural disasters, tracking shoreline
66 changes, and charting the progress of desertification (Mostafiz & Chang, 2018; Shamsuzzoha &
67 Ahamed, 2023; Zanchetta et al., 2016). We used these data alongside modeled precipitation and
68 temperature data to summarize the environment of this population over thirteen years. We
69 analyzed these data in conjunction with demographic data at three different scales representing
70 three distinct levels of field sampling effort—(i) individual microhabitat vs. individual fitness,
71 (ii) population-scale macrohabitat vs. population fitness, and (iii) population-scale macrohabitat
72 vs. population size—to test the suitability of remote sensing data for describing the effects that
73 specific environmental variables can have on population dynamics at different scales. Because
74 populations of banner-tailed kangaroo rats have been the subjects of numerous ecological and
75 evolutionary studies over several decades, we were able to compare the patterns observed in our
76 results against inferences drawn from prior field-based studies.

77 Previous studies of *D. spectabilis* and other heteromyid rodents have described positive
78 relationships between the amount of habitat openness and survival or population size, perhaps
79 because openness facilitates easier detection of or evasion maneuvers against predators or
80 because higher quality food sources tend to grow in such habitats (Bowers et al., 1987; Germano
81 et al., 2001; Waser & Ayers, 2003). We therefore expected to see a positive relationship between
82 the Tasseled Cap brightness index and individual and population fitness, as brightness can
83 indicate the ratio of open soil to plant cover (Crist & Cicone, 1984). We also expected to see a
84 positive effect of precipitation and the Tasseled Cap wetness index—a measure sensitive to soil
85 and vegetative moisture, but primarily characterizing soil moisture (Crist & Cicone, 1984)—on
86 fitness, as increasing water availability may translate into increased food resources (Brown &
87 Zeng, 1989; Munger et al., 1983). Subsequent increases in these resources may be captured by
88 the Tasseled Cap greenness index, a measure shown to be correlated with leaf area index and
89 vegetation biomass (Crist & Cicone, 1984). Specifically, we expected that higher greenness
90 measures in the rainy seasons preceding breeding would lead to increased fitness, as previous
91 studies have found lagged positive responses in rodent biomass or abundance to increased
92 primary productivity (Ernest et al., 2000; Hernández et al., 2005; Previtali et al., 2009; Schooley
93 et al., 2018). Finally, we anticipated that surface and air temperature measures would be
94 negatively correlated with fitness, as increasing surface temperature corresponds to decreasing
95 survival for *D. spectabilis* populations in the Chihuahuan Desert (Moses et al., 2012).

96 Although other studies have drawn important new ecological inferences by linking
97 remotely sensed environmental measurements to approximations or correlates of fitness (where
98 fitness is defined as the number of offspring produced by a single individual), such as apparent
99 survival (Moses et al., 2012; Ward et al., 2018) or clutch size and fledging success (Regos et al.,

2022; Riggio et al., 2023), ours is the first to use direct assessments of individual fitness as response variables. Specifically, the identification of parent-offspring pairs via genetic analysis allows for inclusion of adult individuals known to be alive but producing zero offspring within a year and for linking observations of specific individuals across years. Herein, we leverage this extensive demographic dataset to test our ecological predictions and, through these analyses, develop new ecological hypotheses regarding drivers of banner-tailed kangaroo rat population dynamics. Overall, we demonstrate that, in the absence of locally collected environmental data, remote sensing data can be used to draw novel inferences and generate new questions regarding fitness and population dynamics at multiple spatial scales and degrees of sampling effort.

109 **Methods**

110 *Study system*

111 The study site is located in the Madrean Archipelago ecoregion, which comprises the Sky
112 Islands—forested mountains interspersed among broad, flat desert scrub and grasslands. The
113 Chiricahua Mountains lie just to the north and west of the site, which is situated around a
114 volcanic cinder cone surrounded by flatlands approximately 35 km southwest of Portal, AZ
115 (31°36'27"N, 109°15'48"W) (Fig. 1A). Annual precipitation patterns typically include a summer
116 rainy season from July to August (which supplies 50% of total annual precipitation) and a
117 second, less intense winter rainy season from December to March (Adams & Comrie, 1997). The
118 study area is primarily desert grassland, with rare to occasional half-shrubs and forbs present
119 (Jones et al., 1988; Waser & Ayers, 2003).

120 Banner-tailed kangaroo rats rely on these plant communities for food, caching seeds in
121 large mounds (1-3 m in diameter) constructed for food storage, reproduction, and protection
122 from predators and harsh environmental conditions (Edelman, 2011; Kay & Whitford, 1978).
123 Each mound is typically occupied and defended by a single individual, with the exception of
124 females and their dependent offspring (Schroder, 1979). When the offspring are between two and
125 seven months old, they disperse from their natal mounds to nearby vacant mounds to establish
126 individual territories (Jones, 1984; Waser et al., 2006). Exceptions to typical dispersal patterns
127 may occur in years of high population densities, wherein individuals are more likely to remain in
128 their natal mound to reproduce than to disperse to a new location (Jones et al., 1988; Waser &
129 DeWoody, 2006). Mating typically occurs between December and March with females
130 producing 1-2 litters of 1-3 offspring per year (Jones, 1984). Individuals typically live up to four
131 years, often producing offspring during the first mating season of their lives.

132 *Banner-tailed kangaroo rat data collection*

133 Our banner-tailed kangaroo rat demographic data was collected from a population monitored by
134 Waser et al. from 1990 through 2007 (Sanderlin et al., 2012; Skvarla et al., 2004; Waser &
135 Jones, 1991). Twice annually, three traps were placed around each active mound on three
136 consecutive nights, resulting in near-exhaustive population sampling (98% median capture
137 probability for adults; 93% for juveniles; Skvarla et al., 2004). Each captured individual was
138 uniquely marked with ear tags and sex and mound-specific capture location were recorded. It
139 was also noted whether the individual was a juvenile (*i.e.*, born in that year) or an adult. Ear
140 tagging and subsequent recapture allowed individuals to be tracked across the landscape from
141 year to year, and pinna biopsies were taken for genetic characterization. Biopsy samples were
142 genotyped at nine polymorphic loci (Busch et al., 2009; Waser et al., 2006) and the resulting data

143 were used alongside trapping records to construct a pedigree for the population (Waser &
144 Hadfield, 2011; Willoughby et al., 2019). Briefly, Waser & Hadfield (2011) used MasterBayes to
145 build the pedigree, with parental assignment probabilities influenced by trapping location and
146 parent/offspring genotypes (see Willoughby et al., 2019 for details).

147 *Environmental data curation and transformation*

148 We downloaded all available Landsat 5 TM Collection 2 Level 2 images for our study site from
149 1989-2005. Our site was covered by both paths 34 and 35 in row 38 at 30-m spatial resolution.
150 All images were processed and analyzed in R v4.0.3 (R Core Team, 2020). Because of the small
151 size of our site relative to the footprint of a Landsat 5 scene, each image was cropped to a 2100
152 m x 2750 m extent using the *raster* package prior to further processing (Hijmans, 2022). We
153 manually reviewed the cropped natural color image for each scene to verify absence of clouds or
154 any other source of error.

155 For each of the surface reflectance bands, we applied the multiplicative scale factor
156 (0.0000275) and additive offset (-0.2) specified in the Landsat 4-7 Collection 2 Level 2 Science
157 Product Guide (U.S. Geological Survey, 2021, pp. 4–7). We also converted the surface
158 temperature band to Kelvin (and later to degrees Celsius) using a multiplicative scale factor of
159 0.00341802 and an additive offset of 149. Using the *spectralIndices* function in the *RStoolbox*
160 package, we calculated 3 Tasseled Cap indices for all images: Tasseled Cap brightness,
161 greenness, and wetness (Crist, 1985; Leutner et al., 2019). To check for biased values with
162 respect to path number, we plotted the mean value of each index per scene (*i.e.*, timepoint) over
163 time. Across all years examined, values calculated from path 34 were consistently higher than
164 temporally adjacent values calculated from path 35, leading us to rely exclusively on path 35

165 scenes for downstream analyses. We also limited the dataset to scenes collected from 1993-2005
166 due to limited observations available in 1989-1992, leaving 167 scenes (Fig. A1; Table A1). All
167 cell values across all years were *z*-transformed within each Tasseled Cap index. After observing
168 intra- and interannual patterns for these four variables, we calculated pairwise Pearson
169 correlation coefficients using the *cor* function in R.

170 To link the remote sensing data to specific kangaroo rat mounds, we used GPS
171 coordinates recorded for 188 mounds to assign them to corresponding cells in the raster. For 26
172 mounds, no GPS coordinates were available, but all mounds had been mapped during the
173 original surveys using a custom coordinate system (units in meters) covering the study site (*i.e.*,
174 the position for each mound was recorded against a single reference point). Using the known
175 coordinates for 188 mounds, we overlaid the meter-based locations for all mounds onto the raster
176 and manually assigned the mounds lacking GPS coordinates to cells in the raster. In total, we
177 assigned 214 mounds to raster cells (Fig. 1B).

178 We also obtained precipitation totals and minimum, mean, and maximum temperatures
179 from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) at 4-km
180 resolution (PRISM Climate Group, Oregon State University, 2009). The PRISM model
181 incorporates a digital elevation model and other spatial datasets to calculate gridded estimates of
182 multiple climatic parameters, while accounting for the effects of terrain on precipitation (Daly et
183 al., 1997, 2008). We used these estimated daily precipitation totals (mm) and minimum, mean,
184 and maximum temperatures (°C) to calculate annual and seasonal means for the population-level
185 analysis, as a single value for each PRISM variable was available for the entire population (see
186 below).

187 *Data summarization and statistical analyses*

188 Individual fitness

189 Using the parent-offspring assignments generated by Waser & Hadfield (2011), we determined
190 how many offspring each female produced in each year ($n = 476$ females) and, for females
191 producing at least one offspring, how many of those offspring survived to age one (*i.e.*,
192 reproductive age; $n = 282$ females). We used the capture data to assign each female to a primary
193 mound location within each year. For each female, we summarized remote sensing values by
194 considering the cell containing her mound location and the eight adjacent cells. Given that each
195 cell is 30 m across, the maximum distance from the center of an individual's home range in the
196 raster to the edge is 63 m. Most banner-tailed kangaroo rats disperse < 50 m over their lifetime
197 (*i.e.*, the distance between their natal and home mounds is < 50 m), meaning that their raster-
198 defined home range likely contains both their natal and reproductive environments (Skvarla et
199 al., 2004). For each year, we calculated mean index and surface temperature values in three
200 ways: (i) season-equalized 12-month (*i.e.*, annual) average, wherein the average index values
201 within each meteorological season were averaged to obtain a single annual value for each index;
202 (ii) summary rainy season averages, calculated for July-August; and (iii) winter rainy season
203 averages, calculated for December-March. We applied a 6-month lag to the environmental data,
204 such that: means for July in year $t-1$ through June in year t were used to predict the number of
205 offspring produced in year t ; and means for July in year t through June in year $t + 1$ were used to
206 predict the number of offspring produced in year t surviving to year $t + 1$ (Fig. 2).

207 To check for relationships between individual microhabitat conditions and fitness, we
208 conducted a series of Poisson and negative binomial regressions using the *glm.nb* function from
209 the MASS package (Venables & Ripley, 2002) in R. The response variable was number of

210 offspring produced with mean annual values for brightness, greenness, wetness, and surface
211 temperature (K) as predictor variables. We used backwards stepwise regression, manually
212 removing one predictor variable at a time and examining model coefficients and AIC values until
213 all predictors were significant ($p < 0.05$). We compared the final Poisson and negative binomial
214 regressions using a likelihood ratio test, checked the dispersion parameter for each model, and
215 calculated generalized variance inflation factor (GVIF) values for final models with >1 predictor
216 variable retained using the *gvif* function in the *glmtoolbox* R package to quantify the contribution
217 of collinearity on uncertainty in each model (Hernando Vanegas et al., 2022). We repeated this
218 process for the summer and winter rainy season means and for number of surviving offspring. To
219 visualize the effects of predictor variables in models with multiple retained predictor variables,
220 we used the *effect_plot* function in the *jtools* package in R, setting the non-focal predictor
221 variable equal to its mean value.

222 Because some females were sampled in >1 year, we also constructed negative binomial
223 linear mixed models with female identification number (ID) as a random variable for both
224 number of offspring and number of offspring surviving. These models were built using the
225 *glmmTMB* package in R and we followed the same backwards stepwise regression process as for
226 the models that only included fixed effects (Brooks et al., 2017). For successful mixed models,
227 the final models were compared against the corresponding models lacking random effects with
228 likelihood-ratio tests as implemented in the *lrtest* function in R.

229 Population fitness

230 We used the capture data to determine the number of adult females alive in each year as well as
231 the total number of offspring produced. From these data, we calculated the average number of

232 offspring produced per female and average number of offspring surviving to age 1 per female.
233 To define the set of cells to be analyzed within each year, we began by identifying active mounds
234 (*i.e.*, mounds where a female was captured) within each year. We defined the total set of active
235 cells as all cells containing an active mound plus the eight cells adjacent to each active cell. For
236 each year, we calculated landscape-level means for each remote sensing index and the PRISM
237 variables as we did for the individual data (*i.e.*, annually and for the summer and winter rainy
238 seasons) and again applied a 6-month lag (Fig. 2).

239 We conducted a series of linear regressions to identify relationships between
240 macrohabitat conditions and population-level fitness by testing each combination of a single
241 environmental predictor variable and response variable separately. Two summer rainy season
242 variables (wetness and brightness) were found to be significant predictors for average number of
243 offspring surviving to age 1 ($p < 0.05$). Because neither model met the homoskedasticity
244 assumption, we permuted the y -values and calculated model coefficients 1,000 times per model
245 to generate permuted p -values.

246 Population size

247 Again using capture data, we calculated the number of mounds with resident individuals within
248 each year. We assumed that if a mound was occupied, an experienced surveyor of the site could
249 reasonably identify occupied mounds as active based on signs left by residents (*e.g.*, specific
250 characteristic patterns left by banner-tailed kangaroo rat locomotion, recently excavated soil at
251 mound entrances). We applied the same predictor variables and statistical approaches as for the
252 population fitness data, using annual and summer and winter rainy season means from July in
253 year $t-1$ through June in year t to predict the number of active mounds in year t . After

254 constructing the initial linear regressions, we were left with a single significant predictor variable
255 (mean annual surface temperature; $p < 0.05$) and again permuted the y -values and calculated
256 model coefficients 1,000 times to generate p -values.

257 To confirm that number of active mounds is a reasonable proxy for population size, we
258 constructed linear models to relate number of active mounds to number of adult females and
259 census population size using the capture data. We also tested for relationships between both
260 number of active mounds and number of adult females and fitness rates (number of offspring and
261 number of surviving offspring per female) to determine whether fitness rates could be the result
262 of density-dependent population processes. Finally, to account for the effect of population size in
263 year $t - 1$ on population size in year t , we repeated our statistical approach using (i) absolute
264 change in population size from year $t - 1$ to year t and (ii) proportional change in population size
265 from year $t - 1$ to year t as response variables (*i.e.*, $(N_{year\ t} - N_{year\ t-1})/(N_{year\ t-1})$).

266

267 **Results**

268 We analyzed 167 Landsat 5 TM scenes spanning 13 years (July 1993 – June 2005), calculating
269 surface temperature (°C) and scaled and centered Tasseled Cap greenness, wetness, and
270 brightness indices for each. For surface temperature, patterns matched expectations with
271 maximum temperatures observed during June/July and minima during December/January and
272 with little variation across cells analyzed at each time point as indicated by small standard
273 deviations around mean values (Fig. 3D). For Tasseled Cap greenness, intra-annual patterns
274 largely did not follow our expectation of increased values during or after rainy seasons (Fig. 3A).
275 For example, higher greenness values were observed for the summer rainy season in only 4 of 13

276 years analyzed. Brightness and wetness appeared to be strongly correlated with one another, with
277 both indices perhaps decreasing a bit during the cooler months and increasing during the warmer
278 months (Fig. 3B,C). After observing the similarities between these two variables, we calculated
279 and confirmed strong correlation between wetness and brightness (Pearson's $r = 0.89$; Fig. A2).

280 For individual fitness, we found that mean annual brightness and surface temperature for
281 the area immediately surrounding a female's home location had positive effects on number of
282 offspring produced (Table 1; Fig. 4; Fig. 5A; Fig. A3; see Table A2 for all tested models).
283 Summer rainy season mean brightness and winter rainy season mean wetness and surface
284 temperature also positively affected number of offspring produced (Fig 5B). With respect to the
285 number of offspring surviving to age 1, mean annual surface temperature and mean summer
286 rainy season brightness were positive predictors (Table 1; Fig. 5C; see Table A3 for all tested
287 models). For both number of offspring and number of surviving offspring, greenness was not
288 included in any of the final models. For the two individual fitness models with multiple predictor
289 variables retained, GVIF values were close to 1 and therefore did not indicate an outsized
290 contributed of collinearity to model uncertainty (maximum value was 1.05).

291 Including female ID as a random effect did not affect the results for number of offspring
292 with respect to the identity or significance of retained predictor variables when compared to the
293 negative binomial models that only included fixed effects (tested models presented in Table A4).
294 Likelihood-ratio tests comparing mixed-effects models to models excluding female ID as a
295 random effect were non-significant. For number of offspring surviving, we could not construct
296 reasonable models that included female ID due to convergence issues. These issues were likely
297 due to the over-representation of individuals with only one year of observations (186 of 282
298 females were only observed in one year). For these reasons, we restrict further consideration and

299 discussion to the results of the models that only include fixed effects for both number of
300 offspring and number of offspring surviving.

301 There were only two statistically significant relationships linking environmental variables
302 and population fitness: summer rainy season brightness (Table 2) and wetness (Table 3), when
303 averaged across the active landscape, were positively associated with average number of
304 offspring surviving to age 1 per female (Fig. A4). Despite summer rainy season wetness
305 positively predicting average number of surviving offspring, total precipitation as modeled by
306 PRISM was not correlated with fitness.

307 With respect to population size, only mean annual surface temperature was a significant
308 predictor variable (Table 4; Fig 5D). The direction of this relationship was negative, unlike the
309 positive relationships described between surface temperature and individual fitness. In
310 comparing number of active mounds against number of adult females and census population
311 sizes, we found significant and strong statistical relationships (Fig. A5), suggesting that simply
312 surveying the number of active mounds in an area occupied by banner-tailed kangaroo rats
313 would produce a close estimate of population size. Neither number of adult females nor number
314 of active mounds were significantly associated with fitness rates (Fig. A6), suggesting that
315 fitness is not detectably influenced by population density. We also did not observe any
316 significant relationships between environmental variables and absolute or proportional change in
317 population size from year $t - 1$ to year t . Although previous years' population sizes certainly
318 influence contemporary population size, we were not able to capture these effects in our
319 analyses.

320 Discussion

321 For two variables—Tasseled Cap brightness and wetness—our results matched our expectations
322 that were based on previously published relationships between kangaroo rat demographic
323 measures and environmental conditions. In each individual-level model where brightness was
324 retained as a significant predictor and at the population level, brightness positively affected
325 fitness. This is consistent with previous studies that explicitly tested the relationship between
326 habitat openness (*i.e.*, plant density or shrub cover) and kangaroo rat abundance (Bowers et al.,
327 1987; Waser & Ayers, 2003). However, these studies primarily focused on the effect of shrub
328 density on kangaroo rat populations, whereas the majority of plants at our study site are grasses.
329 Therefore, brightness as measured in our study may be providing a summary of favorable
330 conditions distinct from what was explicitly tested in previous studies of habitat openness and
331 kangaroo rat abundance. Mean winter and summer rainy season wetness values were also
332 positively associated with individual and population fitness, respectively. This mirrors results of
333 previous studies that have demonstrated a positive relationship between precipitation and rodent
334 abundances in dry environments (Cárdenas et al., 2021), although mechanistic links between
335 precipitation and rodent abundances are often complex (Ernest et al., 2000; Thibault et al., 2010;
336 Thibault & Brown, 2008). Positive effects of precipitation on kangaroo rat survival or abundance
337 could be mediated via decreased water stress on individuals or through increased availability of
338 food resources that rely on rainy season precipitation to produce seeds. However, values for
339 wetness and brightness were strongly correlated in our dataset (Pearson's $r = 0.89$; Fig. 3B,C;
340 Fig. A2), making it difficult to definitively interpret changes in either index. This is likely due to
341 the high ratio of bare soil:vegetation cover at our site, with little variation across the cells being
342 compared (Crist, 1985). The strength of this correlation does vary across the year (summer rainy

343 season Pearson's $r = 0.57$; winter rainy season Pearson's $r = 0.92$), indicating that these two
344 indices likely capture distinct soil characteristics, but we cannot explicitly define those
345 characteristics without ground-truthed data.

346 Across all time intervals and scales, Tasseled Cap greenness was never retained as a
347 significant predictor of fitness or population size. We expected greenness to increase during or
348 immediately following the rainy seasons in each year, and this appears to have been the case for
349 some years but not all (Fig. 3). The uninformative nature of this particular index for our study
350 site is likely related to semiarid shrub and grassland characteristics. In such ecosystems, spatial
351 patterns of vegetative land cover are highly heterogeneous with respect to both plant community
352 composition and density (Huenneke et al., 2001), and typically comprise dormant (*i.e.*, non-
353 photosynthetic) vegetative cover for large portions of the year (D. Browning et al., 2017; Okin,
354 2010; Yang & Guo, 2014). Regardless of season, areas with sparse vegetative cover may not
355 reach greenness thresholds required for detection of vegetation in satellite data (Peng et al.,
356 2021). In other words, the low density of green vegetation at our study site may not be sufficient
357 to prompt an increase in Tasseled Cap greenness values on a per-cell basis, even when the plant
358 community has reached maximum greenness. Further investigation would require either higher
359 resolution data than is publicly available (*e.g.*, (Bankert et al., 2021; D. M. Browning et al.,
360 2019)) or ground-truthed data to calibrate conversions of spectral data to per-pixel vegetation
361 fractions (Smith et al., 1990) on a temporal scale capable of capturing the often rapid changes in
362 photosynthetic activity observed in desert plants (Reed et al., 1994). Without such information
363 from the focal system, it may not possible to reliably ascertain aspects of shrub or grassland
364 phenology using multispectral data alone (Allnutt et al., 2002).

365 Whereas the Tasseled Cap indices may require additional data to contextualize their
366 values for a specific location, the Landsat surface temperature band provides a direct measure of
367 a simple physical characteristic. At the individual level, the positive relationships we identified
368 between surface temperature and individual fitness appear to directly contradict other findings in
369 this species (Moses et al., 2012). However, when we analyzed the effect of surface temperature
370 on population size, the direction of this relationship matched previous results describing negative
371 effects of increased temperature on kangaroo rat survival. The apparent mismatch between these
372 two sets of results could be mediated by decoupled processes acting over distinct time frames to
373 increase both individual fitness and subsequent overall mortality in the population. Specifically,
374 the positive effect of surface temperature on individual fitness is partially driven by higher winter
375 temperatures (as was found for the number of offspring response variable), and warmer winters
376 correspond to lower thermoregulatory costs for kangaroo rats (Edelman, 2011; Hinds &
377 MacMillen, 1985). These reduced costs could help the kangaroo rats' seed caches to last longer,
378 allowing females to produce greater numbers of litters in a single season. Whereas higher winter
379 temperatures may correspond to greater numbers of offspring produced, higher summer
380 temperatures may lead to higher rates of mortality. Although we did not detect a significant
381 relationship between summer rainy season surface temperature and population size, hotter
382 summers could perhaps decrease plant productivity, leading kangaroo rats to quickly exhaust
383 their seed caches and spend more time gathering food at night, thereby also increasing their risk
384 of predation. Additional environmental data (*e.g.*, accurate measurements of plant community
385 composition, abundance, and phenology) could provide greater context for interpreting the
386 influence of surface temperature on population dynamics, but satellite-measured surface
387 temperature alone may remain a critical and accessible measure of habitat suitability or

388 population dynamics for many species as climate change progresses, including species of
389 conservation concern and pest species (Albright et al., 2011; Bateman et al., 2023; Blum et al.,
390 2015; Geppert et al., 2023; Moses et al., 2012; Shimada et al., 2021).

391 Although four of our final models included surface temperature as a predictor variable,
392 PRISM temperature estimates were never retained as significant predictors of fitness or
393 population size, nor were PRISM precipitation estimates. One possible explanation is that
394 PRISM estimates may not closely approximate the true values for our study site, which covers
395 roughly 6% of a single PRISM grid cell. PRISM models account for elevation and topography,
396 but precipitation is highly spatially variable in the Chihuahuan Desert, even over short distances
397 (Petrie et al., 2014), making it difficult to assess the accuracy of PRISM estimates over very
398 small areas. Additionally, large precipitation events can contribute the majority of annual rainfall
399 in wet years (Petrie et al., 2014), and extreme weather events could influence kangaroo rat fitness
400 or survival more strongly than the seasonal or annual averages (*e.g.*, due to food resource
401 spoilage (Valone et al., 1995)) we included in our analyses. Spatial variability in air temperatures
402 may also impede detection of relationships between the modeled PRISM temperatures, but a
403 more likely explanation is that surface temperature values are simply more representative of the
404 environment kangaroo rats experience than air temperature estimates, further highlighting the
405 utility of remotely sensed surface temperature measurements in this and similar habitats.

406 For all of the environmental variables we tested, we also checked whether these variables
407 were predictive of either absolute or proportional change in population size from one year to the
408 next. Population size in the preceding year certainly influences contemporary population size,
409 but we did not detect any relationships between environmental variables and either measure of
410 change in population size. It may be that surface temperature—the only variable significantly

411 associated with population size—is also correlated with some unmeasured aspect of the
412 environment that limits population carrying capacity rather than rate of change in population
413 size. We did find that number of active mounds is reliably predictive of population size, as has
414 been previously described for this population over a different set of sampling years (Cross &
415 Waser, 2000). Although visual surveys of the site would not provide information on individual
416 fitness, they could provide close estimates of population size with far less effort than extensive
417 trapping schemes. Future studies of this or other *D. spectabilis* populations could rely on more
418 extensive ground-truthed remote sensing data and active mound surveys to gain additional
419 insights into drivers of population size while minimizing the number of person hours required to
420 collect data.

421 **Conclusions**

422 Through our analysis of remote sensing and modeled climate data, we were able to identify
423 potential ecological drivers of fitness and population size. Although most of our tested variables
424 (*i.e.*, the Tasseled Cap indices) will require pairing with ground-truthed data from the site to
425 confirm, our results and conservative interpretations were consistent with previous findings from
426 our focal population and other systems. The contrasting results for surface temperature across
427 sampling scales demonstrate that, while conducting relatively lower effort mound surveys likely
428 captures demographic trends well enough to identify abiotic determinants of population size, the
429 additional resolution provided by linking parents and offspring via genetic sampling allows for
430 detection of counterintuitive relationships that could influence long-term population stability.

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654 **Author Contributions**

655 AMH and JRW designed the study, AMH analyzed the data and wrote the manuscript with input
656 from all authors. All authors approved of the final manuscript.

657 **Data Availability**

658 Code for all analyses is available at [https://github.com/avril-m-](https://github.com/avril-m-harder/krat_remote_sensing_scripts)
659 [harder/krat_remote_sensing_scripts](https://github.com/avril-m-harder/krat_remote_sensing_scripts). All final datasets are available in Dryad
660 (doi:10.5061/dryad.9p8cz8wnf).

Table 1. Summaries of the best negative binomial models describing individual fitness, with predictor variable values averaged over the time interval indicated.

| Fitness measure | Time interval | Variable | Estimate | SE | z-value | p-value |
|----------------------------------|--|---------------------|-----------------|-----------|----------------|-------------------------|
| Number of offspring (n = 476) | Annual | Intercept | -0.7191 | 0.6523 | -1.102 | 0.2703 |
| | | Brightness | 0.3590 | 0.1566 | 2.292 | 0.0219 |
| | | Surface temperature | 0.0382 | 0.0187 | 2.042 | 0.0412 |
| | Summer rainy | Intercept | 0.7084 | 0.1168 | 6.065 | 1.32 x 10 ⁻⁹ |
| | | Brightness | 0.4664 | 0.1430 | 3.263 | 0.0011 |
| | Winter rainy | Intercept | -0.4845 | 0.4136 | -1.172 | 0.2414 |
| | | Wetness | 0.2070 | 0.0973 | 2.128 | 0.0334 |
| | | Surface temperature | 0.0524 | 0.0120 | 2.628 | 0.0086 |
| | Number of surviving offspring (n = 282) | Annual | Intercept | -3.2547 | 0.7081 | -4.596 |
| Surface temperature | | | 0.0896 | 0.0201 | 4.457 | 8.3 x 10 ⁻⁶ |
| Summer rainy | | Intercept | 0.1346 | 0.1395 | 0.965 | 0.3346 |
| | | Brightness | 0.3752 | 0.1804 | 2.080 | 0.0375 |

Table 2. Summary of the first linear regression model describing population fitness and permuted p -values. The response variable is average number of offspring surviving to age 1 per adult female. The adjusted R^2 for this model was 0.47.

| Variable | Estimate | SE | t-value | Permuted p-value |
|--------------------------------|-----------------|-----------|-----------------------------|--------------------------------------|
| Intercept | 1.215 | 0.210 | 5.790 | < 0.001 |
| Summer rainy season brightness | 0.824 | 0.262 | 3.151 | 0.006 |

Table 3. Summary of the second linear regression model describing population fitness and permuted p -values. The response variable is average number of offspring surviving to age 1 per adult female. The adjusted R^2 for this model was 0.35.

| Variable | Estimate | SE | t-value | Permuted p-value |
|-----------------------------|-----------------|-----------|-----------------------------|--------------------------------------|
| Intercept | 1.155 | 0.237 | 4.866 | 0.010 |
| Summer rainy season wetness | 0.633 | 0.251 | 2.518 | 0.010 |

Table 4. Summary of the linear regression model with number of active mounds as the response variable. P -values were derived from permutation tests. The adjusted R^2 for this model was 0.22.

| Variable | Estimate | SE | t-value | Permuted p-value |
|----------------------------|-----------------|-----------|-----------------------------|--------------------------------------|
| Intercept | 380.383 | 126.632 | 3.004 | 0.018 |
| Annual surface temperature | -7.644 | 3.688 | -2.073 | 0.018 |

Figure captions

Figure 1. A) Map of the area surrounding the study site, which is situated in Arizona near the New Mexico and Mexico borders. The site is located just southeast of the Chiricahua Mountains. B) Map of the study site with all mounds included in this study marked with points. The mounds are located on primarily flat areas surrounding a cinder cone.

Figure 2. Schematic showing temporal alignments between the predictor and response variables tested in the study. For example: annual means used to predict the number of offspring produced in year t were calculated from environmental data collected from July, year $t-1$ through June, year t , whereas winter rainy season means were calculated from data collected from December, year $t-1$ through March, year t . Although not indicated in this figure, PRISM data were only used as predictor variables for population fitness and number of active mounds (*i.e.*, not for measures of individual fitness). Summer and winter rainy season results are indicated by ‘S’ and ‘W’, respectively.

Figure 3. Mean values of Tasseled Cap indices (A-C) and surface temperature (D) across days of the year. Means were calculated using all cells that were occupied in at least one year over the course of the study plus all cells directly adjacent to those occupied cells. Note that the x -axes are offset such that the axis begins with July 1 and ends with June 30. White lines connect dates from July 1 in each year through June 30 in the subsequent year. Vertices for shaded polygons encompass one standard deviation around each mean. The points to the right of the dashed line indicate annual and rainy season mean values within each year.

Figure 4. Schematic summarizing the statistically significant relationships identified between environmental variables and fitness or population size. ‘S’ and ‘W’ indicate summer and winter

rainy season results, respectively. The sign in each colored polygon indicates the direction of the relationship (*i.e.*, the only negative relationship identified was between mean annual surface temperature and number of active mounds). Polygon color indicates environmental predictor variable with outline pattern indicating the scale at which variables were tested (*i.e.*, individual and population fitness and population size).

Figure 5. A-C) Significant positive relationships between surface temperature and measures of individual fitness. Panels A and B present the effects of mean annual and mean winter rainy season surface temperatures, respectively, on number of offspring produced by individual females while setting the non-focal predictor variable in each negative binomial model equal to its mean value. Panel C presents the final negative binomial model predicting number of surviving offspring with mean annual surface temperature. D) Linear regression describing negative effect of mean annual surface temperature on population size, as measured by number of active mounds. For all panels, shaded polygons represent 95% confidence intervals. Statistical results for models are presented in Tables 1-4 and Tables A2.

Appendix

Table A1. Metadata for final list of Landsat 5 TM Collection 2 Level 2 scenes (path 35, row 38) used in analyses (n = 167). Time is provided in Mountain Standard Time (local to the study site).

| Product ID | Scene ID | Date | | | Time | | |
|--|-----------------------|------|-------|-----|------|--------|--------|
| | | Year | Month | Day | Hour | Minute | Second |
| LT05_L2SP_035038_19930104_20200914_02_T1 | LT50350381993004AAA04 | 1993 | 1 | 4 | 10 | 13 | 33 |
| LT05_L2SP_035038_19930309_20200914_02_T1 | LT50350381993068AAA04 | 1993 | 3 | 9 | 10 | 14 | 12 |
| LT05_L2SP_035038_19930325_20200914_02_T1 | LT50350381993084AAA04 | 1993 | 3 | 25 | 10 | 14 | 12 |
| LT05_L2SP_035038_19930410_20200914_02_T1 | LT50350381993100AAA04 | 1993 | 4 | 10 | 10 | 14 | 20 |
| LT05_L2SP_035038_19930512_20200914_02_T1 | LT50350381993132AAA04 | 1993 | 5 | 12 | 10 | 14 | 31 |
| LT05_L2SP_035038_19930528_20200914_02_T1 | LT50350381993148AAA04 | 1993 | 5 | 28 | 10 | 14 | 34 |
| LT05_L2SP_035038_19930613_20200914_02_T1 | LT50350381993164AAA04 | 1993 | 6 | 13 | 10 | 14 | 34 |
| LT05_L2SP_035038_19930629_20200914_02_T1 | LT50350381993180AAA04 | 1993 | 6 | 29 | 10 | 14 | 27 |
| LT05_L2SP_035038_19930731_20200913_02_T1 | LT50350381993212AAA04 | 1993 | 7 | 31 | 10 | 14 | 26 |
| LT05_L2SP_035038_19930917_20200913_02_T1 | LT50350381993260XXX03 | 1993 | 9 | 17 | 10 | 14 | 22 |
| LT05_L2SP_035038_19931003_20200913_02_T1 | LT50350381993276AAA03 | 1993 | 10 | 3 | 10 | 14 | 18 |
| LT05_L2SP_035038_19931104_20200913_02_T1 | LT50350381993308AAA04 | 1993 | 11 | 4 | 10 | 14 | 6 |
| LT05_L2SP_035038_19931120_20200913_02_T1 | LT50350381993324XXX04 | 1993 | 11 | 20 | 10 | 13 | 58 |
| LT05_L2SP_035038_19931206_20200913_02_T1 | LT50350381993340XXX05 | 1993 | 12 | 6 | 10 | 13 | 55 |
| LT05_L2SP_035038_19940107_20200913_02_T1 | LT50350381994007XXX01 | 1994 | 1 | 7 | 10 | 13 | 33 |
| LT05_L2SP_035038_19940328_20200913_02_T1 | LT50350381994087XXX02 | 1994 | 3 | 28 | 10 | 12 | 27 |
| LT05_L2SP_035038_19940413_20200913_02_T1 | LT50350381994103XXX02 | 1994 | 4 | 13 | 10 | 12 | 7 |
| LT05_L2SP_035038_19940429_20200913_02_T1 | LT50350381994119XXX02 | 1994 | 4 | 29 | 10 | 11 | 51 |
| LT05_L2SP_035038_19940515_20200913_02_T1 | LT50350381994135XXX02 | 1994 | 5 | 15 | 10 | 11 | 33 |
| LT05_L2SP_035038_19940616_20200913_02_T1 | LT50350381994167XXX02 | 1994 | 6 | 16 | 10 | 10 | 56 |
| LT05_L2SP_035038_19940702_20200913_02_T1 | LT50350381994183XXX02 | 1994 | 7 | 2 | 10 | 10 | 32 |
| LT05_L2SP_035038_19940803_20200913_02_T1 | LT50350381994215XXX02 | 1994 | 8 | 3 | 10 | 9 | 38 |
| LT05_L2SP_035038_19941022_20200912_02_T1 | LT50350381994295XXX02 | 1994 | 10 | 22 | 10 | 7 | 28 |
| LT05_L2SP_035038_19941209_20200912_02_T1 | LT50350381994343XXX02 | 1994 | 12 | 9 | 10 | 5 | 52 |
| LT05_L2SP_035038_19950110_20200912_02_T1 | LT50350381995010XXX01 | 1995 | 1 | 10 | 10 | 4 | 47 |

| | | | | | | | |
|--|-----------------------|------|----|----|----|----|----|
| LT05_L2SP_035038_19950315_20200912_02_T1 | LT50350381995074AAA01 | 1995 | 3 | 15 | 10 | 2 | 15 |
| LT05_L2SP_035038_19950331_20200912_02_T1 | LT50350381995090XXX01 | 1995 | 3 | 31 | 10 | 1 | 36 |
| LT05_L2SP_035038_19950502_20200912_02_T1 | LT50350381995122XXX01 | 1995 | 5 | 2 | 10 | 0 | 13 |
| LT05_L2SP_035038_19950518_20200912_02_T1 | LT50350381995138XXX02 | 1995 | 5 | 18 | 9 | 59 | 30 |
| LT05_L2SP_035038_19950603_20200913_02_T1 | LT50350381995154XXX01 | 1995 | 6 | 3 | 9 | 58 | 45 |
| LT05_L2SP_035038_19950619_20200913_02_T1 | LT50350381995170XXX03 | 1995 | 6 | 19 | 9 | 58 | 2 |
| LT05_L2SP_035038_19950705_20200912_02_T1 | LT50350381995186XXX02 | 1995 | 7 | 5 | 9 | 57 | 19 |
| LT05_L2SP_035038_19950721_20200912_02_T1 | LT50350381995202XXX02 | 1995 | 7 | 21 | 9 | 56 | 35 |
| LT05_L2SP_035038_19950806_20200912_02_T1 | LT50350381995218AAA02 | 1995 | 8 | 6 | 9 | 55 | 51 |
| LT05_L2SP_035038_19950822_20200912_02_T1 | LT50350381995234XXX02 | 1995 | 8 | 22 | 9 | 55 | 7 |
| LT05_L2SP_035038_19950923_20200912_02_T1 | LT50350381995266XXX02 | 1995 | 9 | 23 | 9 | 53 | 34 |
| LT05_L2SP_035038_19951009_20200912_02_T1 | LT50350381995282XXX03 | 1995 | 10 | 9 | 9 | 52 | 44 |
| LT05_L2SP_035038_19951025_20200912_02_T1 | LT50350381995298AAA01 | 1995 | 10 | 25 | 9 | 51 | 50 |
| LT05_L2SP_035038_19951110_20200912_02_T1 | LT50350381995314XXX00 | 1995 | 11 | 10 | 9 | 51 | 30 |
| LT05_L2SP_035038_19951212_20200911_02_T1 | LT50350381995346XXX01 | 1995 | 12 | 12 | 9 | 52 | 54 |
| LT05_L2SP_035038_19960113_20200911_02_T1 | LT50350381996013XXX01 | 1996 | 1 | 13 | 9 | 55 | 13 |
| LT05_L2SP_035038_19960129_20200912_02_T1 | LT50350381996029AAA01 | 1996 | 1 | 29 | 9 | 56 | 20 |
| LT05_L2SP_035038_19960214_20200912_02_T1 | LT50350381996045XXX01 | 1996 | 2 | 14 | 9 | 57 | 26 |
| LT05_L2SP_035038_19960317_20200911_02_T1 | LT50350381996077XXX01 | 1996 | 3 | 17 | 9 | 59 | 34 |
| LT05_L2SP_035038_19960418_20200911_02_T1 | LT50350381996109AAA02 | 1996 | 4 | 18 | 10 | 1 | 34 |
| LT05_L2SP_035038_19960504_20200911_02_T1 | LT50350381996125AAA01 | 1996 | 5 | 4 | 10 | 2 | 31 |
| LT05_L2SP_035038_19960520_20200911_02_T1 | LT50350381996141XXX02 | 1996 | 5 | 20 | 10 | 3 | 26 |
| LT05_L2SP_035038_19960605_20200911_02_T1 | LT50350381996157XXX02 | 1996 | 6 | 5 | 10 | 4 | 20 |
| LT05_L2SP_035038_19960707_20200911_02_T1 | LT50350381996189XXX03 | 1996 | 7 | 7 | 10 | 6 | 2 |
| LT05_L2SP_035038_19960723_20200911_02_T1 | LT50350381996205AAA02 | 1996 | 7 | 23 | 10 | 6 | 53 |
| LT05_L2SP_035038_19961011_20200911_02_T1 | LT50350381996285XXX02 | 1996 | 10 | 11 | 10 | 11 | 10 |
| LT05_L2SP_035038_19961112_20200911_02_T1 | LT50350381996317XXX02 | 1996 | 11 | 12 | 10 | 12 | 43 |
| LT05_L2SP_035038_19961214_20200910_02_T1 | LT50350381996349XXX02 | 1996 | 12 | 14 | 10 | 14 | 14 |
| LT05_L2SP_035038_19961230_20200910_02_T1 | LT50350381996365AAA02 | 1996 | 12 | 30 | 10 | 15 | 0 |
| LT05_L2SP_035038_19970115_20200910_02_T1 | LT50350381997015XXX02 | 1997 | 1 | 15 | 10 | 15 | 45 |
| LT05_L2SP_035038_19970131_20200910_02_T1 | LT50350381997031XXX01 | 1997 | 1 | 31 | 10 | 16 | 28 |

| | | | | | | | |
|--|-----------------------|------|----|----|----|----|----|
| LT05_L2SP_035038_19970216_20200910_02_T1 | LT50350381997047XXX02 | 1997 | 2 | 16 | 10 | 17 | 9 |
| LT05_L2SP_035038_19970320_20200910_02_T1 | LT50350381997079AAA02 | 1997 | 3 | 20 | 10 | 18 | 26 |
| LT05_L2SP_035038_19970421_20200910_02_T1 | LT50350381997111XXX02 | 1997 | 4 | 21 | 10 | 19 | 35 |
| LT05_L2SP_035038_19970507_20200910_02_T1 | LT50350381997127XXX02 | 1997 | 5 | 7 | 10 | 20 | 8 |
| LT05_L2SP_035038_19970523_20200910_02_T1 | LT50350381997143XXX02 | 1997 | 5 | 23 | 10 | 20 | 42 |
| LT05_L2SP_035038_19970624_20200910_02_T1 | LT50350381997175AAA02 | 1997 | 6 | 24 | 10 | 21 | 49 |
| LT05_L2SP_035038_19970827_20200909_02_T1 | LT50350381997239AAA02 | 1997 | 8 | 27 | 10 | 23 | 55 |
| LT05_L2SP_035038_19970912_20200909_02_T1 | LT50350381997255XXX02 | 1997 | 9 | 12 | 10 | 24 | 22 |
| LT05_L2SP_035038_19970928_20200909_02_T1 | LT50350381997271AAA02 | 1997 | 9 | 28 | 10 | 24 | 50 |
| LT05_L2SP_035038_19971014_20200910_02_T1 | LT50350381997287XXX02 | 1997 | 10 | 14 | 10 | 25 | 16 |
| LT05_L2SP_035038_19971217_20200909_02_T1 | LT50350381997351AAA01 | 1997 | 12 | 17 | 10 | 26 | 52 |
| LT05_L2SP_035038_19980102_20200909_02_T1 | LT50350381998002AAA02 | 1998 | 1 | 2 | 10 | 27 | 15 |
| LT05_L2SP_035038_19980118_20200909_02_T1 | LT50350381998018AAA02 | 1998 | 1 | 18 | 10 | 27 | 35 |
| LT05_L2SP_035038_19980203_20200909_02_T1 | LT50350381998034AAA01 | 1998 | 2 | 3 | 10 | 27 | 57 |
| LT05_L2SP_035038_19980219_20200909_02_T1 | LT50350381998050AAA02 | 1998 | 2 | 19 | 10 | 28 | 16 |
| LT05_L2SP_035038_19980323_20200909_02_T1 | LT50350381998082XXX01 | 1998 | 3 | 23 | 10 | 28 | 45 |
| LT05_L2SP_035038_19980408_20200909_02_T1 | LT50350381998098XXX01 | 1998 | 4 | 8 | 10 | 28 | 57 |
| LT05_L2SP_035038_19980424_20200909_02_T1 | LT50350381998114XXX02 | 1998 | 4 | 24 | 10 | 29 | 9 |
| LT05_L2SP_035038_19980510_20200909_02_T1 | LT50350381998130AAA02 | 1998 | 5 | 10 | 10 | 29 | 24 |
| LT05_L2SP_035038_19980526_20200909_02_T1 | LT50350381998146XXX02 | 1998 | 5 | 26 | 10 | 29 | 40 |
| LT05_L2SP_035038_19980627_20200909_02_T1 | LT50350381998178XXX02 | 1998 | 6 | 27 | 10 | 30 | 4 |
| LT05_L2SP_035038_19980729_20200909_02_T1 | LT50350381998210XXX02 | 1998 | 7 | 29 | 10 | 30 | 23 |
| LT05_L2SP_035038_19980814_20200909_02_T1 | LT50350381998226XXX02 | 1998 | 8 | 14 | 10 | 30 | 30 |
| LT05_L2SP_035038_19981102_20200908_02_T1 | LT50350381998306XXX01 | 1998 | 11 | 2 | 10 | 30 | 56 |
| LT05_L2SP_035038_19981118_20200908_02_T1 | LT50350381998322XXX01 | 1998 | 11 | 18 | 10 | 31 | 4 |
| LT05_L2SP_035038_19981204_20200908_02_T1 | LT50350381998338XXX02 | 1998 | 12 | 4 | 10 | 30 | 59 |
| LT05_L2SP_035038_19981220_20200908_02_T1 | LT50350381998354AAA02 | 1998 | 12 | 20 | 10 | 31 | 4 |
| LT05_L2SP_035038_19990105_20200908_02_T1 | LT50350381999005XXX01 | 1999 | 1 | 5 | 10 | 31 | 6 |
| LT05_L2SP_035038_19990206_20200908_02_T1 | LT50350381999037XXX01 | 1999 | 2 | 6 | 10 | 31 | 12 |
| LT05_L2SP_035038_19990427_20200908_02_T1 | LT50350381999117AAA02 | 1999 | 4 | 27 | 10 | 30 | 45 |
| LT05_L2SP_035038_19990529_20200908_02_T1 | LT50350381999149AAA01 | 1999 | 5 | 29 | 10 | 30 | 11 |

| | | | | | | | |
|--|-----------------------|------|----|----|----|----|----|
| LT05_L2SP_035038_19990630_20200908_02_T1 | LT50350381999181AAA02 | 1999 | 6 | 30 | 10 | 29 | 50 |
| LT05_L2SP_035038_19990817_20200907_02_T1 | LT50350381999229XXX01 | 1999 | 8 | 17 | 10 | 29 | 36 |
| LT05_L2SP_035038_19990918_20200907_02_T1 | LT50350381999261XXX01 | 1999 | 9 | 18 | 10 | 28 | 41 |
| LT05_L2SP_035038_19991004_20200907_02_T1 | LT50350381999277AAA02 | 1999 | 10 | 4 | 10 | 28 | 38 |
| LT05_L2SP_035038_19991105_20200907_02_T1 | LT50350381999309XXX02 | 1999 | 11 | 5 | 10 | 28 | 5 |
| LT05_L2SP_035038_19991121_20200907_02_T1 | LT50350381999325XXX03 | 1999 | 11 | 21 | 10 | 27 | 28 |
| LT05_L2SP_035038_19991223_20200907_02_T1 | LT50350381999357XXX02 | 1999 | 12 | 23 | 10 | 27 | 7 |
| LT05_L2SP_035038_20000108_20200907_02_T1 | LT50350382000008XXX02 | 2000 | 1 | 8 | 10 | 27 | 4 |
| LT05_L2SP_035038_20000328_20200907_02_T1 | LT50350382000088XXX02 | 2000 | 3 | 28 | 10 | 26 | 23 |
| LT05_L2SP_035038_20000515_20200907_02_T1 | LT50350382000136XXX00 | 2000 | 5 | 15 | 10 | 27 | 49 |
| LT05_L2SP_035038_20000531_20200907_02_T1 | LT50350382000152XXX02 | 2000 | 5 | 31 | 10 | 28 | 5 |
| LT05_L2SP_035038_20000616_20200907_02_T1 | LT50350382000168XXX02 | 2000 | 6 | 16 | 10 | 28 | 26 |
| LT05_L2SP_035038_20000718_20200906_02_T1 | LT50350382000200XXX02 | 2000 | 7 | 18 | 10 | 29 | 6 |
| LT05_L2SP_035038_20000803_20200906_02_T1 | LT50350382000216XXX02 | 2000 | 8 | 3 | 10 | 29 | 18 |
| LT05_L2SP_035038_20000819_20200907_02_T1 | LT50350382000232XXX02 | 2000 | 8 | 19 | 10 | 29 | 45 |
| LT05_L2SP_035038_20000904_20200906_02_T1 | LT50350382000248XXX02 | 2000 | 9 | 4 | 10 | 30 | 8 |
| LT05_L2SP_035038_20001123_20200906_02_T1 | LT50350382000328XXX02 | 2000 | 11 | 23 | 10 | 31 | 12 |
| LT05_L2SP_035038_20001225_20200906_02_T1 | LT50350382000360XXX03 | 2000 | 12 | 25 | 10 | 31 | 43 |
| LT05_L2SP_035038_20010126_20200906_02_T1 | LT50350382001026XXX02 | 2001 | 1 | 26 | 10 | 31 | 57 |
| LT05_L2SP_035038_20010211_20200906_02_T1 | LT50350382001042XXX02 | 2001 | 2 | 11 | 10 | 32 | 3 |
| LT05_L2SP_035038_20010315_20200906_02_T1 | LT50350382001074XXX02 | 2001 | 3 | 15 | 10 | 32 | 10 |
| LT05_L2SP_035038_20010331_20200906_02_T1 | LT50350382001090AAA02 | 2001 | 3 | 31 | 10 | 32 | 9 |
| LT05_L2SP_035038_20010416_20200906_02_T1 | LT50350382001106XXX02 | 2001 | 4 | 16 | 10 | 32 | 1 |
| LT05_L2SP_035038_20010502_20200906_02_T1 | LT50350382001122XXX02 | 2001 | 5 | 2 | 10 | 32 | 14 |
| LT05_L2SP_035038_20010806_20200906_02_T1 | LT50350382001218LGS01 | 2001 | 8 | 6 | 10 | 32 | 22 |
| LT05_L2SP_035038_20010822_20200905_02_T1 | LT50350382001234LGS01 | 2001 | 8 | 22 | 10 | 32 | 18 |
| LT05_L2SP_035038_20010907_20200906_02_T1 | LT50350382001250LGS01 | 2001 | 9 | 7 | 10 | 32 | 12 |
| LT05_L2SP_035038_20010923_20200905_02_T1 | LT50350382001266LGS01 | 2001 | 9 | 23 | 10 | 32 | 5 |
| LT05_L2SP_035038_20011025_20200905_02_T1 | LT50350382001298LGS01 | 2001 | 10 | 25 | 10 | 31 | 50 |
| LT05_L2SP_035038_20011228_20200905_02_T1 | LT50350382001362LGS01 | 2001 | 12 | 28 | 10 | 31 | 18 |
| LT05_L2SP_035038_20020113_20200905_02_T1 | LT50350382002013EDC01 | 2002 | 1 | 13 | 10 | 31 | 6 |

| | | | | | | | |
|--|-----------------------|------|----|----|----|----|----|
| LT05_L2SP_035038_20020214_20200905_02_T1 | LT50350382002045LGS01 | 2002 | 2 | 14 | 10 | 30 | 36 |
| LT05_L2SP_035038_20020302_20200905_02_T1 | LT50350382002061LGS01 | 2002 | 3 | 2 | 10 | 30 | 17 |
| LT05_L2SP_035038_20020521_20200905_02_T1 | LT50350382002141LGS01 | 2002 | 5 | 21 | 10 | 28 | 49 |
| LT05_L2SP_035038_20020606_20200905_02_T1 | LT50350382002157LGS01 | 2002 | 6 | 6 | 10 | 28 | 32 |
| LT05_L2SP_035038_20020622_20200905_02_T1 | LT50350382002173LGS03 | 2002 | 6 | 22 | 10 | 28 | 5 |
| LT05_L2SP_035038_20020724_20200905_02_T1 | LT50350382002205LGS01 | 2002 | 7 | 24 | 10 | 27 | 23 |
| LT05_L2SP_035038_20020825_20200905_02_T1 | LT50350382002237LGS01 | 2002 | 8 | 25 | 10 | 26 | 22 |
| LT05_L2SP_035038_20020926_20200905_02_T1 | LT50350382002269LGS01 | 2002 | 9 | 26 | 10 | 25 | 37 |
| LT05_L2SP_035038_20021113_20200905_02_T1 | LT50350382002317EDC01 | 2002 | 11 | 13 | 10 | 24 | 0 |
| LT05_L2SP_035038_20021231_20200905_02_T1 | LT50350382002365LGS01 | 2002 | 12 | 31 | 10 | 24 | 6 |
| LT05_L2SP_035038_20030116_20200905_02_T1 | LT50350382003016LGS01 | 2003 | 1 | 16 | 10 | 24 | 27 |
| LT05_L2SP_035038_20030201_20200905_02_T1 | LT50350382003032LGS01 | 2003 | 2 | 1 | 10 | 24 | 48 |
| LT05_L2SP_035038_20030217_20200904_02_T1 | LT50350382003048LGS01 | 2003 | 2 | 17 | 10 | 25 | 8 |
| LT05_L2SP_035038_20030406_20200904_02_T1 | LT50350382003096LGS01 | 2003 | 4 | 6 | 10 | 26 | 24 |
| LT05_L2SP_035038_20030422_20200905_02_T1 | LT50350382003112LGS01 | 2003 | 4 | 22 | 10 | 26 | 48 |
| LT05_L2SP_035038_20030508_20200905_02_T1 | LT50350382003128LGS01 | 2003 | 5 | 8 | 10 | 27 | 8 |
| LT05_L2SP_035038_20030625_20200905_02_T1 | LT50350382003176LGS01 | 2003 | 6 | 25 | 10 | 28 | 5 |
| LT05_L2SP_035038_20030711_20200905_02_T1 | LT50350382003192PAC02 | 2003 | 7 | 11 | 10 | 28 | 23 |
| LT05_L2SP_035038_20030727_20200904_02_T1 | LT50350382003208PAC02 | 2003 | 7 | 27 | 10 | 28 | 41 |
| LT05_L2SP_035038_20030913_20200904_02_T1 | LT50350382003256PAC02 | 2003 | 9 | 13 | 10 | 29 | 32 |
| LT05_L2SP_035038_20030929_20200904_02_T1 | LT50350382003272PAC02 | 2003 | 9 | 29 | 10 | 29 | 43 |
| LT05_L2SP_035038_20031015_20200904_02_T1 | LT50350382003288PAC02 | 2003 | 10 | 15 | 10 | 29 | 56 |
| LT05_L2SP_035038_20031116_20200904_02_T1 | LT50350382003320LGS01 | 2003 | 11 | 16 | 10 | 30 | 21 |
| LT05_L2SP_035038_20031218_20200904_02_T1 | LT50350382003352PAC02 | 2003 | 12 | 18 | 10 | 30 | 40 |
| LT05_L2SP_035038_20040103_20200904_02_T1 | LT50350382004003LGS01 | 2004 | 1 | 3 | 10 | 30 | 48 |
| LT05_L2SP_035038_20040119_20200904_02_T1 | LT50350382004019LGS01 | 2004 | 1 | 19 | 10 | 30 | 50 |
| LT05_L2SP_035038_20040220_20200903_02_T1 | LT50350382004051LGS01 | 2004 | 2 | 20 | 10 | 30 | 59 |
| LT05_L2SP_035038_20040307_20200903_02_T1 | LT50350382004067PAC02 | 2004 | 3 | 7 | 10 | 31 | 4 |
| LT05_L2SP_035038_20040424_20200903_02_T1 | LT50350382004115PAC02 | 2004 | 4 | 24 | 10 | 32 | 0 |
| LT05_L2SP_035038_20040510_20200903_02_T1 | LT50350382004131PAC04 | 2004 | 5 | 10 | 10 | 32 | 28 |
| LT05_L2SP_035038_20040611_20200903_02_T1 | LT50350382004163PAC02 | 2004 | 6 | 11 | 10 | 33 | 22 |

| | | | | | | | |
|--|-----------------------|------|----|----|----|----|----|
| LT05_L2SP_035038_20040627_20200903_02_T1 | LT50350382004179EDC00 | 2004 | 6 | 27 | 10 | 33 | 51 |
| LT05_L2SP_035038_20040729_20200903_02_T1 | LT50350382004211EDC00 | 2004 | 7 | 29 | 10 | 34 | 41 |
| LT05_L2SP_035038_20040830_20200903_02_T1 | LT50350382004243EDC00 | 2004 | 8 | 30 | 10 | 35 | 28 |
| LT05_L2SP_035038_20040915_20200903_02_T1 | LT50350382004259EDC00 | 2004 | 9 | 15 | 10 | 35 | 53 |
| LT05_L2SP_035038_20041102_20200903_02_T1 | LT50350382004307EDC00 | 2004 | 11 | 2 | 10 | 36 | 55 |
| LT05_L2SP_035038_20041220_20200902_02_T1 | LT50350382004355EDC00 | 2004 | 12 | 20 | 10 | 37 | 50 |
| LT05_L2SP_035038_20050310_20200902_02_T1 | LT50350382005069EDC00 | 2005 | 3 | 10 | 10 | 38 | 57 |
| LT05_L2SP_035038_20050411_20200902_02_T1 | LT50350382005101EDC00 | 2005 | 4 | 11 | 10 | 39 | 9 |
| LT05_L2SP_035038_20050427_20200902_02_T1 | LT50350382005117EDC00 | 2005 | 4 | 27 | 10 | 39 | 13 |
| LT05_L2SP_035038_20050513_20200902_02_T1 | LT50350382005133EDC00 | 2005 | 5 | 13 | 10 | 39 | 19 |
| LT05_L2SP_035038_20050614_20200902_02_T1 | LT50350382005165EDC00 | 2005 | 6 | 14 | 10 | 39 | 35 |
| LT05_L2SP_035038_20050630_20200902_02_T1 | LT50350382005181EDC00 | 2005 | 6 | 30 | 10 | 39 | 39 |
| LT05_L2SP_035038_20050716_20200902_02_T1 | LT50350382005197EDC00 | 2005 | 7 | 16 | 10 | 39 | 49 |
| LT05_L2SP_035038_20050801_20200902_02_T1 | LT50350382005213EDC00 | 2005 | 8 | 1 | 10 | 39 | 59 |
| LT05_L2SP_035038_20050918_20200901_02_T1 | LT50350382005261PAC01 | 2005 | 9 | 18 | 10 | 40 | 10 |
| LT05_L2SP_035038_20051020_20200901_02_T1 | LT50350382005293PAC01 | 2005 | 10 | 20 | 10 | 40 | 5 |
| LT05_L2SP_035038_20051105_20200901_02_T1 | LT50350382005309PAC01 | 2005 | 11 | 5 | 10 | 40 | 12 |
| LT05_L2SP_035038_20051121_20201008_02_T1 | LT50350382005325PAC01 | 2005 | 11 | 21 | 10 | 40 | 36 |

Table A2. Summary of all models tested using backwards stepwise regression for each regression type (P = Poisson, NB = negative binomial) and time interval. For all models in the table, the response variable was individual fitness as measured by number of offspring produced. The final model selected for each time interval is bolded. In all cases, negative binomial was a better fit than Poisson with the same predictor variables, according to a likelihood ratio test for each final model.

| Time interval | Regression type | Model | AIC | Residual df | Dispersion value | Log-likelihood |
|---------------------|-----------------|--|---------------|-------------|------------------|-----------------|
| Annual | P | I + greenness + brightness + wetness + surface temperature | 2980.5 | 786 | 2.40 | -1485.26 |
| Annual | P | I + brightness + wetness + surface temperature | 2978.5 | 787 | 2.39 | -1485.26 |
| Annual | P | I + brightness + surface temperature | 2976.5 | 788 | 2.39 | -1485.26 |
| Annual | NB | I + greenness + brightness + wetness + surface temperature | 2634.5 | 786 | 0.96 | -1311.24 |
| Annual | NB | I + greenness + brightness + surface temperature | 2632.5 | 787 | 0.96 | -1311.25 |
| Annual | NB | I + brightness + surface temperature | 2630.5 | 788 | 0.96 | -1311.27 |
| Summer rainy | P | I + greenness + brightness + wetness + surface temperature | 2968.5 | 786 | 2.40 | -1479.28 |
| Summer rainy | P | I + brightness + wetness + surface temperature | 2966.7 | 787 | 2.40 | -1479.35 |
| Summer rainy | NB | I + greenness + brightness + wetness + surface temperature | 2630.0 | 786 | 0.98 | -1309.00 |
| Summer rainy | NB | I + brightness + wetness + surface temperature | 2628.0 | 787 | 0.98 | -1309.02 |
| Summer rainy | NB | I + brightness + surface temperature | 2627.6 | 788 | 0.98 | -1309.80 |
| Summer rainy | NB | I + brightness | 2626.7 | 789 | 0.97 | -1310.36 |
| Winter rainy | P | I + greenness + brightness + wetness + surface temperature | 2840.1 | 748 | 2.46 | -1415.06 |
| Winter rainy | P | I + brightness + wetness + surface temperature | 2838.2 | 749 | 2.46 | -1415.12 |
| Winter rainy | P | I + wetness + surface temperature | 2839.2 | 750 | 2.46 | -1416.61 |
| Winter rainy | NB | I + greenness + brightness + wetness + surface temperature | 2488.3 | 748 | 0.96 | -1238.14 |
| Winter rainy | NB | I + brightness + wetness + surface temperature | 2486.4 | 749 | 0.96 | -1238.22 |
| Winter rainy | NB | I + wetness + surface temperature | 2486.2 | 750 | 0.95 | -1239.09 |

Table A3. Summary of all models tested using backwards stepwise regression for each regression type (P = Poisson, NB = negative binomial) and time interval. For all models in the table, the response variable was individual fitness as measured by number of offspring produced that survived to age 1. The final model selected for each time interval is bolded. In all cases, negative binomial was a better fit than Poisson with the same predictor variables, according to a likelihood ratio test for each final model.

| Time interval | Regression type | Model | AIC | Residual df | Dispersion value | Log-likelihood |
|---------------------|-----------------|--|---------------|-------------|------------------|----------------|
| Annual | P | I + greenness + brightness + wetness + surface temperature | 1046.4 | 410 | 1.23 | -518.20 |
| Annual | P | I + greenness + wetness + surface temperature | 1044.6 | 411 | 1.23 | -518.29 |
| Annual | P | I + wetness + surface temperature | 1043.6 | 412 | 1.24 | -518.78 |
| Annual | P | I + surface temperature | 1043.1 | 413 | 1.25 | -519.53 |
| Annual | NB | I + greenness + brightness + wetness + surface temperature | 1042.5 | 410 | 1.06 | -515.24 |
| Annual | NB | I + greenness + wetness + surface temperature | 1040.6 | 411 | 1.06 | -515.31 |
| Annual | NB | I + wetness + surface temperature | 1039.5 | 412 | 1.06 | -515.76 |
| Annual | NB | I + surface temperature | 1038.8 | 413 | 1.07 | -516.39 |
| Summer rainy | P | I + greenness + brightness + wetness + surface temperature | 997.4 | 384 | 1.20 | -493.71 |
| Summer rainy | P | I + greenness + brightness + wetness | 996.1 | 385 | 1.20 | -494.03 |
| Summer rainy | P | I + brightness + wetness | 997.5 | 386 | 1.22 | -495.74 |
| Summer rainy | P | I + brightness | 997.2 | 387 | 1.22 | -496.60 |
| Summer rainy | NB | I + greenness + brightness + wetness + surface temperature | 989.5 | 384 | 0.98 | -488.74 |
| Summer rainy | NB | I + greenness + brightness + wetness | 988.0 | 385 | 0.98 | -488.98 |
| Summer rainy | NB | I + brightness + wetness | 988.7 | 386 | 0.98 | -490.34 |
| Summer rainy | NB | I + brightness | 988.0 | 387 | 0.98 | -491.00 |

Table A4. Summary of all negative binomial models tested using backwards stepwise regression for each time interval with female ID included as a random effect. For all models in the table, the response variable was individual fitness as measured by number of offspring produced. The final model selected for each time interval is bolded. The corresponding model without the random variable included is provided in the row following each final model. For all time intervals, the final model retains the same fixed effects as in the final corresponding model without female ID included as a random variable.

| Time interval | Model | AIC | Residual df | Dispersion value | Log- likelihood |
|----------------------|--|---------------|------------------------|-----------------------------|----------------------------|
| Annual | I + greenness + brightness + wetness + surface temperature + (1 female ID) | 2460.0 | 737 | 0.946 | -1223.0 |
| Annual | I + greenness + brightness + surface temperature + (1 female ID) | 2458.4 | 738 | 0.942 | -1223.2 |
| Annual | I + brightness + surface temperature + (1 female ID) | 2456.6 | 739 | 0.940 | -1223.3 |
| Annual | I + brightness + surface temperature | 2455.5 | 740 | 0.871 | -1223.7 |
| Summer rainy | I + greenness + brightness + wetness + surface temperature + (1 female ID) | 2455.4 | 737 | 1.000 | -1220.7 |
| Summer rainy | I + brightness + wetness + surface temperature + (1 female ID) | 2453.4 | 738 | 1.000 | -1220.7 |
| Summer rainy | I + brightness + surface temperature + (1 female ID) | 2453.9 | 739 | 0.978 | -1222.0 |
| Summer rainy | I + brightness + (1 female ID) | 2453.5 | 740 | 0.953 | -1222.7 |
| Summer rainy | I + brightness | 2452.6 | 741 | 0.872 | -1223.3 |
| Winter rainy | I + greenness + brightness + wetness + surface temperature + (1 female ID) | 2456.8 | 737 | 0.971 | -1221.4 |
| Winter rainy | I + brightness + wetness + surface temperature + (1 female ID) | 2454.9 | 738 | 0.972 | -1221.4 |
| Winter rainy | I + wetness + surface temperature + (1 female ID) | 2454.6 | 739 | 0.960 | -1222.3 |
| Winter rainy | I + wetness + surface temperature | 2453.6 | 740 | 0.875 | -1222.8 |

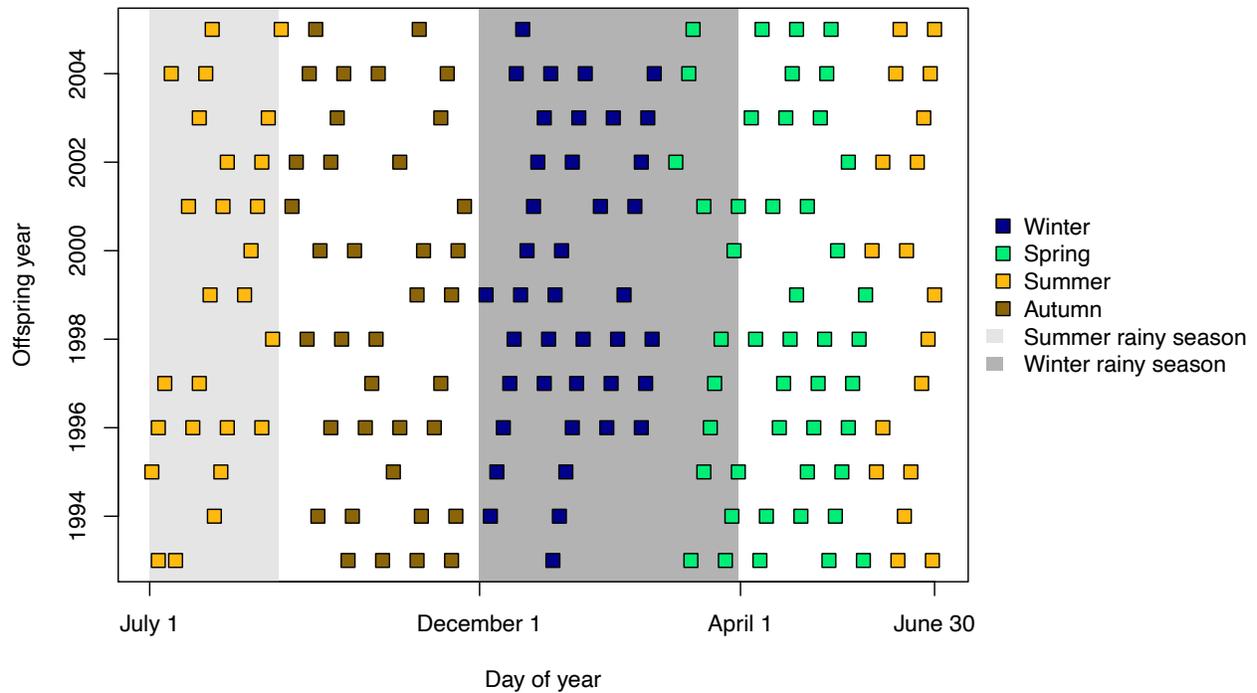


Figure A1. Temporal distribution of retained Landsat 5 scenes ($n = 167$) across rainy seasons and meteorological seasons used for equalizing means within each year. Note that the y-axis indicates offspring year, or the year in which a cohort of offspring was produced. Therefore, the environmental data used to predict the number of offspring produced in year t covers July 1 in year $t - 1$ through June 30 in year t (*i.e.*, the first date included in this plot is July 1, 1992 and the last date included is June 30, 2005).

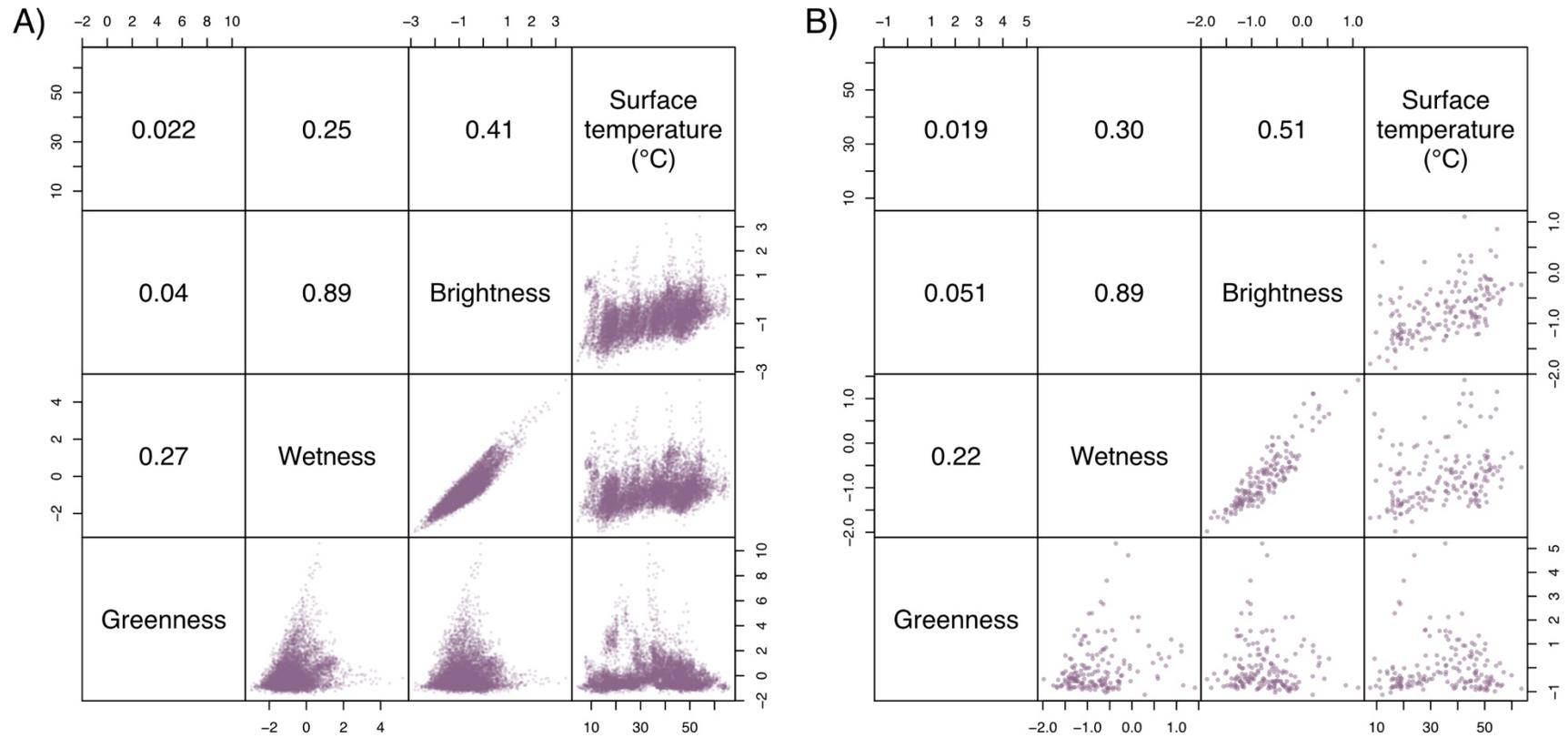


Figure A2. Correlations among remote sensing variables, with Pearson's r presented above the diagonals. A) Points represent 10,000 cells sampled randomly across all time points (*i.e.*, scenes) and all cells active in at least one year ($n = 408$ cells). B) Points represent mean value of active cells within each time point ($n = 167$ scenes). Whereas strong correlation was noted between Tasseled Cap brightness and wetness, the relationships between greenness and these two indices conform to the classic "Tasseled Cap" shape.

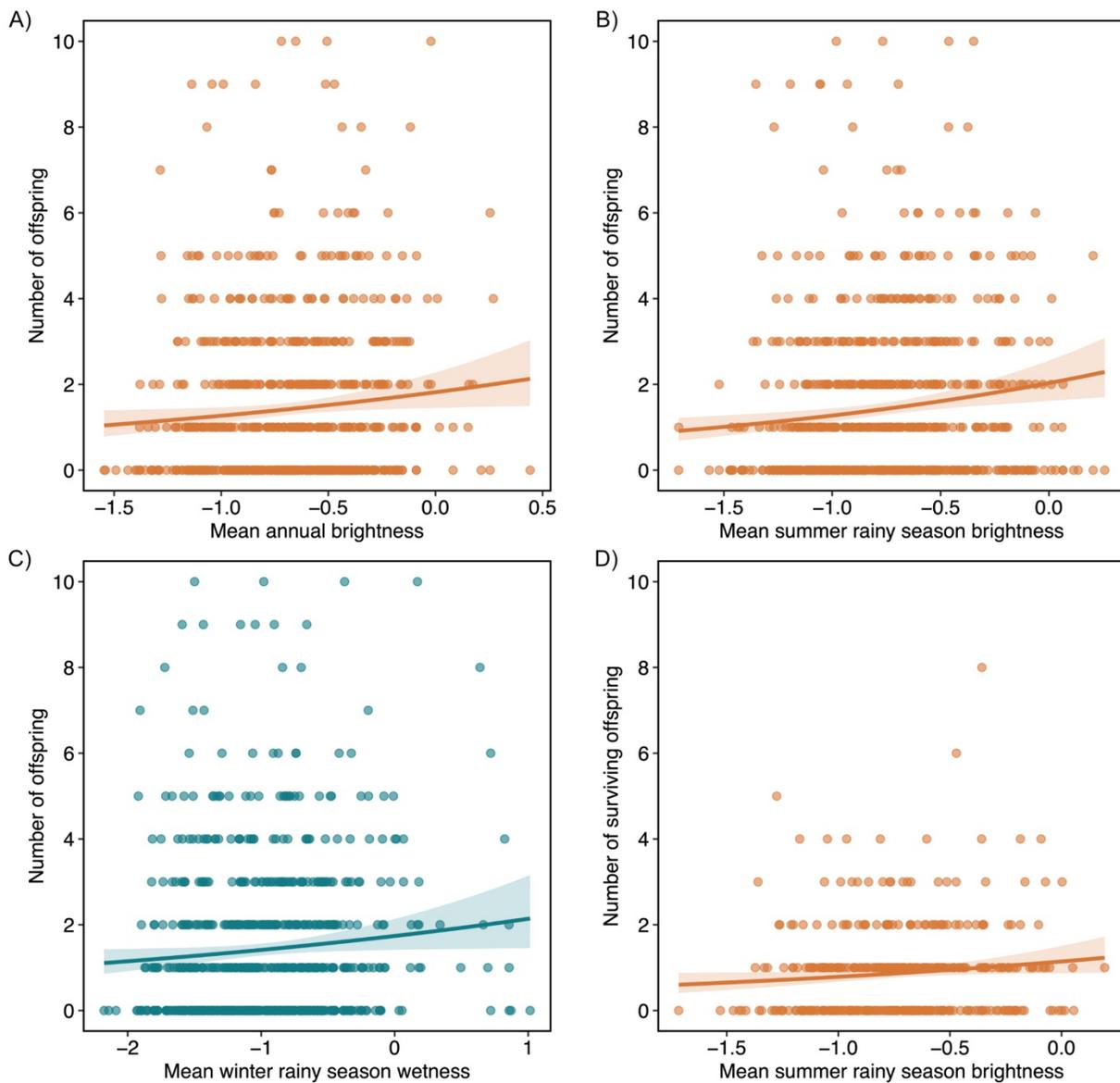


Figure A3. Significant positive relationships between remote sensing measures and individual fitness (A-C, number of offspring; D, number of offspring surviving to age 1). For panels A and C, the effects of each predictor variable were calculated and are presented by setting the non-focal predictor variable in each negative binomial model equal to its mean value. For all panels, shaded polygons represent 95% confidence intervals. Statistical results for models are presented in Tables 1, A2, and A3.

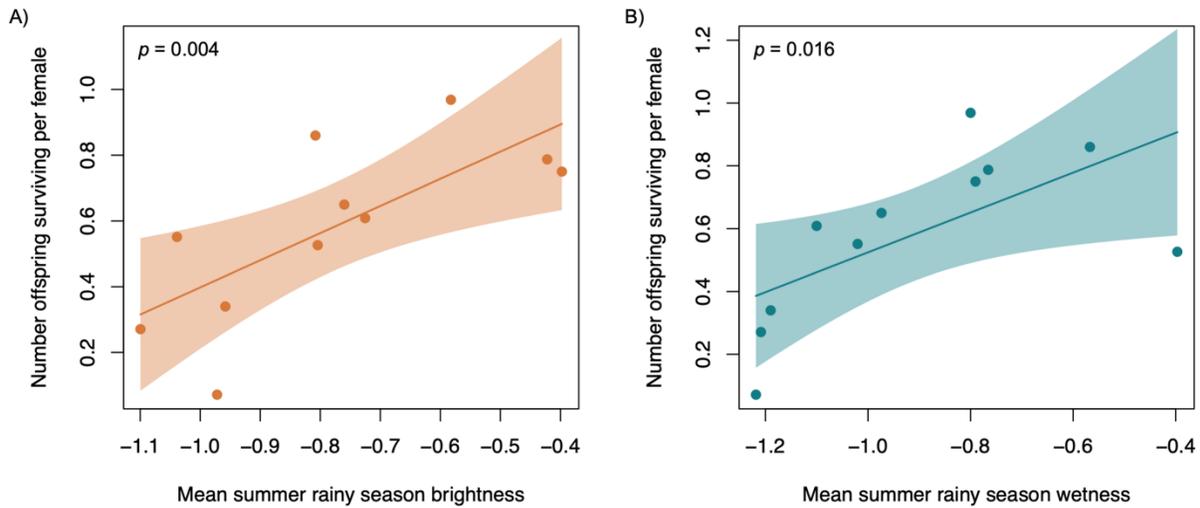


Figure A4. Variables identified as significant predictors of population fitness, specifically the average number of offspring surviving to age 1 per female: mean summer rainy season (A) brightness and (B) wetness. Shaded polygons indicate 95% confidence intervals calculated from the unpermuted linear model. *P*-values were calculated from 1,000 permutations. Model results for brightness and wetness are presented in Tables 2 and 3, respectively.

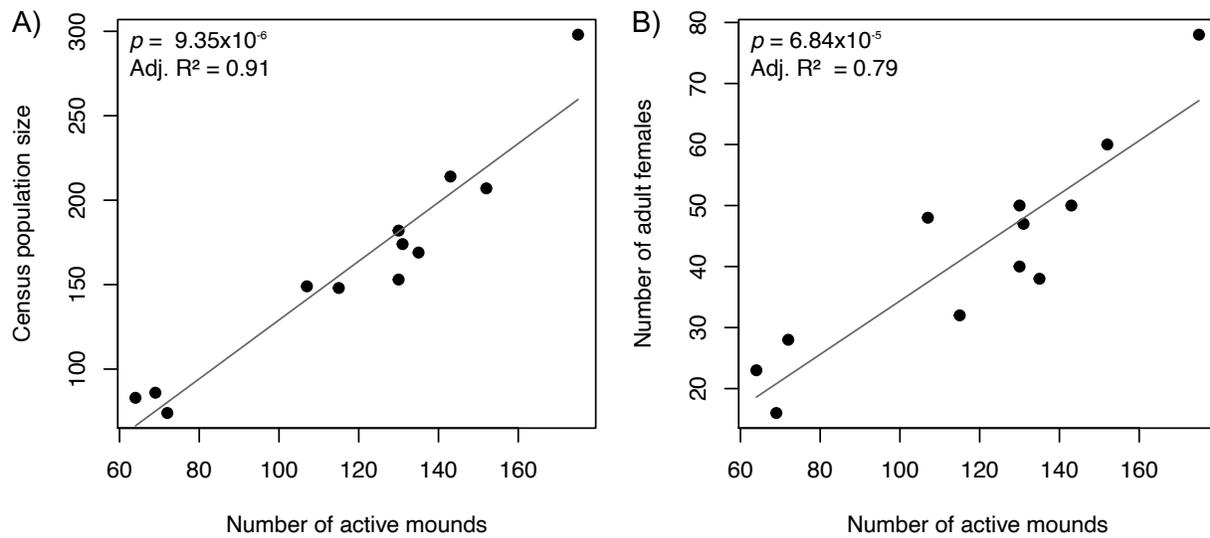


Figure A5. Significant positive relationships between number of active mounds and (A) census population size and (B) number of adult females. Number of active mounds can be reliably ascertained via visual survey of the study site, whereas census population size and number of adult females are both measured via trapping and marking individuals.

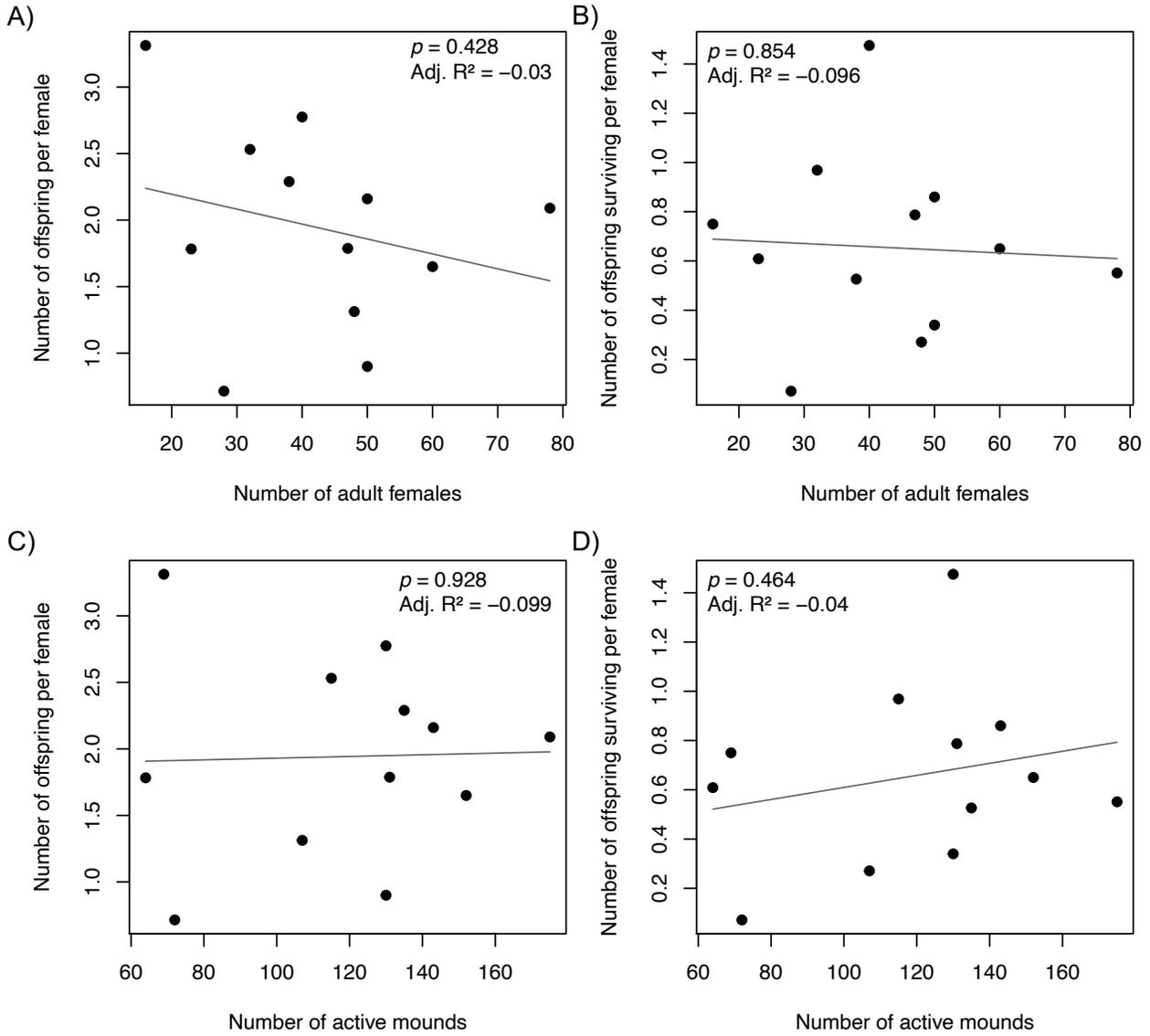


Figure A6. No statistically significant relationships were found between (A-B) number of adult females or (C-D) number of active mounds and average number of offspring per female (A,C) or average number of offspring surviving to age 1 per female (B,D). These patterns suggest a lack of density-dependent influences on individual fitness for the years included in our study.

Figure 1.

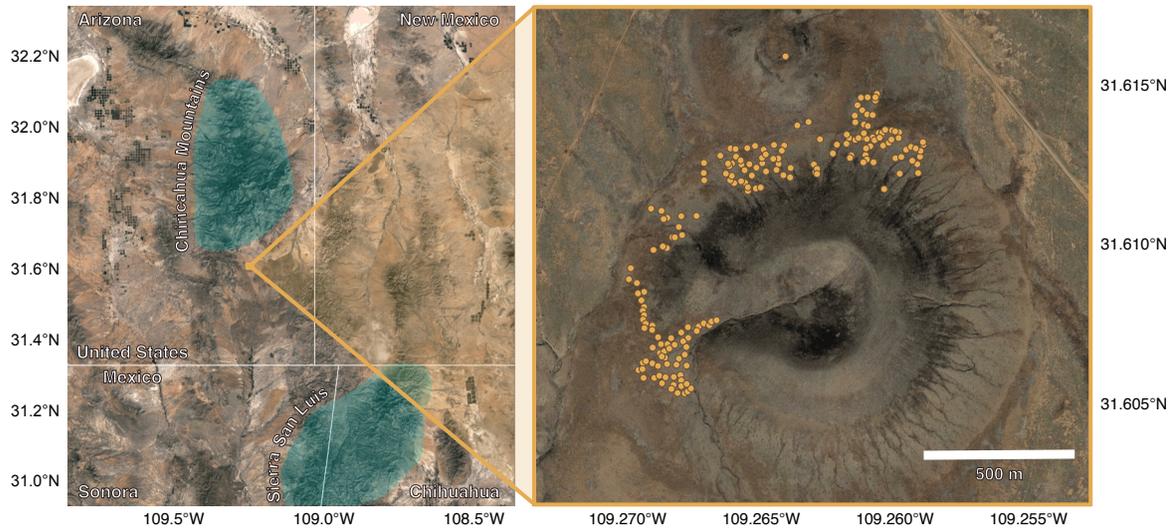


Figure 2.

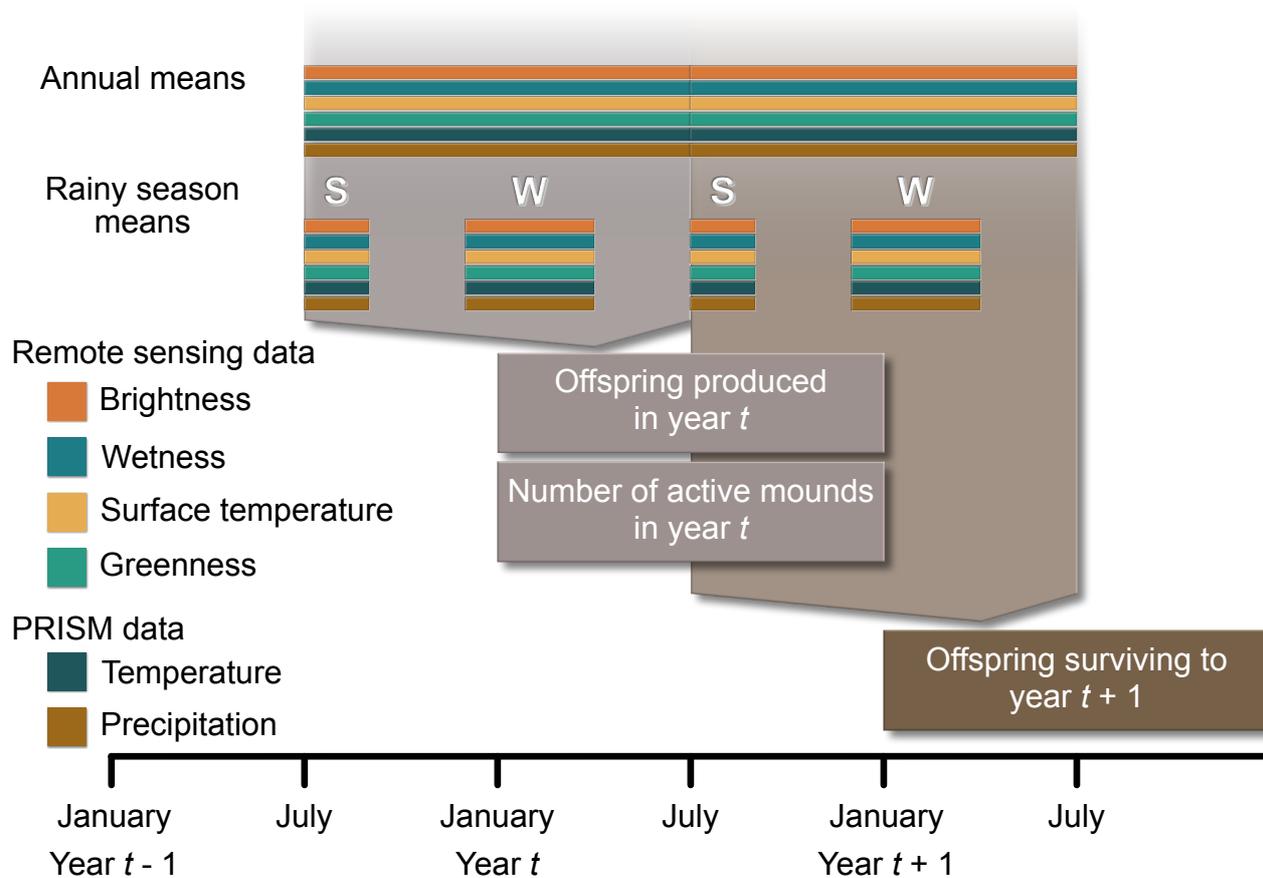


Figure 3.

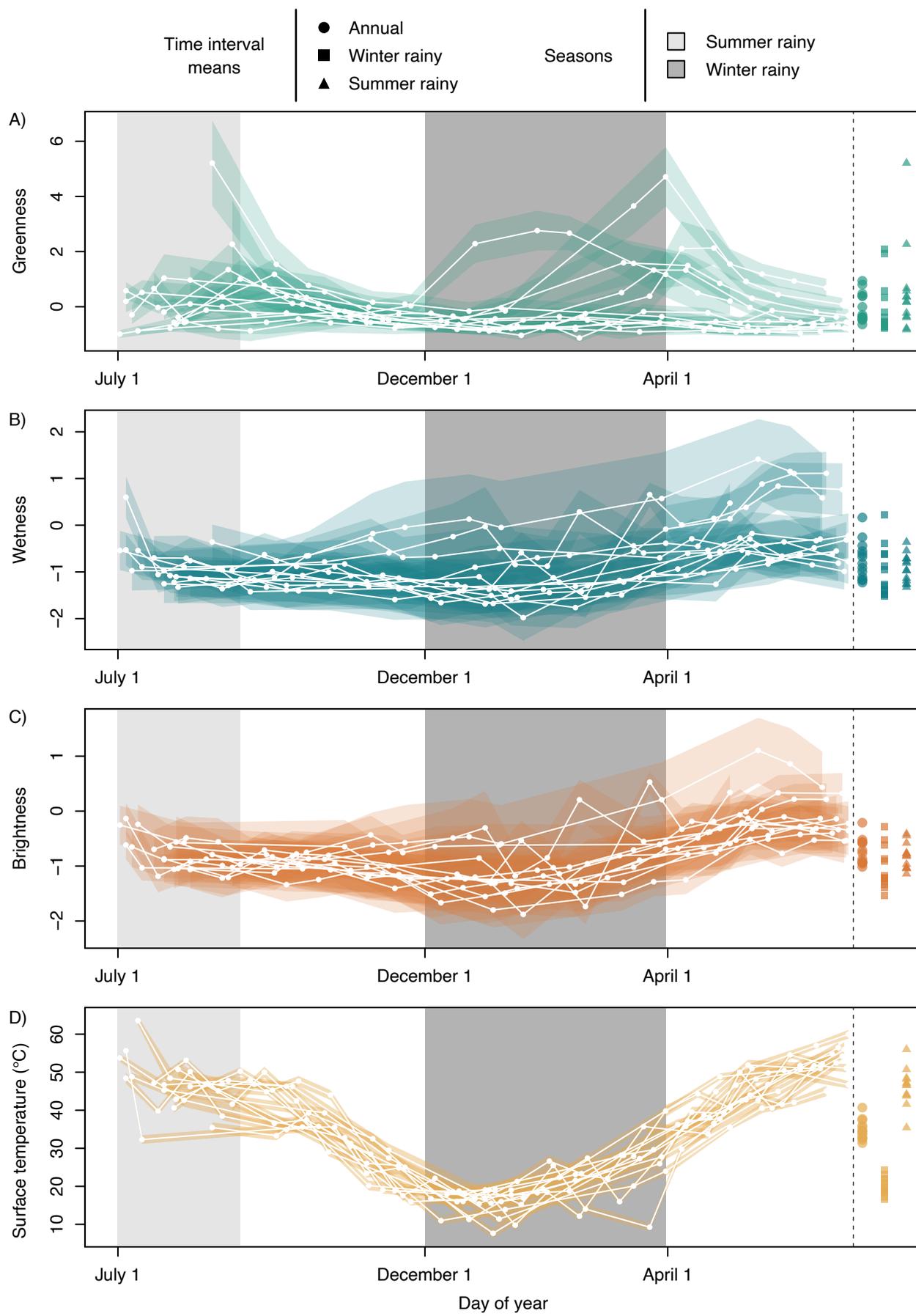


Figure 4.

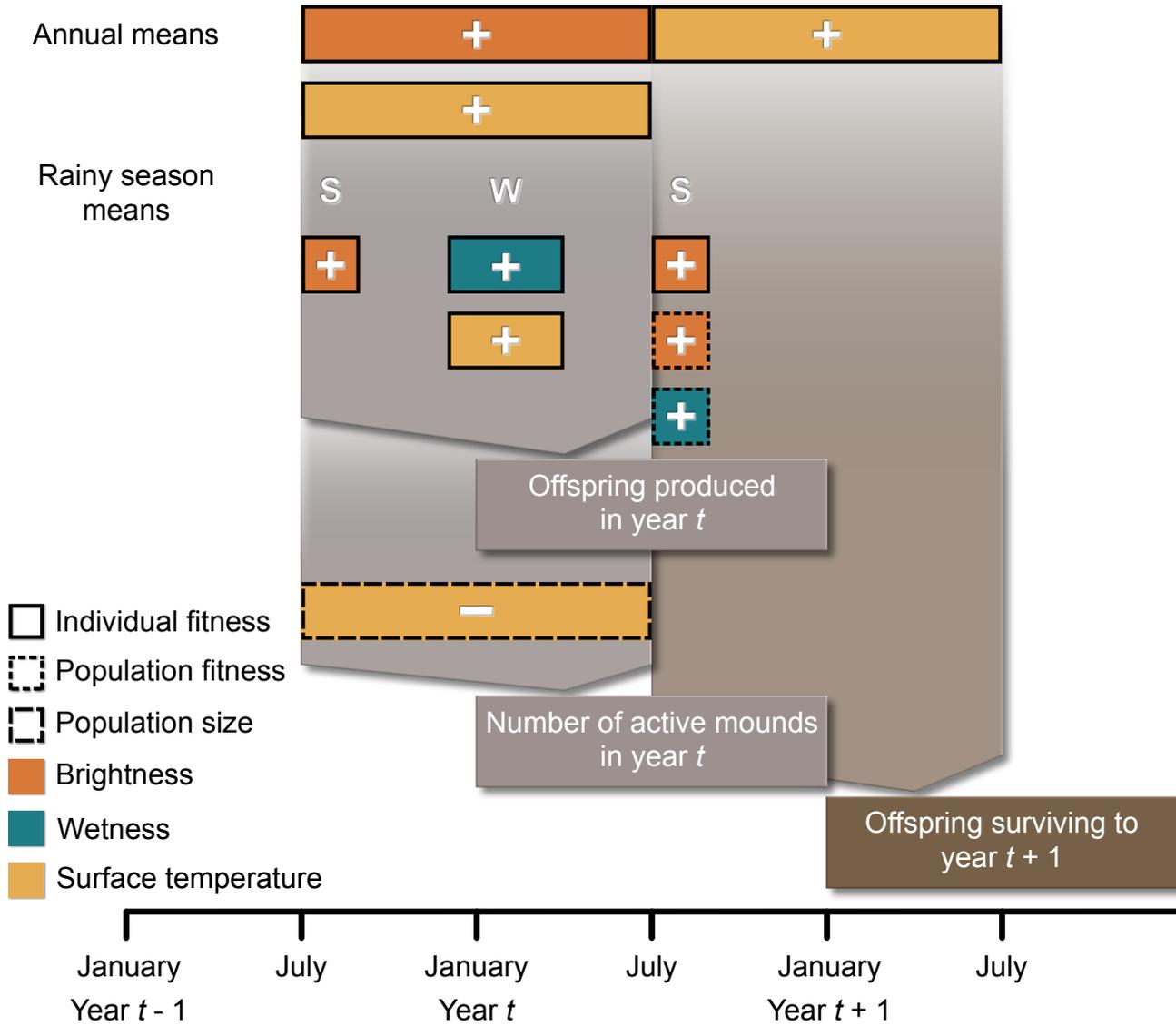


Figure 5.

