

Drivers of burrow use patterns in the Desert
tortoise, *Gopherus agassizii*: Insights towards
social structure

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Summary

1. For several species, refuges (such as burrows, dens, roosts, nests) are an essential resource to obtain protection from predators and extreme environmental conditions. Refuges also serve as focal sites of social interactions including mating, courtship and aggression. Knowledge of refuge use patterns can therefore provide important information about social structure of wildlife populations, especially for species considered to be relatively solitary.
2. In this study, we sought to (a) infer social associations of the desert tortoise, *Gopherus agassizii*, through their asynchronous burrow associations, and (b) examine the effect of various drivers and population stressors influencing burrow use patterns in desert tortoises.
3. Using a graph theoretic approach we found tortoise social networks formed due to asynchronous burrow use to be more clustered, modular, degree centralized and degree homophilic than random networks. Geographical locations had moderate influence on asynchronous burrow associations.
4. We next used regression models combining long-term datasets across nine sites in desert tortoise habitat to test how burrow use patterns are influenced by the environment, density conditions, tortoise characteristics, burrow characteristics and three population stressors - drought, disease, and translocation. We found a large effect of seasonal variation and local tortoise/burrow density on burrow switching patterns. Among the three population stressors tested, translocation had the largest effect on burrow switching, with translo-

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cated animals surprisingly visiting fewer unique burrows than residents. We also found less seasonal variation in burrow popularity and a greater effect of burrow age and surrounding topographical condition instead.

5. Our study emphasizes the role of combining graph theoretic and statistical approaches to examine the social structure of (relatively) solitary species through their refuge use patterns. Detailed knowledge of refuge use behavior at an individual level and its population level consequences can be used to design effective conservation and management strategies including control of future infection spread.

Keywords

behavioral stress response; bipartite networks; clustering; generalized linear mixed models; modularity; Mycoplasma agassizii; seasonality; translocation; URTD

Introduction

1 Incorporating behavior into conservation and management of species has garnered
2 increased interest over the past twenty years (Clemmons, 1997; Swaisgood, 2007;
3 Festa-Bianchet & Apollonio, 2013). Adaptive behavioral responses such as habitat
4 selection, patch use, and foraging that affect fitness (Morris *et al.*, 2009; Berger-Tal
5 *et al.*, 2011), can be more efficient indicators of population disturbances because,
6 unlike population dynamics, they can respond instantaneously to altered condi-
7 tions. Refuge use can similarly affect fitness as refuges, by providing shelter,
8 protection from predators and sites for nesting, are central to survival and repro-

9 ductive success. Altered patterns of refuge use may therefore indicate a distur-
10 bance or change in population fitness and provide an early warning to conservation
11 biologists.

12 Quantifying patterns of refuge use is especially useful for relatively solitary
13 species, as it can provide important information about their social structure. So-
14 cial structure of wildlife populations is typically derived from observational studies
15 on direct social interactions (e.g. in primates (Griffin & Nunn, 2011; MacIntosh
16 *et al.*, 2012), dolphins (Lusseau *et al.*, 2006), ungulates (Cross *et al.*, 2004; Vander
17 Wal, Paquet & Andrés, 2012) etc.). Direct interactions are less frequent and thus
18 harder to quantify for relatively solitary species. For such species, social interac-
19 tions may be limited to certain areas within their habitat, such as refuges (e.g.,
20 roost, den, burrow, nest) or watering holes that provide increased opportunities of
21 direct contact between individuals. Monitoring these resources can therefore help
22 establish relevant social patterns among individuals. In addition to establishing
23 social structure, knowledge of refuge use patterns can serve as a key tool in efforts
24 to control the spread of infection in solitary species. Transmission of pathogens
25 occurs either through close contacts among hosts or through fomites. Host contact
26 patterns therefore either directly or indirectly influence the dynamics of infectious
27 disease in a population. As refuges often serve as focal sites of host contacts in
28 solitary species, patterns of refuge use can be used to establish relevant contact
29 network for infectious disease spread.

30 Here we investigate patterns of burrow use in the desert tortoise, *Gopherus*
31 *agassizii*. Desert tortoise is a long-lived, terrestrial species in the Testudinidae
32 family that occurs throughout the Mojave Desert north and west of the Colorado
33 River. Desert tortoises use subterranean burrows (excavated by both adults and

34 non-reproductives) as an essential adaptation to obtain protection from tempera-
35 ture extremes and predators. Constructing new burrows can be an energy-intensive
36 process, and tortoises often use existing burrows when available (Duda & Krzysik,
37 1998). Because tortoises utilize existing refuges and spend a majority of their
38 time in or near burrows, most of their social interactions are associated with bur-
39 rows (Bulova, 1994). Documenting asynchronous burrow use can therefore provide
40 insights towards sociality in desert tortoises.

41 Social behavior in desert tortoises is not well understood, though evidence
42 suggests some dominance hierarchies or structure may be present (Niblick, Rostal
43 & Classen, 1994; Bulova, 1997) which can influence burrow choice in tortoises. In
44 addition to social structure, environmental conditions and burrow attributes can
45 likely influence burrow-use behavior. Multiple tortoises have been observed visiting
46 a subset of burrows on the landscape, suggesting popularity of a burrow may
47 increase the likelihood of social interaction (Bulova, 1994). At an individual scale,
48 previous research suggests factors such as sex (Harless *et al.*, 2009), age (Wilson
49 *et al.*, 1999), season (Bulova, 1994); and environmental conditions (Duda, Krzysik
50 & Freilich, 1999; Franks, Avery & Spotila, 2011) to influence burrow use in desert
51 tortoises. However, we currently lack a mechanistic understanding of heterogeneity
52 in burrow use patterns, as the relative effect of various factors influencing burrow
53 switching in desert tortoises and popularity of burrows is unknown.

54 If conspecific cues and environmental factors exhibit strong influence on bur-
55 row use, population stressors impacting these characteristics could alter typical
56 burrow behavior. Desert tortoises are currently listed as a threatened species
57 under the US Endangered Species Act (Department of the Interior: US Fish and
58 Wildlife Service, 2011). Three major threats have been identified for desert tortoise

59 populations, the first being anthropogenic interference such as overgrazing, urban
60 development, solar power plants development etc. (Boarman, 2002). The recovery
61 guidelines recommend translocating animals in affected populations in response
62 to these anthropogenic disturbances (Department of the Interior: US Fish and
63 Wildlife Service, 2011). Translocation attempts on other reptilian species, how-
64 ever, has had limited success due to high rates of mortality (Dodd & Seigel, 1991;
65 Germano & Bishop, 2009). The second threat is an infectious disease called upper
66 respiratory tract disease caused by *Mycoplasma agassizii* and *Mycoplasma tes-*
67 *tudineum* (Brown *et al.*, 1994; Sandmeier *et al.*, 2009; Jacobson *et al.*, 2014). The
68 third threat to desert tortoise populations is extreme environmental conditions,
69 particularly drought (Lovich *et al.*, 2014). All three of these stressors: translo-
70 cation, disease, and drought, have been linked to differences in tortoise behavior
71 (Duda, Krzysik & Freilich, 1999; Nussear *et al.*, 2012; McGuire *et al.*, 2014).

72 In this study we combined graph theoretic and statistical approaches to: 1)
73 investigate social structure in desert tortoises populations as reflected by their
74 asynchronous burrow use, and 2) analyze the relative contribution of tortoise at-
75 tributes, burrow attributes, environment, density conditions as well as population
76 stressors towards patterns of burrow use in desert tortoises. To achieve this goal
77 we combined data-sets from nine study sites in desert tortoise habitat (Fig.1),
78 spanning more than 15 years to derive burrow use patterns and tease apart the
79 effect of various drivers and population stressors. We first constructed bipartite
80 networks of burrow use in desert tortoise to infer social associations due to asyn-
81 chronous burrow use. We then used generalized linear mixed models to examine
82 the potential variables influencing burrow use patterns from the perspective of (1)
83 animals, by examining the total number of unique burrows used by individuals,

84 and (2) burrows, by examining the total number of unique tortoises visiting the
85 burrows. Our analysis, unlike previous research, attempts to describe the popu-
86 lation level consequences of asynchronous burrow use as well as tease apart the
87 role of various drivers of burrow use while controlling for others. In addition, as
88 desert tortoises are long lived species, quantifying demographic consequences of
89 population stressors can be difficult. Our analysis instead focuses on behavioral
90 consequence of population stressors that is linked to foraging and mating, and
91 thereby survival success.

92 **Materials and methods**

93 **Dataset**

94 We combined datasets from nine study sites across desert tortoise habitat in the
95 Mojave desert (Fig.1) of California, Nevada, and Utah. At each site, individuals
96 were monitored at least weekly during their active season and at least monthly
97 during winter months using radio telemetry. All tortoises were uniquely tagged,
98 and during each tortoise encounter, data were collected to record the individual
99 identifier of the animal, date, GPS location, microhabitat of the animal (e.g.,
100 vegetation, pallet, or a burrow), any visible signs of injury or upper respiratory
101 tract disease, and environmental conditions. The unique burrow identification was
102 recorded for cases where an animal was located in a burrow. New burrow ids were
103 assigned when an individual was encountered at a previously unmarked burrow.
104 Each site was monitored over multiple but not simultaneous years (SI Table1).

105 Network analysis

106 We constructed burrow use networks of desert tortoises in five out of the nine
107 sites (CS, HW, MC, PV, SL; where no translocations occurred) during active
108 (March - October) and inactive season (November - February) of each surveyed
109 year as a two-mode *bipartite network* that consisted of burrow and tortoise nodes
110 (Fig.2). An edge connecting a tortoise node to a burrow node indicates usage of
111 that burrow by the individual. Edges in a bipartite network always connect the
112 two different node types, thus edges connecting two tortoise nodes or two burrow
113 nodes are not permitted. The power of using bipartite networks of burrow use
114 is to represent both animals and burrows as nodes, thus representing interaction
115 between individual tortoises and burrows. To reduce bias due to uneven sampling,
116 we did not assign edge weights to the bipartite networks.

117 We further examined the social structure of desert tortoises by converting the
118 bipartite network into a single-mode projection of tortoise nodes (Tortoise social
119 network, Fig.2). For these tortoise social networks, we calculated network density,
120 degree centralization, modularity, clustering, and assortativity of individuals by
121 degree and sex/age class. Network density is calculated as the fraction of observed
122 edges to the total possible edges in a network. Degree centralization measures
123 the variation in node degree across the network, such that high values indicate
124 a higher heterogeneity in node degree and that a small number of nodes have a
125 higher degree than the rest. Modularity measures the strength of the division
126 of nodes into subgroups (Girvan & Newman, 2002) and clustering measures the
127 tendency of neighbours of a node to be connected (Bansal, Khandelwal & Meyers,
128 2009). The values of modularity and clustering can range from 0 to 1, and larger

129 values indicate stronger modularity or clustering. To establish the significance of
130 the observed network metrics, we generated 1000 random network counterparts
131 to each empirical network using the configuration model (Molloy & Reed, 1995).
132 The generated random networks had the same degree distribution, average network
133 degree, and number of nodes as empirical networks, but were random with respect
134 to other network properties.

135 We next examined the spatial dependence of asynchronous burrow associations
136 by using coordinates of burrows visited by tortoises to calculate centroid location
137 of each tortoise during a particular season of a year. Distances between each tor-
138 toise pair (i, j) was then calculated as $d_{ij} = d_{ji} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}$ where
139 (x, y) is the coordinate of tortoise centroid location. Pearson correlation coefficient
140 was used to calculate the correlation between observed social associations and ge-
141 ographical distances between the tortoises. We compared the observed correlation
142 to a null distribution of correlation values generated by randomly permuting spa-
143 tial location of burrows 10,000 times and recalculating correlation between social
144 associations and distance matrix for each permutation.

145 Regression Analysis

146 We used generalized linear mixed regression models with Poisson distribution and
147 log link function to assess burrow use patterns. To capture seasonal variation in
148 burrow use, we aggregated the response counts over six periods (Jan-Feb, Mar-
149 Apr, May-Jun, Jul-Aug, Sep-Oct and Nov-Dec). Patterns of burrow use were
150 analyzed in two ways. First, we investigated factors affecting burrow switching,
151 which we define as the number of unique burrows used by a tortoise in a par-

152 ticular sampling period. Second, we investigated burrow popularity, defined as
153 the number of unique individuals using a burrow in a particular sampling period.
154 Model variables used for each analysis are summarized in Table 1. All continuous
155 model variables were centered (by subtracting their averages) and scaled to unit
156 variances (by dividing by their standard deviation). This standard approach in
157 multivariate regression modeling assigns each continuous predictor with the same
158 prior importance in the analysis (Schielzeth, 2010). All analyses were performed
159 in R (version 3.0.2; R Development Core Team 2013).

160 **Investigating burrow switching of desert tortoises:**

161 In this model, the response variable was burrow switching, defined as the total
162 number of unique burrows used by desert tortoises during each sampling period.
163 An individual was considered to be using a burrow if it was reported either inside
164 a burrow or within 25 sqm grid around a burrow. The predictors included in the
165 model are described in Table 1. In addition to the fixed effects, we considered
166 three interactions in this model (i) sampling period \times sex, (ii) sampling period \times
167 seasonal rainfall and (iii) local tortoise density \times local burrow density. Tortoise
168 identification and year \times site were treated as random effects.

169 **Investigating burrow popularity:**

170 For this model, the response variable was burrow popularity defined as the total
171 number of unique tortoises using a focal burrow in a sampling period. The pre-
172 dictors included in the model are also described in Table 1. In this model, we
173 also tested for three interactions between predictors including (i) sampling period
174 \times seasonal rainfall, (ii) sampling period \times local tortoise density, and (iii) local

175 tortoise density \times local burrow density. We treated burrow identification and year
176 \times site as random effects.

177 **Population stressors:**

178 *Disease as a stressor:* We considered field observations of tortoises exhibiting
179 typical signs of URTD including nasal discharge, swollen (or irritated/ sunken)
180 eyes and occluded nares to be indicative of an unhealthy animal. As diagnostic
181 testing was not the focus of the studies collecting the data, we were unable to
182 confirm the infection status of individuals. Knowledge of confirmed infection status
183 of animals, however, was not central to our study as our aim was to measure
184 behavioral response of symptomatic individuals only. We included health condition
185 in the regression model as a categorical variable with two levels - healthy and
186 unhealthy. An individual was considered to be unhealthy if it was reported to
187 display clinical signs of URTD at least once during the sampling period.

188 *Translocation as a stressor:* Translocations were carried out at four (BSV,
189 FI, LM, SG) out of nine sites in our dataset for purposes described in previous
190 studies (Drake *et al.*, 2012; Nussear *et al.*, 2012). We categorized all animals
191 native to the site prior to translocation as controls. Post translocation, all control
192 animals at translocation sites were categorized as residents and introduced animals
193 as translocated. Translocated and resident animals were labeled as ex-translocated
194 and ex-residents, respectively, after a year of translocation to account for potential
195 acclimatization of introduced animals (Nussear *et al.*, 2012). We note that one of
196 four translocation sites (SG) did not have native animals prior to translocation.
197 No translocations were carried out at the rest of the five sites, so all animals
198 surveyed at those sites were labeled as controls. We accounted for translocation

199 in the regression model by giving each surveyed tortoise one of the following five
200 residency status at each sampling period: Control (C), Resident (R), Translocated
201 (T), Ex-Resident (ER) or Ex-Translocated (ET).

202 *Drought as a stressor:* The desert tortoise habitat in Mojave desert typically
203 receives most of the rainfall during the winter season. We therefore use winter
204 rainfall to assess drought conditions in desert tortoise habitat. We defined winter
205 rain during a year as average rainfall from November to February and used it
206 as a proxy of drought condition for the following year. We note that summer
207 rainfall in desert tortoise habitat varies from west to east, where summer rainfall
208 becomes a larger component of the total annual precipitation in East Mojave
209 desert (Henen *et al.*, 1998). Therefore, although we used winter rainfall as a proxy
210 of drought conditions, we considered the effects of summer precipitation implicitly
211 by including seasonal rainfall as a separate predictor (see Table1).

212 **Model selection and validation**

213 Following Harrell (2002) we avoided model selection to remove non-significant pre-
214 dictors and instead present results of our full model. Using the full model with
215 insignificant predictors allows model predictions conditional on the values of all the
216 model predictors and results in more accurate confidence interval of effects of in-
217 terest (Harrell, 2002). The Bayesian information criterion (BIC) of model selection
218 was used only to identify the best higher order interactions. A potential drawback
219 of including all independent variables in the final model is multicollinearity. We
220 therefore estimated Generalized Variance Inflation Factor (GVIF) values for each
221 predictor. GVIF is a variant of traditional VIF used when any predictor in the
222 model has more than 1 degree of freedom (Fox & Monette, 1992). To make GVIF

223 comparable across dimensions, Fox & Monette (1992) suggest using $\text{GVIF}^{(1/(2 \cdot \text{Df}))}$
224 which we refer to as adjusted GVIF. We sequentially removed predictors with high
225 adjusted GVIFs, recalculated adjusted GVIF, and repeated the process until all
226 adjusted GVIF values in the model were below 3 (Zuur, Ieno & Elphick, 2010).

227 We carried out graphical diagnostics by inspecting the Pearson residuals for
228 the conditional distribution to check if the models fit our data in each case. We
229 detected under-dispersion in both the regression models. Under-dispersed mod-
230 els yield consistent estimates, but as equi-dispersion assumption is not true, the
231 maximum-likelihood variance matrix overestimates the true variance matrix which
232 leads to over-estimation of true standard errors (Winkelmann, 2003). We therefore
233 estimated 95% confidence intervals of fixed and random effects using bootstrapping
234 procedures implemented in 'bootMER' function in package lme4.

235 We tested for the significance of fixed factors in both the models using likelihood
236 ratio test (R function mixed from afex package Singmann (2013)). For significant
237 categorical predictors, we used Tukey's HSD (R function glht from the multcomp
238 package, (Hothorn, Bretz & Westfall, 2008)) as a post-hoc test of significant pair-
239 wise differences among means. All reported p-values of post-hoc tests are adjusted
240 for multiple comparisons using single-step method (Hothorn, Bretz & Westfall,
241 2008).

242 Results

243 Network analysis

244 We constructed bipartite networks of asynchronous burrow use in desert tortoises
245 for active and inactive seasons of each year at five sites where no translocation
246 were carried out. An example is shown in Fig.2. Tortoise nodal degree in the
247 bipartite network denotes the number of unique burrows used by the individual
248 and burrow nodal degree is the number of unique individuals visiting the burrow.
249 Bipartite networks demonstrated considerable heterogeneity in tortoise degree and
250 burrow degree (Fig.3). Tortoises visited more unique burrows on an average (= 4.03 ± 3.43 SD)
251 and had a greater range of burrows visited (1-9) in active seasons
252 than in inactive seasons (average = 1.46 ± 0.72 SD, range = 1-5). More than 60%
253 of tortoises used a single burrow during Nov-Feb (inactive) months (Fig.3a). Most
254 of the burrows in desert tortoise habitat were visited by a single tortoise during
255 active and inactive season (Fig.3b). Heterogeneity in total unique animals visiting
256 burrows, however, was slightly more during the months of March-November than
257 November-February (active = 1.21 ± 0.56 SD, inactive = 1.08 ± 0.35 SD).

258 Single mode projection of tortoise nodes from the bipartite network (henceforth
259 call as the tortoise social network) demonstrated moderate clustering (0.36 ± 0.21
260 SD) and modularity (0.53 ± 0.15 SD). Out of the total 24, 23 social networks
261 had higher clustering and 18 social networks were more modular than random
262 networks. Thirteen social networks out of the total 20 demonstrated significant
263 degree homophily and 11 of those had positive associations (SI Table S3). Positive
264 degree homophily (when nodes with similar degree tend to be connected) suggests
265 that tortoises using many unique burrows often use the same set of burrows and

266 are therefore connected in the social network. Tortoise social networks also had a
267 moderate positive degree centralization which indicates a small subset of individ-
268 uals used more burrows than the rest in the surveyed population. Within sexes,
269 positive degree centralization was observed both within males (0.20 ± 0.08 SD)
270 and females (0.17 ± 0.06 SD). Homophilic association by sex ranged from -0.6
271 to 0.11 indicating preference of opposite sex to associate with each other. These
272 negative sexwise associations, however, were not different than those expected by
273 chance.

274 The magnitude of correlation between geographical distances and social associ-
275 ation in tortoise social network due to asynchronous burrow use ranged from -0.22
276 – -0.89 with an average value of -0.49 (Fig. 4). P-value of the permutation test
277 for all sites across active seasons of all surveyed years was less than 0.05, indicat-
278 ing a significant effect of geographical location on social associations. This result
279 of spatial constraints driving social interactions is not surprising as geographical
280 span of surveyed sites were much larger ($>1500\text{m}$) than normal movement range
281 of desert tortoises (Franks, Avery & Spotila, 2011). However, moderate value of
282 correlations suggest other factors (such as environmental, social, density) could
283 play an important role in desert tortoise’s asynchronous burrow associations.

284 **Regression analysis**

285 Based on the observed heterogeneity in bipartite networks, we next investigated
286 the relative effect of natural variables and population stressors on burrow switching
287 patterns of desert tortoises (*viz* degree of animal nodes in bipartite networks) and
288 popularity of burrows in desert tortoise habitat (*viz* degree of burrow nodes in bi-

289 partite networks). SI Table4 presents the best models of BIC values for interactive
290 predictors that explain burrow switching in desert tortoises and burrow popularity.
291 The three interactions tested for burrow switching model were sampling period \times
292 sex, sampling period \times seasonal rainfall and local tortoise density \times local burrow
293 density. We tested all possible combinations of the three interactions. The best
294 model contained interaction of sampling period \times seasonal rainfall (SI Table4).
295 The evidence ratio of this model was over 92 times higher than the second best
296 model containing an additional interaction of local tortoise density \times local bur-
297 row density. We note that previous studies report sex difference in activity levels
298 of adult tortoises between different seasons, with adult female tortoises moving
299 longer distances and having larger home ranges during nesting season, and males
300 being more active during mating season (Bulova, 1994). The lack of support for
301 sex \times sampling period interaction as a candidate predictor in our model, however,
302 suggests seasonal differences in burrow use behavior between adults to be minor
303 as compared to other drivers of burrow use.

304 For the burrow popularity model, we tested all possible combination of sam-
305 pling period \times seasonal rainfall, sampling period \times local tortoise density and local
306 tortoise density \times local burrow density interactions. The best model included the
307 sampling period \times local tortoise density and local tortoise density \times local bur-
308 row density interaction term. All three measures of temperature (average, max
309 and min) had adjusted GVIF values of >3 and were therefore removed from the
310 models. We also removed sampling period \times tortoise density interaction from the
311 burrow popularity model as it inflated adj GVIF value of tortoise density to >3 .
312 σ^2 estimate of tortoise id and burrow id was negligible (tortoise id: $\sigma^2 = 0$, CI =
313 0-0.004, burrow id: $\sigma^2 = 0$, CI = 0-0.003). Both the random effects were therefore

314 removed from the regression models.

315 **Effect of animal attributes**

316 Sex/age class had a significant effect on burrow switching ($\chi^2=16.75$, $P=0.0002$).

317 Overall, adults used more unique burrows than non-reproductives. Among adults,
318 males used slightly higher number of unique burrows than females (Fig. 5). There
319 was no effect of body size on individuals' burrow switching behavior ($\chi^2= 0.2$,
320 $P=0.65$).

321 **Effect of burrow attributes**

322 Out of the six burrow attributes included in the model, burrow age and surface
323 roughness around burrow had the highest impact on burrow popularity, i.e., num-
324 ber of unique individuals visiting the burrow (burrow age: $\chi^2= 46.07$, $P < 0.0001$,
325 surface roughness: ($\chi^2= 14.37$, $P < 0.0001$). Burrow popularity was positively
326 correlated with surface roughness indicating that burrows in flat sandy areas were
327 visited by less unique tortoises than burrows in rough rocky areas. Older burrows
328 were visited by more unique individuals, with burrow popularity increasing $\exp^{0.08}$
329 times with each increment of age (Fig. 5). Burrows in areas with higher topo-
330 graphical position as indicated by GIS raster images were also more popular ($\chi^2=$
331 5.71 , $P= 0.02$).

332 **Effect of environmental conditions**

333 Sampling period had a large effect on number of unique burrows used by desert
334 tortoises ($\chi^2= 160.96$, $P < 0.0001$) as well as on burrow popularity ($\chi^2= 176.25$,
335 $P < 0.0001$). Burrow switching of desert tortoises was highest during the months

336 of May-June and September-October when they are typically more active, and
337 lowest in winter months (Fig. 5). In the late summer (July-August), tortoises
338 demonstrated slightly lower burrow switching than during the active season, but
339 higher than the winter season. Within a particular year, the direction of the effect
340 of seasonal rainfall varied across different sampling periods (sampling period \times
341 seasonal rain: $\chi^2= 107.46$, $P < 0.0001$). For example, high rainfall during the
342 months of March-April reduced burrow switching in desert tortoises. On the other
343 hand, individuals exhibited higher burrow switching with higher rain during the
344 months of July-August (SI Fig. S3b).

345 In contrast to the large variation in individuals' burrow switching behavior be-
346 tween sampling periods, popularity of burrows did not vary during a large portion
347 of the year (May - December). Total unique animals visiting burrows tended to be
348 lower in the months of January-February and March-April, as compared to other
349 months of the year (Fig. 5, S4c). Seasonal rainfall had a positive correlation with
350 burrow popularity ($\chi^2= 6.02$, $P= 0.01$).

351

352 **Effect of density conditions**

353 An increase in the number of active burrows around individuals promoted bur-
354 row switching, whereas an individual used fewer burrows when there were more
355 tortoises in the vicinity (Fig. 5). In the burrow popularity model, higher tortoise
356 density around burrows increased number of individuals visiting these burrows
357 (Fig. 5). There was a significant interactive effect of the two density conditions on
358 burrow popularity ($\chi^2= 177.37$, $P < 0.0001$) – increase in burrow popularity with
359 higher tortoise density was lower when there more burrows in the vicinity of the

360 focal burrow (SI Fig. S4d).

361

362 **Effect of population stressors**

363 Population stressors of drought, health and translocation had variable influences
364 on burrow switching of desert tortoises (Fig.5, S5). As compared to residents
365 and controls, translocated animals demonstrated lower burrow switching during
366 the year of translocation and also in the subsequent years. We did not find any
367 differences between burrow switching levels of individuals exhibiting clinical signs
368 of URTD and clinically healthy individuals ($\chi^2 = 2.51$, $P = 0.11$). Burrow switching
369 levels of all surveyed animals (indicated by lower winter rainfall), however, was
370 slightly lower in comparison to non-drought years (burrow switching: $\chi^2 = 3.5$, P
371 $= 0.06$).

372 **Discussion**

373 Burrow switching in desert tortoises is associated with costs of increasing exposure
374 to heat, predators and benefits of finding food and mates. A tortoises' decision to
375 switch burrows must be, therefore, made based on the balance between costs and
376 benefits of being outside the refuge. These decisions and the consequent outcome
377 of burrow switching patterns observed in desert tortoise populations is important,
378 as theoretical models predict reduced survival of populations due to suboptimal
379 refuge use decisions (Cooper Jr, 2015). Burrow switching has an additional cost
380 of infection risk where refuges are focal points of pathogen transfer. Modeling
381 optimal burrow switching that maximizes fitness in desert tortoises is difficult

382 as it is hard to quantify fitness costs in a long-lived species. Our study instead
383 provides a baseline of burrow use patterns in desert tortoises. Any large deviation
384 to these baseline levels may lower the survival and thus (long-term) fitness of the
385 population. As direct measurements of survival (or fitness) is often unavailable in
386 long-lived species such as the desert tortoise, burrow switching can be used as an
387 immediate indicator of potential long-term fitness consequences of a population.

388 We detected non-random structure in desert tortoise social networks based on
389 asynchronous burrow associations. Desert tortoises form tight and closed soci-
390 eties as demonstrated by higher modularity and clustering coefficient values than
391 random null networks. There were clear spatial constraints behind asynchronous
392 burrow associations in desert tortoises. As the average distances between burrows
393 across the study sites were well beyond the normal movement range of individuals,
394 we believe the spatial constraint reflects tortoises' preference to move and use spa-
395 tially proximate burrows than geographically distant ones. The spatial constraints
396 to asynchronous burrow associations along with positive degree associations, clus-
397 tering and modularity can have important implication in infection spread through
398 desert tortoise populations. Few connections between communities in tortoise so-
399 cial network can, on one hand, effectively localize new infections to few individuals.
400 For chronic infections such as URTD, these pockets of infection, however, can serve
401 as sources of re-infection to other uninfected communities, eventually leading to
402 high and consistent level of infection across the entire population.

403 Our analysis of drivers of individual-level heterogeneity of asynchronous burrow
404 associations revealed local burrow density and time of the year to have the largest
405 influence on burrow switching behavior of desert tortoises. Low burrow switching
406 during winter and summer months reflects reduced movement of desert tortoises

407 to avoid severe weather conditions (Eubanks, Michener & Guyer, 2003). High bur-
408 row switching in May-June and September-October coincides with high activity
409 of nesting and mating in adults. Among individuals, the differences in burrow use
410 behavior between adults and non-reproductives were much larger than differences
411 among adult males and females. These differences may reflect the different costs
412 and benefits of switching burrows for reproductive adults and non-reproductive
413 tortoises. Leaving a refuge may present a greater risk to non-reproductives that
414 are more vulnerable to predation and do not benefit from the mating opportuni-
415 ties gained by burrow switching. Future studies and management plans should
416 consider differences in burrow switching between different non-reproductive tor-
417 toises including neonates, juveniles and subadults in order to mitigate increased
418 predation risk by pervasive predators such as ravens.

419 Earlier studies report only one-fourth of burrows in desert tortoise habitat to be
420 popular, i.e., used by more than one animal in a year (Bulova, 1994; Harless *et al.*,
421 2009). We show variables such as topographical variables (of surface roughness
422 and elevation), age of burrow and density of tortoises around the burrow affect
423 burrow popularity, which may explain why only a small fraction of burrows are
424 visited by multiple animals. Knowledge of active and popular burrows can have
425 two important implications for the management of the species. First, population
426 density estimates usually rely on observations of animals located above ground.
427 Desert tortoises, however, spend most of the time in a year in burrows (Bulova,
428 1994), which may lead to underestimation of actual population densities (Nussear
429 & Tracy, 2007; Inman, Nussear & Richard Tracy, 2010). Survey of active popular
430 burrows at high tortoise density areas can augment the current survey methods
431 in order to get a more accurate estimate of population density of desert tortoises.

432 Our results suggest that popular burrows can be identified using certain burrow
433 characteristics such as surrounding topographical variables and age. As actual
434 burrow age is often hard to determine, we demonstrate the use of historical survey
435 data to estimate proxy age of burrows. Once identified, these popular burrows can
436 be surveyed throughout the year as there is only a minor effect of sampling period
437 and seasonal rainfall on burrow popularity. Secondly, declines of popular burrows
438 in desert tortoise habitat can indicate reduced social interactions and thus mating
439 opportunities for individuals. Reduced burrow popularity can also be indicative
440 of higher mortality risk - Esque *et al.* (2010) found higher mortality in flat open
441 areas where burrows, as our results indicate, are less popular as compared to rough
442 higher elevation sites. Active popular burrows can be therefore used (a) as sentinels
443 of population health and (b) to identify critical core habitat of desert tortoises for
444 conservation and adaptive management of the species.

445 We investigated the effect of three population stressors - drought, translocation
446 and disease - associated with major threats to the conservation of this species. Out
447 of the three, our results suggests translocation to have the strongest impact on
448 burrow switching behavior of desert tortoises. Although translocated animals are
449 known to have high dispersal tendencies (Nussear *et al.*, 2012; Hinderle *et al.*, 2015)
450 and hence are expected to encounter and use more burrows, we found translocated
451 individuals to use fewer unique burrows than residents. Our results are however
452 supported by evidences of translocated tortoises spending more time on the surface
453 and taking shelter under vegetation rather than using burrows (Hinderle, 2011).
454 Surprisingly, even after one year of translocation, relocated animals continued use
455 fewer burrows than residents in the population. The use of fewer burrows coupled
456 with movement rates can increase expose translocated animals to predation and

457 dehydration, potentially increasing mortality. Therefore, to improve translocation
458 success, a fruitful area of investigation for future research will be to determine
459 potential causes of this change in burrow use behavior in translocated tortoises.

460 There was no major effect of drought or disease on burrow switching patterns
461 of tortoises in our data-set. Severe clinical signs of URTD have been associated
462 with changes in burrow use pattern in Gopher tortoises (McGuire *et al.*, 2014).
463 Our results do not indicate any effect of disease quite possibly because we could
464 not distinguish severe clinical signs with milder forms in the dataset. Although
465 there was no evidence of disease influencing burrow use behavior in the present
466 study, we note that it is likely for burrow use behavior (and in particular the
467 burrows themselves) to drive infectious disease patterns in desert tortoises either
468 directly, through cohabitation instances, or indirectly, by serving as focal sites
469 of social interactions. We used winter rain as a proxy of drought conditions as
470 the Western Mojave receives most of its annual rainfall during the months of
471 November-February. Winter rain is important for the availability of food for desert
472 tortoises in the spring and has therefore been used in previous studies to assess the
473 effect of drought on tortoise behavior (Duda, Krzysik & Freilich, 1999; Lovich *et al.*,
474 2014). Our results show average number of unique burrows visited by tortoises were
475 slightly reduced during drought years. Reduced burrow switching may correspond
476 to smaller homeranges of desert tortoises observed during drought years (Duda,
477 Krzysik & Freilich, 1999). Years of low winter rainfall have been known to cause
478 increased predation of desert tortoises due to diminished prey resources (Peterson,
479 1994; Esque *et al.*, 2010). Lower burrow switching during drought years can also be
480 a behavioral response to avoid predation or reduce energy expenditure and water
481 loss in years of low resource availability (Nagy & Medica, 1986).

482 Conclusions

483 We examined the patterns of burrow use in *G. agassizii* by modeling variation in
484 burrow use in two different ways. We first considered animals as units of interest
485 and examined their burrow switching behavior. Using burrows as units we next ex-
486 amined patterns of burrow popularity in desert tortoise habitat. We describe how
487 various factors of tortoise attributes, burrow attributes, environment and popula-
488 tion stressors affect burrow use patterns in desert tortoises. Burrows are essential
489 for survival of individuals and are the focal points of most social interactions.
490 Burrow switching patterns, therefore, may correlate to reproductive and foraging
491 success in desert tortoises. Reduced burrow use due to population stressors can
492 increase risk of predation and mortality due to overheating of animals. Burrow
493 use is therefore an important aspect of tortoise' behavior and burrow use patterns
494 can be particularly important to consider before implementing any management
495 or conservation strategy. Burrows might also play an important role in spread of
496 infectious diseases by either providing refuge for prolonged contact or facilitating
497 indirect transmission. Understanding the drivers of burrow use patterns can there-
498 fore provide insights towards the social (contact) structure in desert tortoise and,
499 in future, help design models of infectious disease spread such as URTD.

500 Acknowledgments

501 TODO

502 Data accessibility

503 The data used for burrow switching and burrow popularity model can be accessed
504 at <http://dx.doi.org/10.7910/DVN/S5KZBS>

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650 **Table captions**

651 **Table 1.** Potential variables considered to characterize burrow use patterns in the
652 desert tortoise, *Gopherus agassizii*.

653

654 **Figure captions**

655 **Figure 1.** Critical habitat range of the desert tortoise within the Mojave desert,
656 USA as determined by the US Fish and Wildlife Services in 2010(<http://www.fws.gov/carlsbad/GIS/>)
657 Critical habitat is defined as those geographical areas that contain physical or bi-
658 ological features essential to the conservation and management of the species (US
659 Fish & Wildlife Service, 1973). Points represent centroids of survey sites where
660 tortoises were monitored using radio-telemetry. Point size is proportional to the
661 number of animals monitored at the site.

662

663 **Figure 2.** (a) Bipartite network of burrow use patterns at MC site during the year
664 2012. Node type indicated by color (Blue = adult males and red = adult females).
665 Node positions were fixed using Yifan Hu's multilevel layout in Gephi. In this
666 paper, we quantify burrow switching and burrow popularity as degree of tortoise
667 nodes and burrow nodes, respectively, in the bipartite network. For example,
668 burrow switching of the female tortoise X is five and burrow popularity of burrow
669 Y is one. (b) Single-mode projection of the bipartite network into tortoise social
670 network.

671 **Figure 3.** Frequency distribution of (a) Tortoise degree i.e., unique burrows used
672 by desert tortoises and (b) Burrow degree i.e., unique tortoises visiting burrows
673 during active (Mar-Oct) and inactive (Nov-Feb) seasons. Values are averaged over
674 each surveyed year and study site. y-axis represents normalized frequency counts
675 of tortoises/burrows.

676 **Figure 4.** Spatial constraints on asynchronous burrow associations during active
677 seasons at study sites with control animals. Correlation between geographical

Table 1:

Variables	Variable type	Description
Tortoise attributes (Burrow switching model only)		
Sex/age class	Categorical	Three levels - adult males, adult females and non-reproductive individuals
Size	Continuous	Midline carapace length averaged over the year for each individual
Burrow attributes (Burrow popularity model only)		
Burrow azimuth	Categorical	Direction in which burrow entrance faces forward. We converted the 1 to 360° range of possible azimuth values to eight categorical azimuth directions: Q1 (1-45), Q2 (46-90), Q3 (91-135), Q4 (136-180), Q5 (181-225), Q6 (226-270), Q7 (271-315) and Q8 (316-360)
Burrow surveyed age	Continuous	Number of years between the first report of burrow and current observation
Soil condition	Categorical	The soil conditions at the nine sites varied from sandy to mostly rocky. We therefore categorized burrow soil into four categories - mostly sandy, sand and rocky, mostly rocky and caliche and rocky
Percentage wash	Continuous	Percentage area covered by dry bed stream within 250 sqm area around burrow
Surface roughness	Continuous	See (Inman <i>et al.</i> , 2014)
Topographic position	Continuous	See (Inman <i>et al.</i> , 2014)
Environmental characteristics		
Sampling period	Categorical	The period of observation as described before. We divided a year into six periods of two months each
Seasonal rainfall*	Continuous	Total rainfall recorded at weather station nearest to the study site (in inches) during a particular sampling period
Temperature*	Continuous	Average, maximum and minimum temperature recorded at the weather station nearest to the study site and calculated over each sampling period in our model
Population stressors**		
Tortoise health	Categorical	Burrow switching model only. Two categories - healthy and unhealthy
Residency status	Categorical	Burrow switching model only. Each individual was assigned one of the five residency status for each sampling period - Control (C), Resident (R), Translocated (T), Ex-Resident (ER) or Ex-Translocated (ET)
Drought condition	Continuous	Average rainfall from November to February used as a proxy of drought condition for the following year
Density condition		
Local tortoise density	Continuous	For burrow switching model: the average number of individuals found within 10,000 sqm grid around the focal tortoise each day of sampling period when the animal was surveyed. For burrow popularity model: number of individuals found in 10,000 sqm grid around the focal burrow averaged each surveyed day of the sampling period
Local burrow density	Continuous	For burrow switching model: the average number of active burrows in 10,000 sqm grid around the focal tortoise each day of the sampling period when the animal was reported. For burrow popularity model: the number of active burrows in 10,000 sqm grid around the focal burrow. A burrow was considered to be active if it was reported to be occupied at least once during the current or any previous sampling period
Survey condition		
Sampling days	Continuous	Total survey days during the sampling period
Individual level bias	Continuous	Burrow switching model: Total number of days when the focal tortoise was reported using any burrow to account for any survey biases between individuals. Burrow popularity model: Total tortoises surveyed during the sampling period

* Rainfall and temperature data was obtained from the nearest weather station to the study site using database available at National Oceanic & Atmospheric Administration website (<http://www.ncdc.noaa.gov>).

** See text for details.

678 distance and edge occurrence in tortoise social network. Correlation values are
679 averaged over each surveyed year and error vars are standard errors. P-value
680 associated with each correlation measure was < 0.05 .

681 **Figure 5.** The effect of various predictors on the two models of burrow use
682 patterns in desert tortoises. Error bars indicate 95% confidence intervals around
683 the estimated coefficient value. For continuous predictors, the vertical dashed
684 line indicates no effect - positive coefficients indicate increase in burrow popular-
685 ity/switching with increase in predictor value; negative coefficients indicate de-
686 crease in burrow popularity/switching with higher values of predictors. For each
687 categorical predictor, the base factor straddles the vertical line at 0 and appears
688 without a 95% CI. Positive and negative coefficients for categorical predictors de-
689 note increase and decrease, respectively, in burrow popularity/switching relative to
690 the base factor.

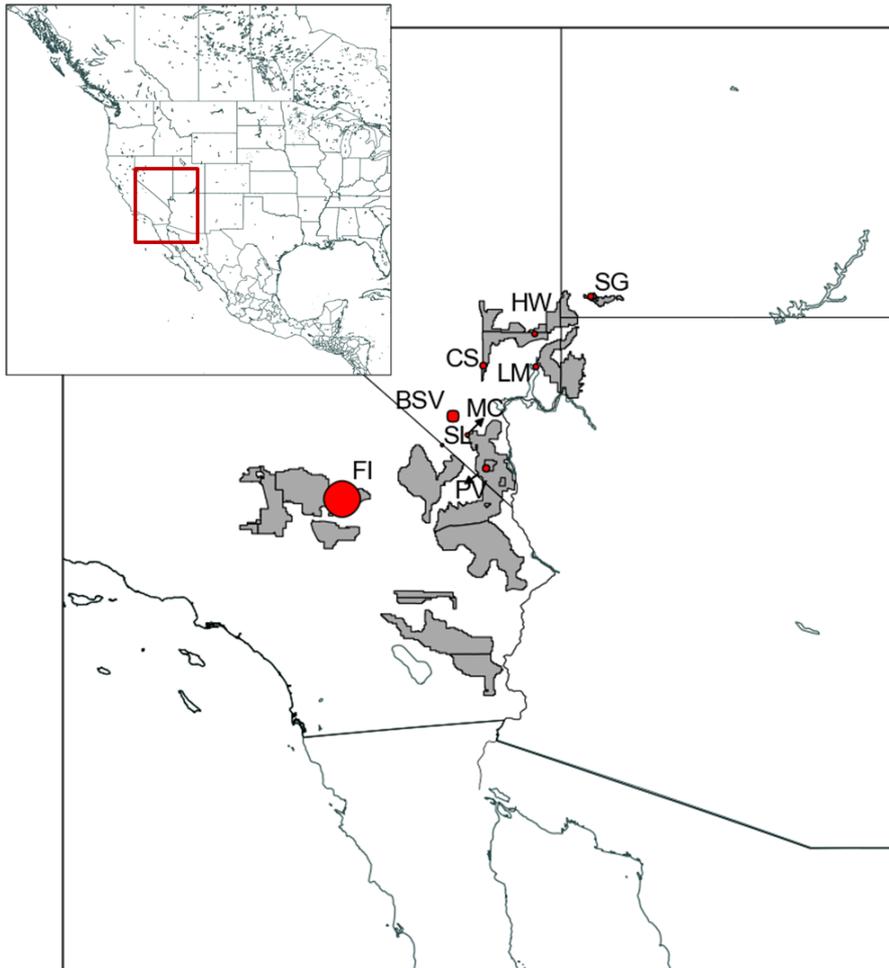


Figure 1:

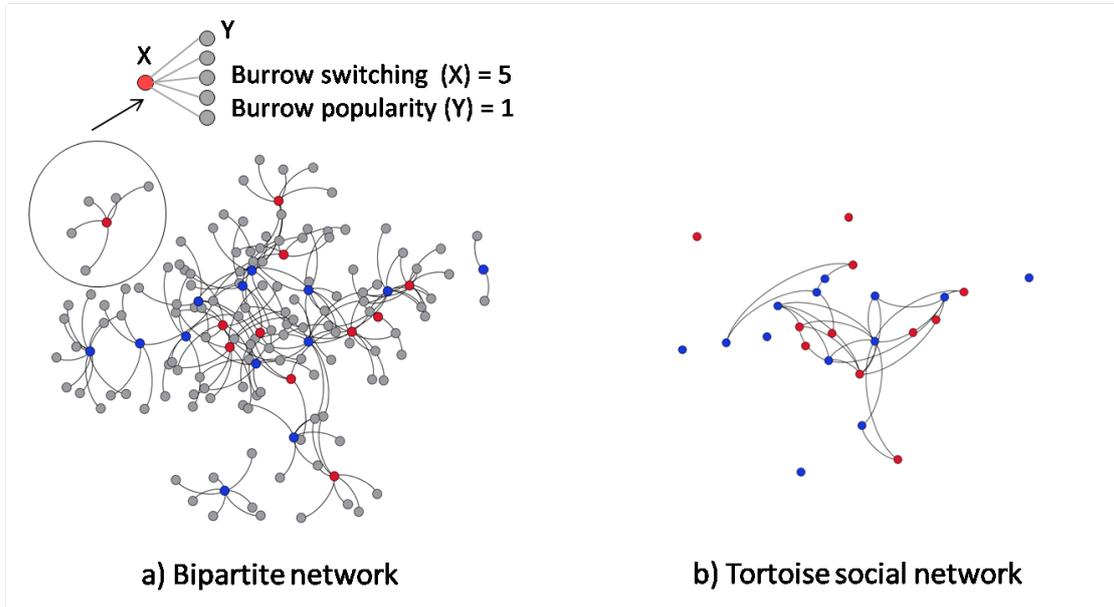


Figure 2:

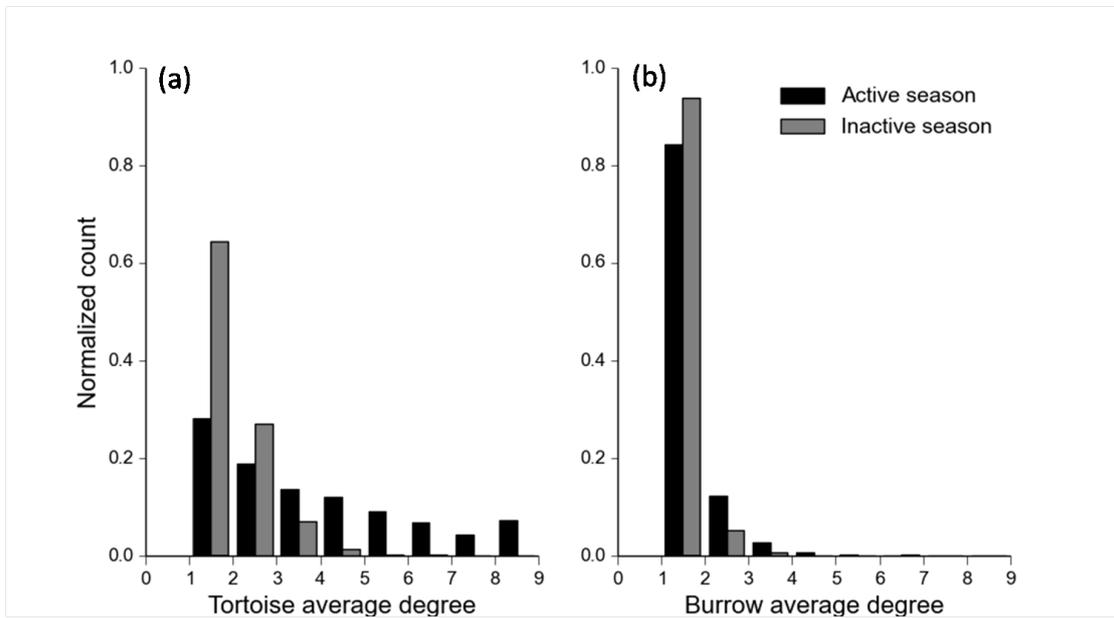


Figure 3:

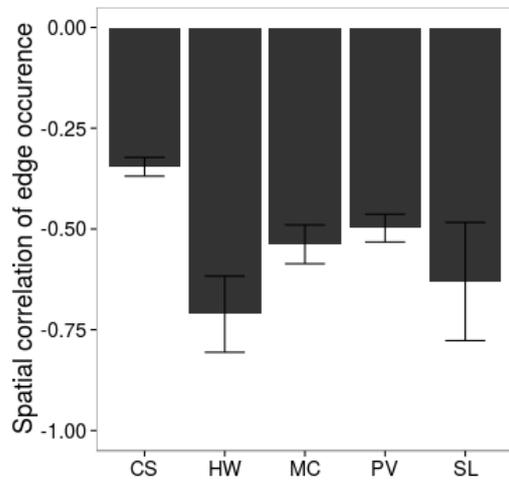


Figure 4:

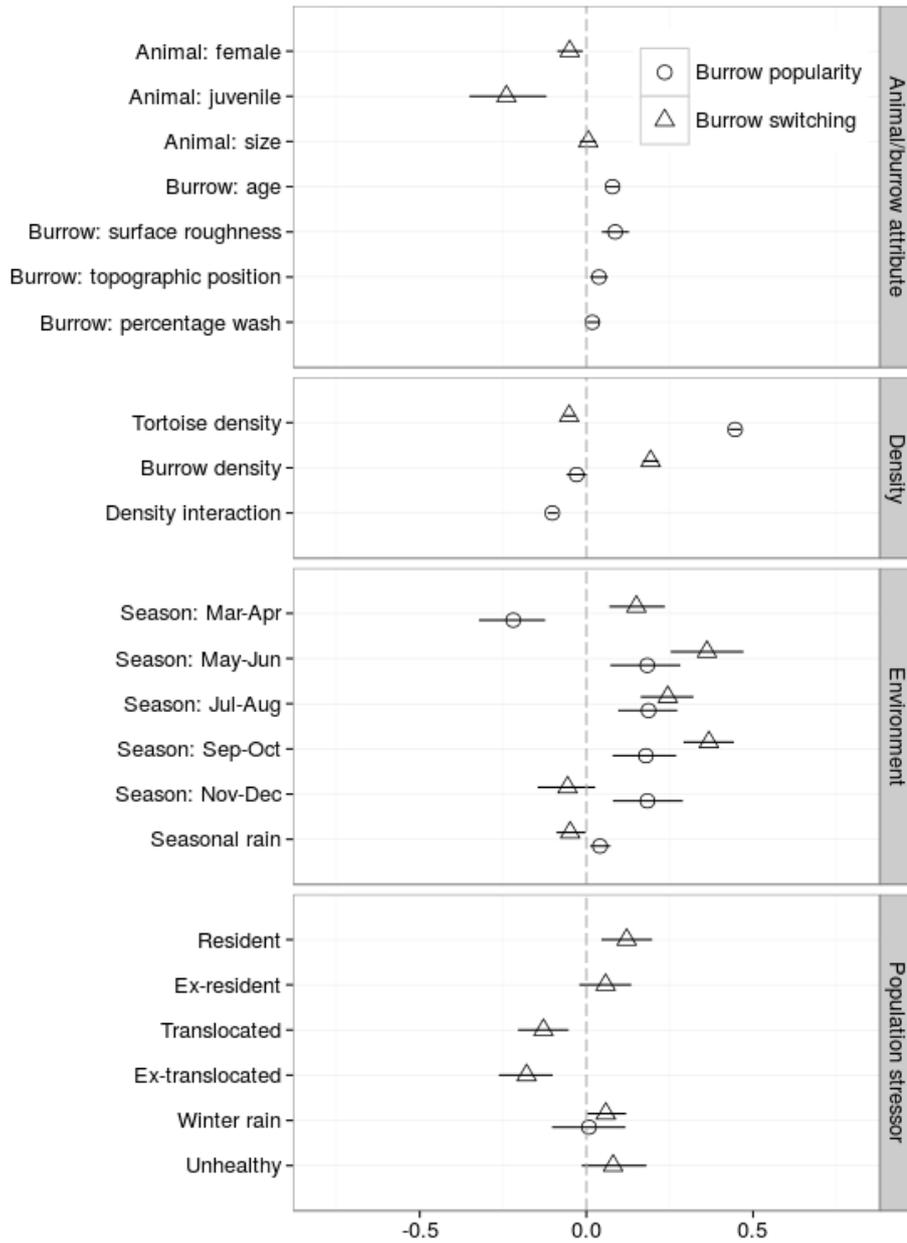


Figure 5: