

13

Abstract

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For several species, refuges (such as burrows, dens, roosts, nests) are an essential resource for protection from predators and extreme environmental conditions. Refuges also serve as focal sites for social interactions including mating, courtship and aggression. Knowledge of refuge use patterns can therefore provide information about social structure, mating and foraging success, as well as the robustness and health of wildlife populations, especially for species considered to be relatively solitary. In this study, we construct networks of burrow use to infer social associations in a threatened wildlife species typically considered solitary - the desert tortoise. We show that tortoise social networks are significantly different than null networks of random associations, and have moderate spatial constraints. We next use statistical models to identify major mechanisms behind individual-level variation in tortoise burrow use, popularity of burrows in desert tortoise habitat and test for stressor-driven changes in refuge use patterns. We show that seasonal variation has a strong impact on tortoise burrow switching behavior. On the other hand, burrow age and topographical condition influence the number of tortoises visiting a burrow in desert tortoise habitat. Of three major population stressors affecting this species (translocation, drought, disease), translocation alters tortoise burrow switching behavior, with translocated animals visiting fewer unique burrows than residents. In a species that is not social, our study highlights the importance of leveraging refuge use behavior to study the presence of and mechanisms behind non-random social structure and individual-level variation. Our analysis of the impact of stressors on refuge-based social structure further emphasizes the potential of this method to detect environmental or anthropogenic disturbances.

Significance statement: Adaptive and social behavior that affects fitness is now being increasingly incorporated in the conservation and management of wildlife species. However, direct observations of social interactions in species considered to be solitary are difficult, and therefore integration of behavior in conservation and management decisions in such species has been infrequent. For such species, we propose quantifying refuge use behavior as it can provide insights towards their (hidden) social structure, establish relevant contact patterns of infectious disease spread, and provide early warning signals of population stressors. Our study highlights this approach in a long-lived and threatened species, the desert tortoise. We provide evidence towards the presence of and identify mechanisms behind the social structure in desert tortoises formed by their burrow use preferences. We also show how individuals burrow use behavior responds to the presence of population stressors.

Key words: behavioral stress response, bipartite networks, *Gopherus agassizii*, generalized linear mixed models, modularity, *Mycoplasma agassizii*.

44 **Introduction**

45 Social structure of wildlife populations is typically derived from observational studies on direct social interactions
46 [e.g. affiliative interactions in primates (Griffin and Nunn 2011; MacIntosh et al. 2012), group association in dolphins
47 (Lusseau et al. 2006) and ungulates (Cross et al. 2004; Vander Wal et al. 2012), food sharing in vampire bats (Carter
48 and Wilkinson 2013)]. In relatively solitary species, individuals spend a considerable amount of time alone and have
49 minimal direct interactions with conspecifics except during mating and occasional aggressive encounters (Scott and
50 Carrington 2011). Examples of such species include raccoons, red foxes, orangutans, and some species of bees, wasps
51 and bats. For these wildlife populations, social interactions may be limited to certain areas within their habitat, such as
52 refuges (e.g., roost, den, burrow, nest) or watering holes that provide increased opportunities of direct contact between
53 individuals. Monitoring these resources can therefore help establish relevant social patterns among individuals.

54 In addition to establishing social structure, refuges provide shelter, protection from predators and serve as sites for
55 nesting and mating. Refuge use patterns of individuals are therefore central to survival, mating and foraging success
56 and can serve as efficient indicators of population disturbances. Unlike traditional population dynamics indicators
57 such as mortality and birth rate, refuge use behavior can respond instantaneously to sub-optimal conditions (Morris
58 et al. 2009; Berger-Tal et al. 2011). Altered patterns of refuge use may thus indicate a disturbance or change in
59 population fitness and provide an early warning to conservation biologists. Changes in habitat or refuge use have
60 indeed been linked to the presence of natural population stressors such as increased predation (van Gils et al. 2009),
61 drought (Kerr and Bull 2006; Gough et al. 2012) and disease transmission risk (Behringer and Butler IV 2010), as well
62 as anthropogenic population stressors of translocation (Jachowski et al. 2012) and urbanization (Moule et al. 2015).

63 While the importance of refuge use in social interactions, survival and mating success, as well as indicators of
64 environmental and anthropogenic stressors has been long appreciated, biologists are only beginning to understand
65 individual level heterogeneity in refuge use and its population-level consequences in relatively solitary species (Fortuna
66 et al. 2009; Leu et al. 2010; Godfrey 2013). The general absence of studies quantifying pairwise interactions due
67 to preferences in refuge-use implies a lack of knowledge of the baseline social organization that could be used to
68 evaluate changes in robustness or health of these wildlife populations. To overcome these shortcomings we explore
69 a modeling framework that combines network theory with statistical models to infer the presence of and mechanisms
70 behind the social organization in the desert tortoise, *Gopherus agassizii*, formed by their refuge-use preferences. The
71 desert tortoise is a long-lived, terrestrial species that occurs throughout the Mojave Desert north and west of the
72 Colorado River. Individuals of this species use subterranean burrows as an essential adaptation to obtain protection
73 from temperature extremes and predators. Because tortoises spend a majority of their time either in or near burrows,
74 most of their social interactions are associated with burrows (Bulova 1994).

75 Social behavior in desert tortoises is not well understood, though evidence suggests the presence of dominance

Pratha Sah

76 hierarchies (Niblick et al. 1994; Bulova 1997) which may influence social structure and burrow choice in desert
77 tortoises. In addition to social hierarchies, previous research suggests factors such as sex (Harless et al. 2009), age
78 (Wilson et al. 1999), season (Bulova 1994); and environmental conditions (Duda et al. 1999; Franks et al. 2011)
79 may influence burrow use in desert tortoises. If conspecific cues and environmental factors exhibit strong influence
80 on burrow use, population stressors impacting these characteristics could alter typical burrow behavior. The two
81 major population threats that have been identified in desert tortoise populations include upper respiratory tract disease
82 (URTD) caused by *Mycoplasma agassizii* and *Mycoplasma testudineum* (Brown et al. 1994; Sandmeier et al. 2009;
83 Jacobson et al. 2014), and extreme environmental conditions, particularly drought (Longshore et al. 2003; Lovich et al.
84 2014). In addition to these threats, the primary management strategy in desert tortoises is to translocate animals out
85 of areas affected by anthropogenic disturbances (Department of the Interior 2011). Translocation in other reptilian
86 species, however, has had limited success due to high rates of mortality (Dodd and Seigel 1991; Germano and Bishop
87 2009) and may also act as a population stressor. In desert tortoises, all three population stressors have been linked to
88 differences in individual behavior (Duda et al. 1999; Nussear et al. 2012; McGuire et al. 2014). Although previous
89 studies provide insights towards potential factors that may affect burrow use, we lack a mechanistic understanding
90 behind the role of these factors in driving heterogeneity in burrow use patterns in desert tortoises. A large impact of
91 population stressors on refuge use can affect mating and foraging opportunities of desert tortoises and also reduce their
92 likelihood of survival.

93 In this study, we combine data-sets from nine study sites in desert tortoise habitat, spanning more than 15 years to
94 derive burrow use patterns of individuals in these populations. We first construct bipartite networks to infer their social
95 associations due to asynchronous use of burrows. We then use generalized linear mixed models to explain mechanisms
96 behind heterogeneity in burrow use behavior of individuals and effect of population stressors. As the desert tortoise is a
97 long lived species, evaluating the impact of population stressors on burrow use patterns provides an efficient alternative
98 to using traditional demographic metrics (such as mortality). We also investigate the use of burrows through a bipartite
99 network model to identify why certain burrows are more popular than others in desert tortoise habitat. Overall, our
100 analysis of refuge-based associations provide further insights into the structure and dynamics of social organization
101 in a species traditionally considered as solitary and provides mechanisms behind individual variation within these
102 associations.

103 **Methods**

104 ***Dataset***

105 We combined datasets from nine study sites monitored from 1996 to 2014 across desert tortoise habitat in the Mojave
106 desert of California, Nevada, and Utah (Fig. 1). Each site was monitored over multiple years, but not all sites were
107 monitored in each year of the 15 year span. At each site, individuals were monitored at least weekly during their active
108 season and at least monthly during winter months using radio telemetry. The total number of animals sampled and
109 average number of observations per tortoise at each site is included in Supplementary Table S1. All tortoises were
110 individually tagged, and during each tortoise encounter, data were collected to record the individual identifier, date
111 of observation, GPS location, micro-habitat currently used by the animal (e.g., vegetation, pallet, or a burrow), any
112 visible signs of injury or upper respiratory tract disease. As the dataset involved monitoring tagged individuals, it was
113 not possible to record data blind. The unique burrow identification (id) was recorded for cases where an animal was
114 located in a burrow. New burrow ids were assigned when an individual was encountered at a previously unmarked
115 burrow.

116 ***Network Analysis***

117 We constructed *bipartite networks* of asynchronous burrow use in desert tortoises for active (March - October) and
118 inactive season (November - February) of each year at five sites (CS, HW, MC, PV, SL) where no translocations were
119 carried out. An example of a burrow use bipartite network is shown in Fig. 2. The network consisted of burrow and
120 tortoise nodes and undirected edges. An edge connecting a tortoise node to a burrow node indicated burrow use by the
121 individual (Fig. 2). To reduce bias due to uneven sampling, we did not assign edge weights to the bipartite networks.
122 Edges in a bipartite network always connect the two different node types, thus edges connecting two tortoise nodes
123 or two burrow nodes are not permitted. Tortoise nodal degree in the bipartite network therefore denotes the number
124 of unique burrows used by the individual and burrow nodal degree is the number of unique individuals visiting the
125 burrow. Networks were generated using Networkx package in Python (Hagberg et al. 2008).

126 We further examined the social structure of desert tortoises by converting the bipartite network into a single-mode
127 projection of tortoise nodes (Tortoise social network, Fig. 2). For these tortoise social networks, we calculated network
128 density, degree centralization, modularity, clustering coefficient, and homophily of individuals by degree and sex/age
129 class. Network density is calculated as the ratio of observed edges to the total possible edges in a network (Scott
130 and Carrington 2011). Degree centralization measures the variation in node degree across the network, such that high
131 values indicate a higher heterogeneity in node degree and that a small proportion of nodes have a higher degree than
132 the rest (Scott and Carrington 2011). Modularity measures the strength of the division of nodes into subgroups (Girvan

133 and Newman 2002) and clustering coefficient measures the tendency of neighbours of a node to be connected (Bansal
134 et al. 2009). The values of modularity and clustering coefficient can range from 0 to 1, and larger values indicate
135 stronger modularity or clustering coefficient. We generated 1000 random network counterparts to each empirical
136 network using double-edge swap operation in NetworkX (Hagberg et al. 2008) to determine if the observed network
137 metrics were significantly different from random expectation. The generated random networks had the same degree
138 sequence as empirical networks, but were random with respect to other network properties.

139 We next examined the spatial dependence of asynchronous burrow associations by using coordinates of burrows
140 visited by tortoises to calculate centroid location of each tortoise during a particular season of a year. Distances be-
141 tween each tortoise pair (i, j) were then calculated as $d_{ij} = d_{ji} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}$ where (x, y) is the coordinate
142 of tortoise centroid location. Pearson correlation coefficient was used to calculate the correlation between observed
143 edges in social network and geographical distances between the tortoises. We compared the observed correlation to
144 a null distribution of correlation values generated by randomly permuting spatial location of burrows 10,000 times
145 and recalculating correlation between social associations and distance matrix for each permutation. Correlation were
146 calculated using MantelTest package in Python (Carr 2015).

147 ***Regression Analysis***

148 We used generalized linear mixed regression models with Poisson distribution and log link function to assess burrow
149 use patterns. To capture seasonal variation in burrow use, we aggregated the response counts over six periods (Jan-Feb,
150 Mar-Apr, May-Jun, Jul-Aug, Sep-Oct and Nov-Dec). Patterns of burrow use were analyzed in two ways. First, we
151 investigated factors affecting burrow switching, which we define as the number of unique burrows used by a tortoise in
152 a particular sampling period. Second, we investigated burrow popularity, defined as the number of unique individuals
153 using a burrow in a particular sampling period. Model variables used for each analysis are summarized in Table 1.
154 All continuous model variables were centered (by subtracting their averages) and scaled to unit variances (by dividing
155 by their standard deviation). This standard approach in multivariate regression modeling assigns each continuous
156 predictor with the same prior importance in the analysis (Schielezeth 2010). All analyses were performed in R (version
157 3.0.2; R Development Core Team 2013).

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

159 In this model, the response variable was burrow switching, defined as the total number of unique burrows used by
160 desert tortoises during each sampling period. An individual was considered to be using a burrow if it was reported
161 either inside a burrow or within 25 m^2 grid around a burrow. The predictors included in the model are described in
162 Table 1. In addition to the fixed effects, we considered three interactions in this model (i) sampling period \times sex, (ii)

Pratha Sah

163 sampling period \times seasonal rainfall and (iii) local tortoise density \times local burrow density. Tortoise identification and
164 year \times site were treated as random effects.

165 ***Investigating burrow popularity:***

166 For this model, the response variable was burrow popularity defined as the total number of unique tortoises using a
167 focal burrow in a sampling period. The predictors included in the model are also described in Table 1. In this model,
168 we also tested for three interactions between predictors including (i) sampling period \times seasonal rainfall, (ii) sampling
169 period \times local tortoise density, and (iii) local tortoise density \times local burrow density. We treated burrow identification
170 and year \times site as random effects.

171 ***Population stressors:***

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

179 *Translocation:* We accounted for translocation in the regression model by giving each surveyed tortoise one of the
180 following five residency status at each sampling period: Control (C), Resident (R), Translocated (T), Ex-resident (ER)
181 or Ex-translocated (ET). Translocations were carried out at four (BSV, FI, LM, SG) out of nine sites in our dataset for
182 purposes described in previous studies (Drake et al. 2012; Nussear et al. 2012). All animals native to the site were
183 categorized as Controls (C) during sampling periods before translocation occurred. For sampling periods post translo-
184 cation, all native animals were categorized as Residents (R), and introduced animals were categorized as Translocated
185 (T). One year after translocation, translocated and resident tortoises were considered to be Ex-translocated (ET) and
186 Ex-residents (ER), respectively, to account for potential acclimatization of introduced animals (Nussear et al. 2012).
187 We note that one of the four translocation sites (SG) did not have native animals prior to translocation. No transloca-
188 tions were carried out at the rest of the five sites, so all animals surveyed at those sites were labeled as controls in all
189 sampling periods.

190 *Drought:* The desert tortoise habitat in Mojave desert typically receives most of the rainfall during the winter
191 season. We therefore used winter rainfall to assess drought conditions in desert tortoise habitat. We defined winter
192 rain during a year as average rainfall from November to February and used it as a proxy of drought condition for the

193 following year. We note that summer rainfall in desert tortoise habitat varies from west to east, where summer rainfall
194 becomes a larger component of the total annual precipitation in East Mojave desert (Henen et al. 1998). Therefore,
195 although we used winter rainfall as a proxy of drought conditions, we considered the effects of summer precipitation
196 implicitly by including seasonal rainfall as a separate predictor (see Table1).

197 ***Model selection and validation***

198 Following Harrell (2002) we avoided model selection to remove non-significant predictors and instead present results
199 of our full model. Using the full model allows model predictions conditional on the values of all predictors and results
200 in more accurate confidence interval of effects of interest (Harrell 2002). The Bayesian information criterion (BIC)
201 of model selection was used to identify the best higher order interactions. A potential drawback of including all
202 independent variables in the final model is multicollinearity. We therefore estimated Generalized Variance Inflation
203 Factor (GVIF) values for each predictor. GVIF is a variant of traditional VIF used when any predictor in the model
204 has more than 1 degree of freedom (Fox and Monette 1992). To make GVIF comparable across dimensions, Fox and
205 Monette (1992) suggest using $GVIF^{(1/(2 \cdot Df))}$ which we refer to as adjusted GVIF. We sequentially removed predictors
206 with high adjusted GVIFs, recalculated adjusted GVIF, and repeated the process until all adjusted GVIF values in the
207 model were below 3 (Zuur et al. 2010).

208 We carried out graphical diagnostics by inspecting the Pearson residuals for the conditional distribution to check
209 if the models fit our data in each case. We detected under-dispersion in both the regression models. Under-dispersed
210 models yield consistent estimates, but as equidispersion assumption is not true, the maximum-likelihood variance
211 matrix overestimates the true variance matrix which leads to over-estimation of true standard errors (Winkelmann
212 2003). We therefore estimated 95% confidence intervals of fixed and random effects using bootstrapping procedures
213 implemented in 'bootMER' function in package lme4.

214 We tested for the significance of fixed factors in both the models using likelihood ratio test (R function mixed from
215 afex package (Singmann 2013)). For significant categorical predictors, we used Tukeys HSD (R function glht from
216 the multcomp package, (Hothorn et al. 2008)) as a post-hoc test of significant pair-wise differences among means. All
217 reported P-values of post-hoc tests are adjusted for multiple comparisons using the single-step method (Hothorn et al.
218 2008).

219 **Results**

220 *Network Analysis*

221 Bipartite networks of asynchronous burrow use across all sites demonstrated considerable variation in degree of tor-
222 toise nodes and burrow nodes (Fig. 3). Tortoises visited more unique burrows on average (4.03 ± 3.43 SD) and had a
223 greater range of burrows visited in active seasons (1-9) than in inactive seasons (average = 1.46 ± 0.72 SD, range = 1-5).
224 Less than 40% of tortoises used more than one burrow during Nov-Feb (inactive) months (Fig. 3a). Most burrows in
225 desert tortoise habitat were visited by a single tortoise during active and inactive season (Fig. 3b). Heterogeneity in
226 the number of animals visiting burrows, however, tended to be slightly more during the months of March-November
227 than November-February (active = 1.21 ± 0.56 SD, inactive = 1.08 ± 0.35 SD).

228 The tortoise social network (constructed as a single mode projection of tortoise nodes from the bipartite network)
229 demonstrated moderate clustering coefficient (0.36 ± 0.21 SD) and modularity (0.53 ± 0.15 SD). Twenty three of
230 the 24 social networks we analyzed had higher clustering coefficient and 18 social networks were more modular than
231 random networks (Supplementary Table S3). Thirteen social networks out of the total 24 demonstrated significant
232 degree homophily (when nodes with similar degree tend to be connected) and 11 of those had positive associations
233 (Supplementary Table S3). Positive degree homophily suggests that tortoises using many unique burrows often use the
234 same set of burrows and are therefore connected in the social network. Tortoise social networks also had a moderate
235 positive degree centralization which indicates a small subset of individuals used more burrows than the rest in the
236 sampled population. Within sexes, positive degree centralization was observed both within males (0.20 ± 0.08 SD)
237 and females (0.17 ± 0.06 SD). Homophilic association by sex ranged from -0.6 to 0.11 indicating a preference for
238 one sex to associate with the opposite. These negative sexwise associations, however, were not different than those
239 expected by chance.

240 The association between tortoises in their social network was inversely correlated with geographical distances
241 between them, indicating that individuals closer to each other preferred using the same set of burrows. The magnitude
242 of correlation ranged from -0.22 to -0.89 with an average value of -0.49 (Fig. 4). The P-value of the permutation test
243 for all sites across active seasons of all surveyed years was less than 0.05, indicating a significant effect of geographical
244 location on social associations (Supplementary Table S4). This result of spatial constraints driving social interactions
245 is not surprising as geographical span of surveyed sites were much larger (>1500 m) than the normal movement range
246 of desert tortoises (Franks et al. 2011). However, the moderate value of correlations suggest other factors (such as
247 environmental, social, density) could play an important role in desert tortoise's asynchronous burrow associations.

248 ***Regression Analysis***

249 Based on the observed heterogeneity in bipartite networks, we next investigated the relative effect of natural variables
250 and population stressors on burrow switching patterns of desert tortoises (*viz* degree of animal nodes in bipartite
251 networks) and popularity of burrows in desert tortoise habitat (*viz* degree of burrow nodes in bipartite networks).
252 Supplementary Table S5 presents the best models of BIC values for interactive predictors that explain burrow switching
253 in desert tortoises and burrow popularity. The three interactions tested for burrow switching models were sampling
254 period \times sex, sampling period \times seasonal rainfall and local tortoise density \times local burrow density. We tested all
255 possible combinations of the three interactions. The best model contained an interaction of sampling period \times seasonal
256 rainfall (Supplementary Table S5). For the burrow popularity model, we tested all possible combinations of the
257 sampling period \times seasonal rainfall, the sampling period \times the local tortoise density and the local tortoise density \times
258 local burrow density interactions. The best model included the sampling period \times the local tortoise density and the
259 local tortoise density \times the local burrow density interaction term.

260 Multicollinearity tests revealed all three measures of temperature (average, max and min) to have adjusted GVIF
261 values of >3 . The three predictors were therefore dropped from both the models. We also removed the sampling period
262 \times tortoise density interaction from the burrow popularity model as it inflated adj GVIF value of tortoise density to >3 .
263 σ^2 estimate of tortoise identification and burrow identification random effect was negligible (tortoise identification:
264 $\sigma^2 = 0$, CI = 0-0.004, burrow identification: $\sigma^2 = 0$, CI = 0-0.01). Both random effects were therefore removed from
265 the regression models.

266 ***Effect of animal attributes***

267 Sex/age class had a significant effect on burrow switching ($\chi^2=16.75$, $P = 0.0002$). Overall, adults used more unique
268 burrows than non-reproductives. Among adults, males used a slightly higher number of unique burrows than females
269 (Fig. 5). There was no effect of body size on individuals' burrow switching behavior ($\chi^2_1 = 0.2$, $P = 0.65$).

270 ***Effect of burrow attributes***

271 Out of the six burrow attributes included in the model, burrow age and surface roughness around burrow had the
272 highest impact on burrow popularity, i.e., number of unique individuals visiting the burrow (burrow age: $\chi^2_1 = 46.07$,
273 $P < 0.0001$, surface roughness: $\chi^2_1 = 14.37$, $P = 0.0002$). Burrow popularity was positively correlated with surface
274 roughness indicating that burrows in flat sandy areas were visited by fewer unique tortoises than burrows in rough
275 rocky areas (Fig. 5). Older burrows were visited by more unique individuals, with burrow popularity increasing $e^{0.08}$
276 times with each increment of age (Fig. 5). Burrows in areas with higher topographical position as indicated by GIS
277 raster images were also more popular ($\chi^2_1 = 5.71$, $P = 0.02$).

278 ***Effect of environmental conditions***

279 Sampling period had a large effect on number of unique burrows used by desert tortoises ($\chi^2_5 = 160.96$, $P < 0.0001$)
280 as well as on burrow popularity ($\chi^2_5 = 176.25$, $P < 0.0001$) as compared to other model predictors. Burrow switching
281 of desert tortoises was highest during the months of May-June and September-October when they are typically more
282 active, and lowest in winter months (Fig. 5). In the late summer (July-August), tortoises demonstrated slightly lower
283 burrow switching than during the active season, but higher than the winter season. Within a particular year, the
284 direction of the effect of seasonal rainfall varied across different sampling periods (sampling period \times seasonal rain:
285 $\chi^2_5 = 107.46$, $P < 0.0001$). For example, high rainfall during the months of March-April reduced burrow switching in
286 desert tortoises. On the other hand, individuals exhibited higher burrow switching with higher rain during the months
287 of July-August (Supplementary Fig. S3b).

288 In contrast to the large variation in individuals' burrow switching behavior between sampling periods, popularity
289 of burrows did not vary during a large portion of the year (May - December). Total unique animals visiting burrows
290 tended to be lower in the months of January-February and March-April, as compared to other months of the year (Fig.
291 5, S4c). Seasonal rainfall had a positive correlation with burrow popularity ($\chi^2_1 = 6.02$, $P = 0.01$).

292

293 ***Effect of density conditions***

294 An increase in the number of active burrows around individuals promoted burrow switching, whereas an individual
295 used fewer burrows when there were more tortoises in the vicinity (Fig. 5). In the burrow popularity model, higher tor-
296 toise density around burrows increased number of individuals visiting these burrows (Fig. 5). There was a significant
297 interactive effect of the two density conditions on burrow popularity ($\chi^2_1 = 177.37$, $P < 0.0001$) – increase in burrow
298 popularity with higher tortoise density was lower when there were more burrows in the vicinity of the focal burrow
299 (Supplementary Fig. S4d).

300

301 ***Effect of population stressors***

302 Population stressors of drought, health and translocation had variable influences on burrow switching of desert tortoises
303 (Fig. 5, Supplementary Fig. 5). As compared to residents and controls, translocated animals demonstrated lower
304 burrow switching during the year of translocation and also in the subsequent years (Fig. 5, Supplementary Fig. S5a).
305 We did not find any differences between burrow switching levels of individuals exhibiting clinical signs of URTD and
306 clinically healthy individuals ($\chi^2_1 = 2.51$, $P = 0.11$). Burrow switching levels of all surveyed animals during drought
307 years (indicated by lower winter rainfall), however, tended to be slightly lower in comparison to non-drought years

308 (burrow switching: $\chi_1^2 = 3.5$, $P = 0.06$).

309 **Discussion**

310 Although direct social interactions among solitary species are relatively infrequent, individual preference for certain
311 shared refuge and foraging spaces may lead to a highly structured social system (Leu et al. 2011). In such species,
312 knowledge of social network structure formed through refuge or forage associations can identify key influential indi-
313 viduals (Fortuna et al. 2009; Leu et al. 2011), and provide early-warning signals for environmental (or anthropogenic)
314 disturbances (Jachowski et al. 2012; Moule et al. 2015) that may ultimately affect population fitness. In this study, we
315 infer social associations between individuals of a relatively solitary species, the desert tortoise, by their asynchronous
316 use of burrows. While descriptive approaches are common in the field of animal social networks (Pinter-Wollman et al.
317 2013), we sought to gain a mechanistic understanding behind individual variation in burrow-use associations of desert
318 tortoises. The degree of an individual in a bipartite network has biological and ecological importance as it indicates
319 a decision to switch refuges. Refuge switching is associated with a tradeoff between the costs of increasing exposure
320 to heat, predators, increased risk of infection, and the benefits of finding food and mates. The outcome of observed
321 refuge switching patterns is important as theoretical models predict reduced survival of populations due to suboptimal
322 refuge use decisions (Cooper 2015). Modeling optimal burrow switching that maximizes fitness in desert tortoises is
323 challenging as it is difficult to quantify fitness costs in a long-lived species. Our study instead provides an approach
324 to build baseline models of burrow use patterns. Any large deviation to baseline levels may indicate lower survival,
325 foraging, and reproductive success for tortoises and thus burrow switching can serve as an immediate indicator of
326 population stressors affecting long-term fitness consequences.

327 We show that social networks in desert tortoises formed due to burrow use preferences cannot be explained by
328 random associations. In several wildlife systems, spatial constraints can play a large role in shaping social networks
329 (Davis et al. 2015), and non-random associations may not be definitive evidence of social organization in a population.
330 Desert tortoise social associations, however, were only moderately correlated to spatial distances, which corroborates
331 earlier studies that report social organization in desert tortoises (Niblick et al. 1994; Bulova 1997). In general, the
332 social networks were also clustered (0.23-0.59) and modular (0.34 - 0.68). However, higher clustering coefficient
333 values have been reported in other social species [e.g. 0.54-0.57 in bottlenose dolphins (Mann et al. 2012), 0.57-
334 0.87 in guppies (Croft et al. 2004), 0.81 in squirrels (Manno 2008), 0.57-0.67 in primates (Pasquaretta et al. 2014)]
335 and even in a few relatively solitary species that have been studied [e.g., 0.7 in raccoons (Hirsch et al. 2013), 0.59
336 in brushtail possum (Porphyre et al. 2011)]. The low (but significant) clustering coefficient value in desert tortoise
337 social networks suggests that they do not form tight social bonds as compared to other social wildlife species. In
338 social species, the network structure is known to affect population stability (Kurvers et al. 2014) and resistance to

Pratha Sah

339 disease outbreaks (Cross et al. 2004; Godfrey et al. 2009; MacIntosh et al. 2012). Modular social networks of desert
340 tortoises in particular can have important implications in the spread and persistence of infections. For example, few
341 connections between communities in a social network can effectively localize new infections to a few individuals. For
342 chronic infections such as URTD, these pockets of infection, however, can serve as sources of re-infection to other
343 uninfected communities, eventually leading to persistent infection across the entire population.

344 Our analysis of burrow use heterogeneity in desert tortoises reveals that the period of the year and density of
345 burrows around an individual are the main drivers behind the individual's burrow switching decision. Low burrow
346 switching levels in tortoises during winter and summer months reflects reduced movement to avoid severe weather
347 conditions (Eubanks et al. 2003). Individuals visit more burrows in the months of May-June and September-October
348 which coincides with high activity of nesting and mating in adults. Seasonal rainfall also influences burrow switching
349 in desert tortoises. Tortoises use fewer burrows in high rainfall conditions in March-April months, which possibly
350 reflects reduced activity during cold weather associated with spring storms. Infrequent summer rains, on the other
351 hand, increase tortoise activity as individuals emerge from burrows to rehydrate (Nagy and Medica 1986; Peterson
352 1996). Our results of high burrow switching during summer rains (July-August) are consistent with these reports
353 of increased activity. We also find that non-reproductive tortoises use fewer burrows than adults, which may reflect
354 differences in costs and benefits associated with switching burrows. Leaving a refuge can present a greater risk to
355 non-reproductives that are more vulnerable to predation (Wilson 1991), are prone to thermal stress due to their smaller
356 size (Mushinsky et al. 2003), and do not benefit from the mating opportunities gained by burrow switching. Indeed,
357 previous studies have found juveniles forage closer to their burrows and minimize time spent out of burrows (Mcrae
358 et al. 1981; Mushinsky et al. 2003; Halstead et al. 2007). Future studies and management plans of desert tortoises may
359 consider differences in burrow switching between different non-reproductive tortoises in order to mitigate increased
360 predation risk by pervasive predators such as ravens.

361 While it has been shown that a small fraction of burrows in desert tortoises are visited by multiple animals (Bulova
362 1994; Harless et al. 2009), the mechanisms behind burrow popularity were previously unknown. Our results suggest
363 that popular burrows can be identified using certain burrow characteristics such as surrounding topographical variables
364 and age. As true burrow age is often hard to determine, we demonstrate the use of historical survey data to estimate
365 proxy age of burrows. Once identified, these popular burrows can be surveyed throughout the year as there is only a
366 minor effect of time of the year and seasonal rainfall on burrow popularity. Knowledge of active and popular refuges
367 can have two important implications for the conservation and management of wildlife species. First, population density
368 estimates usually rely on observations of animals located outside refuge space (Witmer 2005). For species that spend
369 most of the time in a year in a refuge, survey of popular refuges can augment the current survey methods to get a more
370 accurate estimate of population density. Secondly, declines of popular refuges can indicate reduced social interactions
371 and mating opportunities for individuals. Reduced refuge popularity can also be indicative of higher mortality risk -

Pratha Sah

372 Esque et al. (2010) found higher mortality of desert tortoise in flat open areas where burrows, as our results indicate,
373 are less popular compared to rough higher elevation sites. Active popular burrows can therefore be used (a) as sentinels
374 of population health and (b) to identify critical core habitat for conservation and adaptive management of a wildlife
375 species.

376 Of three potential population stressors that we included in our model (disease, drought, translocation), translocation
377 caused a change in burrow switching behavior of desert tortoises. Although translocated animals are known to have
378 high dispersal tendencies (Nussear et al. 2012; Hinderle et al. 2015) and hence are expected to encounter and use more
379 burrows, we found translocated individuals use fewer unique burrows than residents. Our results are supported by
380 evidence of translocated tortoises spending more time on the surface and taking shelter under vegetation rather than
381 using burrows (Hinderle 2011). The use of fewer burrows coupled with high dispersal rates can increase exposure
382 of translocated animals to thermal stress and dehydration, potentially increasing mortality. Therefore, to improve
383 translocation success, a fruitful area of investigation for future research will be to determine potential causes of this
384 change in burrow use behavior in translocated tortoises. We used winter rain as a proxy of drought conditions as the
385 Western Mojave receives most of its annual rainfall during the months of November-February and is important for
386 the availability of food for desert tortoises in the spring (Duda et al. 1999; Lovich et al. 2014). Our results show a
387 slight (but not significant) reduction in burrow use by tortoises during drought years. Reduced burrow switching may
388 correspond to smaller home-ranges of desert tortoises observed during drought years (Duda et al. 1999). Low winter
389 rainfall condition is also known to increase predation of desert tortoises due to diminished prey resources (Peterson
390 1994; Esque et al. 2010). Lower burrow use during drought years can be therefore a behavioral response of desert
391 tortoises to avoid predation or to reduce energy expenditure and water loss in years of low resource availability (Nagy
392 and Medica 1986). Contrary to previous studies (McGuire et al. 2014), we did not find any effect of disease on burrow
393 use behavior, possibly because we could not distinguish severe clinical signs with milder forms in our data. Although
394 there was no evidence of disease influencing burrow use behavior in the present study, we note that it is likely for
395 burrow use behavior (and in particular the burrows themselves) to drive infectious disease patterns in desert tortoises
396 either directly, through cohabitation instances, or indirectly, by serving as focal sites of social interactions.

397 **Conclusions**

398 Our study demonstrates non-random associations in desert tortoises based on refuge use patterns. We formulate sta-
399 tistical models of burrow switching and popularity of burrows to investigate the mechanisms including environmental,
400 topographical, density factors, and population stressors behind refuge use preferences of desert tortoises. In combina-
401 tion, these models help infer the mechanisms behind heterogeneity in refuge use from the perspective of individuals
402 as well as from the perspective of the refuges. This approach is particularly useful for species that are not overtly

Pratha Sah

403 gregarious. For these species, refuge switching often correlates to reproductive and foraging success, and patterns
404 of refuge use can be an important aspect to consider before implementing any management or conservation strategy.
405 For example, popular refuges can be used to identify core habitat areas. In addition, sudden changes in the refuge
406 switching behavior of individuals can be used as an early warning signal of disturbances that may ultimately affect
407 population fitness. More broadly, our study provides insights towards the presence of and mechanisms behind non-
408 random social structure and individual variation in a relatively solitary species by analyzing refuge-based associations.
409 The structure of networks in social species is known to affect population stability and resilience to infectious diseases.
410 Future studies are needed to establish such functional roles of social networks in relatively solitary species.

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421 **Conflict of interest**

422 The authors declare that they have no conflict of interest.

423 **Ethical approval**

424 All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.
425 This article does not contain any studies with human participants performed by any of the authors.

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Pratha Sah

569 **Table captions**

570 **Table 1** Model variables considered to characterize burrow use patterns in the desert tortoise, *Gopherus agassizii*

571

572 **Figure captions**

573 **Fig. 1** Critical habitat range of the desert tortoise within the Mojave desert, USA as determined by the US Fish and
574 Wildlife Services in 2010 (<http://www.fws.gov/>). Critical habitat is defined as those geographical areas that contain
575 physical or biological features essential to the conservation and management of the species (Department of the Inte-
576 rior 1973). Points represent centroids of survey sites where tortoises were monitored using radio-telemetry. Point size
577 is proportional to the number of animals monitored at the site. Site abbreviations: BSV - Bird Spring Valley, CS -
578 Coyote Springs, FI - Fort Irwin, HW - Halfway, LM - Lake Meade, MC - McCullough Pass, PV - Piute Valley, SG -
579 St. George, SL - Stateline Pass

580

581 **Fig. 2** (a) Bipartite network of burrow use patterns at MC site during the year 2012. Node type indicated by color
582 (Blue = adult males and red = adult females). Node positions are fixed using Yifan Hu's multilevel layout in Gephi
583 (Bastian et al. 2009). In this paper, we quantify burrow switching and burrow popularity as degree of tortoise nodes
584 and burrow nodes, respectively, in the bipartite network. For example, burrow switching of the female tortoise X is
585 five and burrow popularity of burrow Y is one. (b) Single-mode projection of the bipartite network into tortoise social
586 network. Nodes with zero degree have been removed for clarity of illustration

587

588 **Fig. 3** Frequency distribution of (a) Tortoise degree i.e., unique burrows used by desert tortoises and (b) Burrow degree
589 i.e., unique tortoises visiting burrows during active (Mar-Oct) and inactive (Nov-Feb) seasons, excluding zero degree
590 nodes. Values are averaged over each surveyed year and study site. y-axis represents normalized frequency counts of
591 tortoises/burrows

592

593 **Fig. 4** Spatial constraints on asynchronous burrow associations during active seasons at study sites with control asyn-
594 imals. At each site, correlation is calculated between geographical distance and edge occurrence in tortoise social
595 network, and averaged over each surveyed year. Error bars represent standard errors with n=8 (CS), n=3 (HW), n=2
596 (MC), n=7 (PV) and n=2 (SL). P-value associated with each correlation measure is < 0.05

597

598 **Fig. 5** The effect of various predictors on the two models of burrow use patterns in desert tortoises. Error bars indicate
599 95% confidence intervals around the estimated coefficient value. For continuous predictors, the vertical dashed line
600 indicates no effect - positive coefficients indicate increase in burrow popularity/switching with increase in predictor
601 value; negative coefficients indicate decrease in burrow popularity/switching with higher values of predictors. For
602 each categorical predictor, the base factor (solid data points) straddles the vertical line at 0 and appears without a 95%
603 CI. Positive and negative coefficients for categorical predictors denote increase and decrease, respectively, in burrow

Pratha Sah

604 popularity/switching relative to the base factor

Table 1:

Variables	Variable type	Description
Tortoise attributes (Burrow switching model only)		
Sex/age class	Categorical	Three levels - adult males, adult females and non-reproductives (including neonates, juveniles and subadults)
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 et al. (2014)
Topographic position	Continuous	Index of landscape elevation around 250 sqm of burrow. High values are indicative of dry lakebeds or valley bottoms, and low values represent ridges and mountain tops. See Inman et al. (2014) for details.
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 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 Supplementary Table S2 for details

** See text for details

Pratha Sah

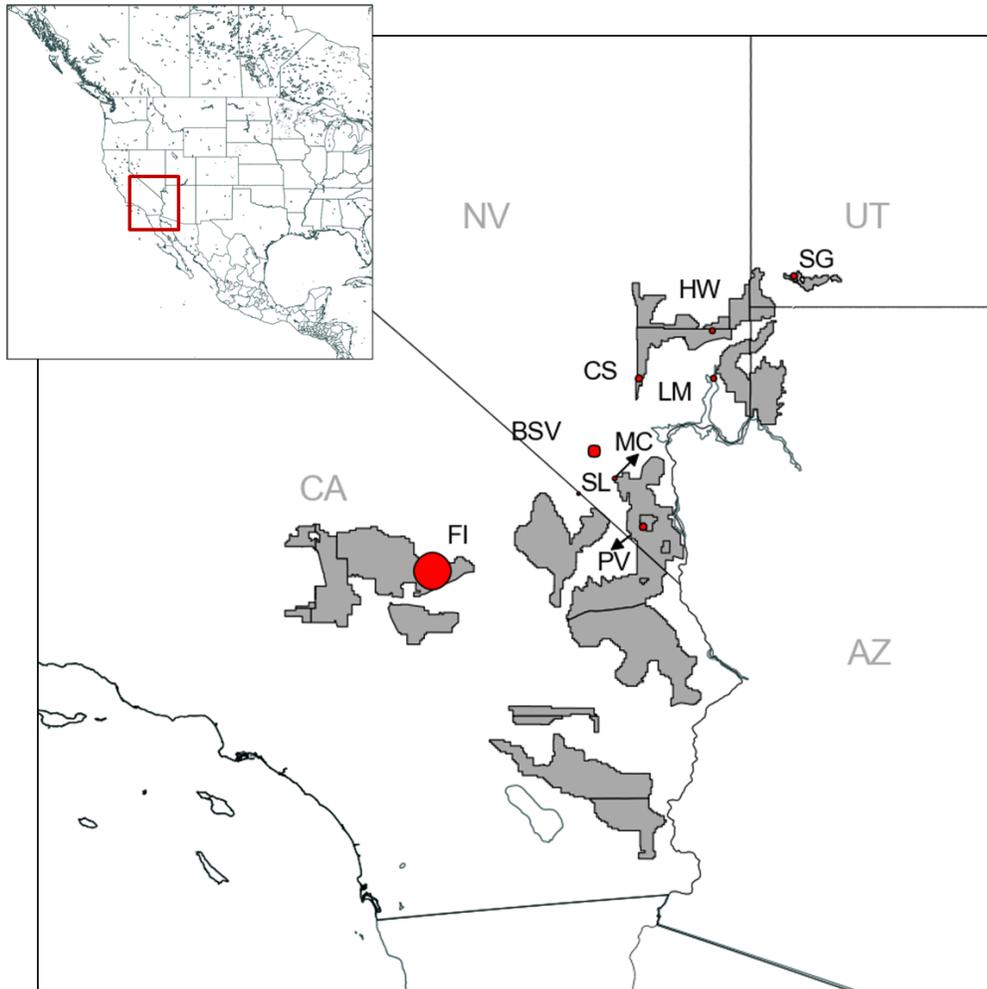


Figure 1:

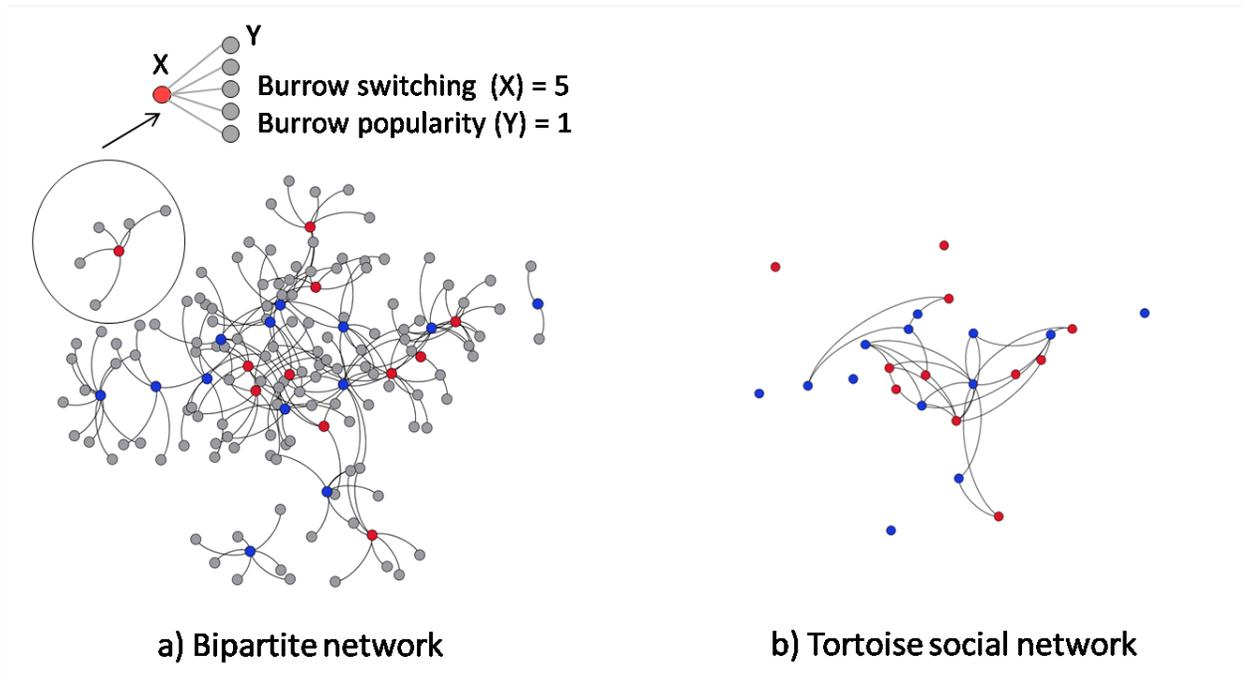


Figure 2:

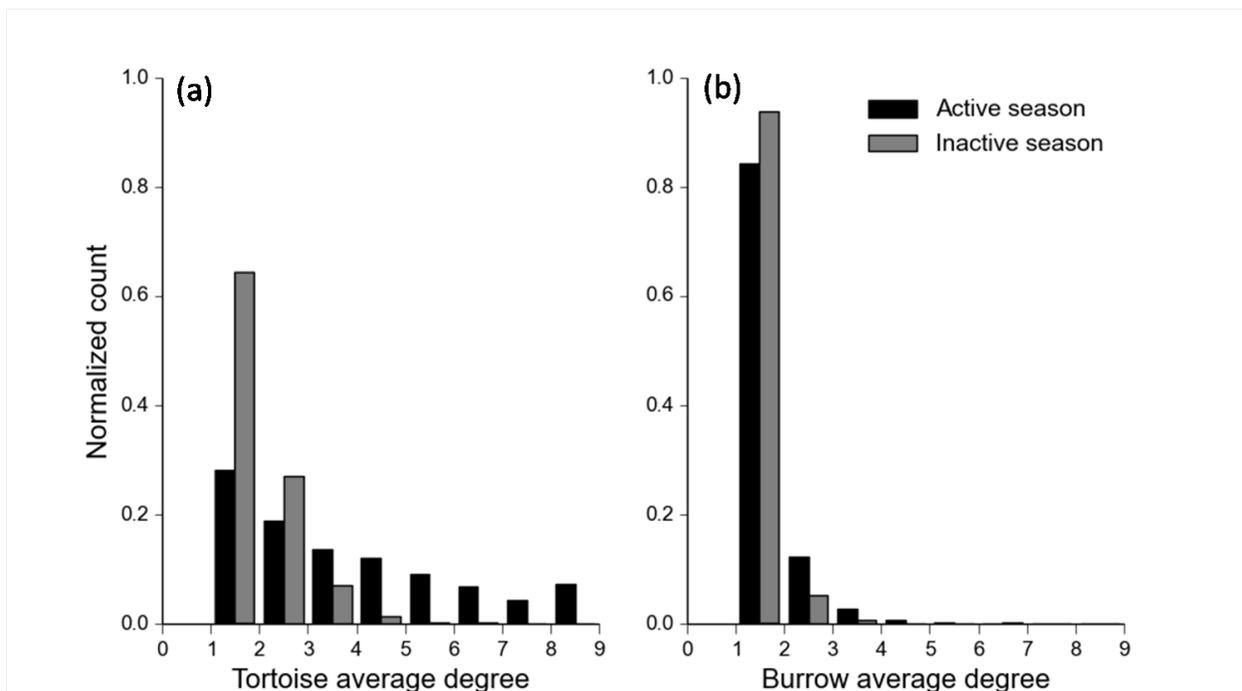


Figure 3:

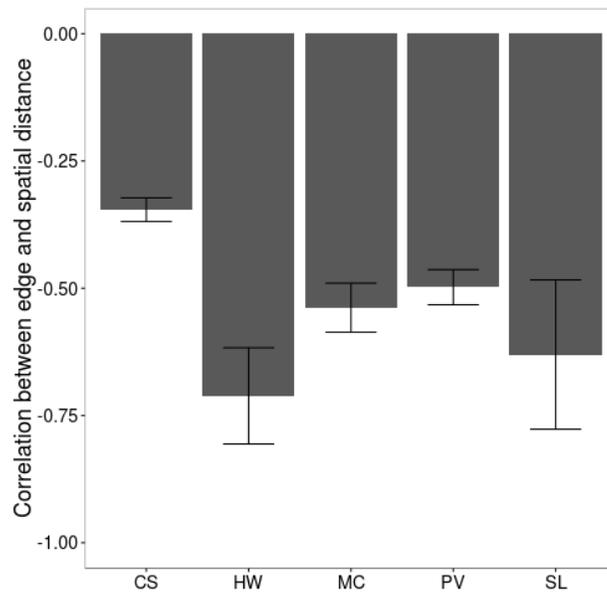


Figure 4:

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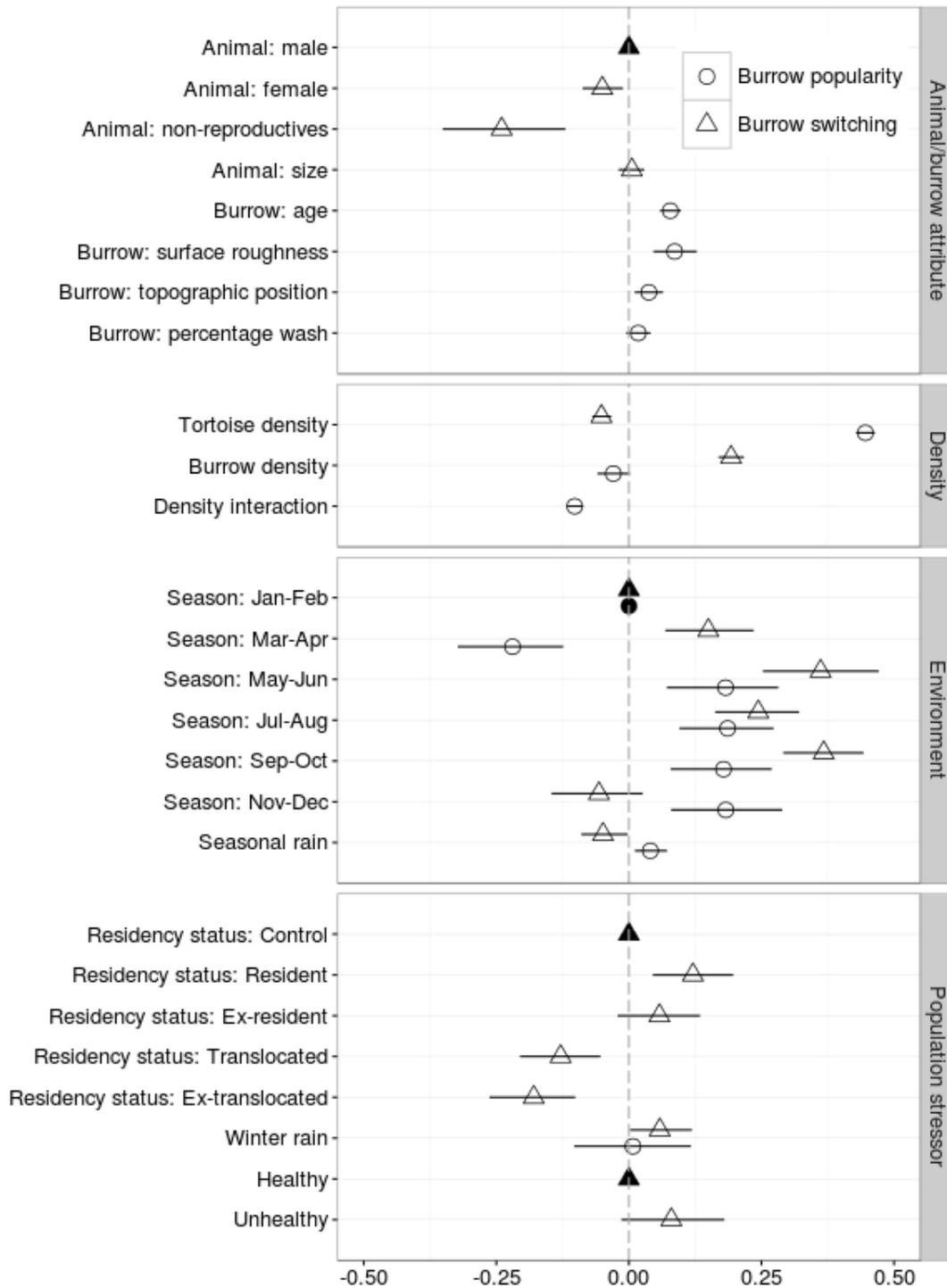


Figure 5: