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1 **When the going gets tough: behavioral type dependent space use in the sleepy**
2 **lizard changes as the season dries**

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9 **Short title:** behavioral type dependent space use

10 **Summary**

11 Understanding space use remains a major challenge for animal ecology, with implications for
12 species interactions, disease spread and conservation. Behavioral type may shape space use of
13 individuals within animal populations. Bolder or more aggressive individuals tend to be more
14 exploratory and disperse further. Yet, to date we have limited knowledge on how space use other than
15 dispersal depends on behavioral type. To address this question we studied behavioral type dependent
16 space-use patterns of sleepy lizards (*Tiliqua rugosa*) in southern Australia. We combined high-resolution
17 GPS tracking of 72 free ranging lizards with repeated behavioral assays, and with a survey of the spatial
18 distributions of their food and refuge resources. Bayesian Generalized Linear Mixed Models showed that
19 lizards responded to the spatial distribution of resources at the neighborhood scale and to the intensity
20 of space use by other conspecifics (showing apparent conspecific avoidance). Behavioral type (especially
21 aggressiveness) affected space use by lizards and their response to ecological and social factors, in a
22 seasonally dependent manner. Many of these effects and interactions were stronger later in the season
23 when food became scarce and environmental conditions got tougher. For example, refuge and food
24 availability became more important later in the season and unaggressive lizards were more responsive
25 to these predictors. These findings highlight a commonly overlooked source of heterogeneity in animal
26 space use and improve our mechanistic understanding of processes leading to behaviorally driven
27 disease dynamics and social structure.

28 **Key words:** animal personality, Bayesian GLMM, behavioral syndromes, GPS-telemetry, movement
29 ecology, spatial ecology.

30 **Introduction**

31 Understanding what shapes spatial dynamics and animal space use is a major challenge in ecology
32 and evolution as they link processes at the individual and population levels. Space use is critical for
33 many, if not most, ecological processes because it determines interaction rates that organisms have
34 with conspecifics, with other species (e.g., prey, predators, competitors, or parasites) and with key
35 abiotic factors (e.g., heat stress). Yet, the factors shaping spatial dynamics in natural systems remain
36 poorly understood, presumably because animal movements result from complex feedbacks between the
37 state and traits of focal individuals and their environment [1,2]. Well-known environmental factors
38 include the local distribution of resources, predators and competitors [3,4], but the effects of consistent
39 behavioral differences among individuals within a population, remain elusive [5,6]. Such differences
40 among individuals are often referred to as behavioral types (BTs) or animal personalities and here we
41 test how BTs interact with ecological conditions to affect animal space use.

42 BTs are known to influence various ecological processes [7–11]. In particular, individuals that are
43 more exploratory, bolder, more aggressive or more asocial than others tend to disperse more frequently
44 and over larger distances [12–15]. Other BT-dependent aspects of space use may include home range
45 (HR) size, relative use of patches that differ in resources or risks, and movement patterns [5,16–18], but
46 these have received less attention. Within-species differences in space use can generate spatial and
47 temporal variability in interactions within and among species that can, in turn, have major impacts on
48 population and community dynamics (REF). For example, the fact that some individuals move more
49 widely than others or have different habitat preferences than others can have major impacts on disease
50 spread (REF) or ecological invasions (REF). Our fundamental hypothesis is that individual differences in
51 BT within a population can help to explain individual differences in space use. Acknowledging BT-
52 dependent space use can also help to advance the burgeoning field of movement ecology by (partially)
53 explaining the commonly-observed intraspecific variation in movement patterns, and the deviations of
54 individuals from theoretically expected optimal behaviors [5,6,16]. Although the idea of BT-dependent
55 space use seems intuitive, it's generality, temporal (e.g., seasonal) dynamics and how it interacts with
56 spatiotemporal variation in ecological conditions are still poorly understood.

57 To date, empirical evidence is particularly scarce and limited by several methodological issues. First,
58 many studies of animal personality have used captive individuals where their space use in nature cannot
59 be addressed. Second, many previous studies suggesting that BT affects habitat preference or space use
60 of mammals [18,23], birds [24,25] and fish [26–29] have derived their measures of space use and BT
61 non-independently, from the same *in-situ* movement data. For example, activity or exploration
62 tendency (both widely used BTs) are commonly estimated from movement data, often through
63 dimension reduction by principal component analysis [e.g., 23,24,30]. Third, to understand the role of
64 social interactions (conspecific attraction or avoidance) in shaping space use, movements of nearby
65 conspecifics should be also studied. Thus, to more rigorously examine relationships between BT and
66 space use, we need to track space use of free ranging individuals, assay their BT independently of
67 movement, and aim to include all (or at least most) individuals in the relevant sub-population. This is
68 feasible for strongly site-faithful, territorial species, but usually difficult for others.

69 We tracked free ranging sleepy lizards (*Tiliqua rugosa*) and ran independent assays to determine
70 their BTs. Simultaneously tracking most resident adults in our study site allowed us to quantify how BT-
71 dependent responses to conspecific presence influenced individual space use. We also explored how
72 individual BTs exhibited differential responses to ecological conditions by mapping relevant factors, such
73 as refuge and food availability. Since their preferred food source, annual food plants, tend to dry out as
74 summer progresses, lizards have a short activity season (spring to early summer). They occupy stable
75 overlapping HRs with exclusive HR cores (shared only with partners) and form monogamous pair bonds
76 with males following females for several weeks during early spring [31]. We predicted that (i) lizards will
77 spend more time at resource rich sites and (ii) the importance of these ecological factors will increase
78 with deteriorating environmental conditions as the season dries. We further predicted that (iii) BTs
79 influence how lizards respond to the ecological predictors and (iv) the effect of lizard BT on space use
80 will intensify as environmental conditions deteriorate. For instance, since aggressive individuals in
81 general explore more superficially and show lower sociability [32] and aggressive male sleepy lizards
82 have weaker social bonds and female following behavior [31] we predicted that aggressive individuals
83 would be less responsive to changing ecological conditions and the space use of conspecifics.

84 **Methods**

85 **Study system.** Sleepy lizards are large, long-lived Australian scincid lizards with a varied diet of
86 mostly annual plants [33]. Adults are rarely threatened by predators [34], normally walk 100-500m per
87 day [35,36] and are mainly active during the austral spring (September-December), with activity ceasing

88 by mid summer. Pairing behavior lasts for 6–8 weeks before mating in late October [31,37,38]. Social
89 network of sub-populations remain stable among years [39].

90 The study was conducted in a 1.2 km² area of semi-arid chenopod shrubland near Bunday Bore
91 Station (33°54' S, 139°20' E) in South Australia (Figure 1). The area has cool wet winters and hot dry
92 summers. Vegetation includes annual plants between scattered chenopod shrubs (bluebush; *Maireana*
93 *sedifolia*) and patches of sparsely distributed black oak (*Casuarina cristata*). Since annual plants grow in
94 the spring and then dry out in the summer, leaving increasingly rare patches of food plants for lizards as
95 the season progresses, there is a strong seasonal effect within each year on available food resources
96 [33,40]. This seasonality affects the movements and behavior of lizards, and shaded refuges (typically
97 large dome-shaped shrubs, fallen trees or mammal burrows) become important later in the season as
98 lizards seek to avoid high heat stress [40–42]. The study area has a dirt road crossing it from east to
99 west, with two building ruins and two seasonal dams that retain water and soil moisture for longer than
100 other parts of the area. The ruins and the roadside have more food plant resources because they are
101 fenced to exclude livestock (but allow access to lizards).

102 **Lizard tracking and behavioral assays.** Tracked lizards were part of a continuous population
103 inhabiting similar surrounding habitat that has been studied for more than 30 years [41,43]. Tracking
104 techniques and behavioral assays have been previously described [31,44,45]. In 2009 and 2010, at the
105 beginning of each spring (September), we captured 60 lizards and fitted them with data loggers (43
106 lizards were tagged in both years). The loggers recorded GPS locations every 10 min for periods when
107 the lizards were assessed to be active from an integrated step counter. Data were downloaded every
108 two weeks each year until late December when lizards had become largely inactive.

109 In 2010, we measured BTs for each lizard three times about 24 days apart, using two assays: (1)
110 **Aggressiveness**- was the tendency (on a scale of 1-11; least to most aggressive) for a lizard to flee or to
111 give a threat display as an observer slowly approached to within 0.3 m (see Table 1 in [31] for further
112 details). Performance in this assay correlated with assayed responses to a lizard model and with
113 measured scale damage [31]. (2) **Boldness**- was the tendency (on a scale of 1-7; shyest to boldest) for a
114 lizard to approach and inspect an unusual food item (novel in the first trial), a banana piece placed 5 cm
115 from its head in the presence of a potential threat from a stationary nearby observer (2 m away). Scores
116 were repeatable (0.474 and 0.304, respectively; see Appendix 1§1 for 'adjusted repeatability' of BT
117 estimates while accounting for sex and trial [sensu 46]), and summed over the trials. Both assays were
118 conducted sequentially before normal morning activity had started, and after the focal lizard had been

119 held in an incubation chamber *in situ* for 40 min at 34° C. For lizards tracked in 2009 BTs were only
120 available for the lizards also tracked in 2010.

121 **Habitat ground survey.** We conducted a survey in late October- early Nov 2013 to assess habitat
122 properties that may affect lizard space use. We evaluated 1400 adjacent 20 x 20 m quadrats along 36
123 north-south transects (Fig 1). For each quadrat we defined a categorical **habitat type**: ‘Open’– chenopod
124 shrubland; ‘Wooded’–black oak trees; ‘Mixed’– a combination of these two; and ‘Anthropogenic’– site
125 directly modified by humans (road, dam or ruin). In addition, we ranked each quadrat from 1 – 5 for four
126 **ecological factors** (see Appendix 1§2 for more details): 1) Refuge– the best available refuge in the
127 quadrat with well-developed wombat burrows ranked highest. 2) Cover of annuals– proportion of open-
128 ground covered by annual plants. Mostly dry at the time of our survey. 3) Late food– presence during
129 the survey period of other plant food resources including berries of the ruby saltbush (*Enchylaena*
130 *tomentosa*), live Ward’s weed (*Carrichtera annua*) and other annuals that were still green. 4) Abundance
131 of Ward’s weed and *Compositae spp.* (hereafter WW&Comp) –although these were mainly dry at the
132 time of the survey we assumed they could indicate food availability earlier during the spring.
133 Additionally, we measured 5) elevation in the center of each quadrat with a handheld Garmin GPS unit;
134 and 6) distance to the nearest dam (hereafter DistDam). We surveyed after lizard tracking ended to
135 ensure we included the entire area used by tagged lizards. Because transects were 40 m apart (and
136 quadrats 20 m wide) we collected habitat data from 50% of this area. Because local plant community
137 structures largely reflect soil type and topography, that interact to determine water runoff and soil
138 moisture, we assumed the spatial configuration of annual plants (the major food resource) and refuges
139 remained constant over years.

140 **Data processing and analyses.** Due to strong seasonal differences at our study site we divided data
141 for each year (2009, 2010) into **Early** (September-October) and **Late** seasons (November- December).
142 During the Early season, male and female lizards are paired, the temperature is moderate and food and
143 water are relatively abundant. In contrast, the post-mating Late season is hotter and drier, and food and
144 water are scarce and food is concentrated in fewer patches. Our focal response variable was space-use
145 intensity, assessed by the number of GPS locations within each quadrat for each focal lizard during each
146 season of each year. Quadrats that were within the minimum convex polygon HR of a lizard, but not
147 visited by it, were scored as zero for space-use intensity. The HR center for each lizard was defined as
148 the center of mass of its activity for each year. We considered how lizards responded to environmental
149 heterogeneity at two spatial scales: a local scale, where a quadrat was scored according to the ranks for

150 ecological factors of the quadrat itself; and a neighborhood scale score including values from the two
151 adjacent quadrats inversely weighted by distance from the quadrat center (normally 20 m; see Appendix
152 1§4 for details). GPS median horizontal accuracy of 6 m [42] prevented consideration of smaller spatial
153 scales and larger scales were probably beyond a lizard's perceptual range [47]. We accounted for spatial
154 autocorrelation in the data by including quadrat identity as a random factor in the statistical models.
155 Since use intensity decreased at the HR periphery, we also included a factor of quadrat distance from
156 the HR center of the focal lizard (DistHRc).

157 We included social effects by calculating for each quadrat and lizard the relative **use intensity by**
158 **conspecifics** (hereafter Conspcfc). To avoid biases from unequal tracking durations or from variation in
159 the local proportions of GPS-tagged individuals (for instance there may be more untagged lizards using
160 quadrats towards the site edges) we calculated Conspcfc as follows. For each lizard we calculated the
161 proportional use intensity across all quadrats within its HR. Then, for each focal lizard in a quadrat we
162 averaged this proportion over all *other* lizards whose HR included this quadrat. This reflects the relative
163 usage by all tagged non-focal lizards for each quadrat. A quadrat that has been used intensively by a few
164 tagged individuals will have a higher value than a quadrat used infrequently (or avoided) by more tagged
165 individuals. Since most quadrats were included in the HR of several lizards (mean 6.1 ± 3.9 lizards; max
166 21, <16% of quadrats were within HR of only 2 lizards), visitation rate by a single non-focal individual
167 (e.g., followed sexual partner) is unlikely to bias the results.

168 To evaluate how space-use intensity by lizards (the dependent variable, as defined above) was
169 influenced by all considered factors and the spatial scale (local vs neighborhood) we used general linear
170 mixed models (GLMMs) with a Poisson distribution and log-link function. We built our models in a
171 Bayesian framework with weakly informative priors (priors were drawn from a normal distribution
172 centered around zero with a S.D.= 100, thus constraining possible parameter ranges) and Markov chain
173 Monte Carlo (MCMC) fitting techniques (see Appendix 1§4 for details; [48]). Sixty lizards with known BTs
174 were included as focal lizards in these models. The main predictors (or factors) included three focal
175 lizard properties (sex, aggressiveness and boldness) and nine quadrat properties: DistHRc, Conspcfc,
176 habitat type and the six measured ecological factors (Refuge, Cover, Late-food, WW&Comp, Elevation
177 and DistDam). Sex and habitat type were assigned dummy variable scores. All non-dummy variables
178 were standardized around the mean. Pairwise comparison showed these factors were not strongly
179 correlated (28 pairs, Pearson's $r = 0.20 \pm 0.11$; max $r = 0.45$ between Late-food and WW&Comp).

180 We considered two-way interactions between the three lizard and eight quadrat properties,
181 excluding habitat type and sex*DistHRc (due to co-linearity with DistHRc as a main effect), leaving 23
182 interactions. For each dataset (Early, Late) we considered a set of 27 possible competing models that
183 included individual lizards, quadrats and years as random factors and some or all of these predictors and
184 their two way interactions (see Tables 1 for partial and A4 for full lists of model structures). We tested
185 our predictions by ranking models using deviance information criterion (DIC) and examined seasonal
186 effects by modeling the two seasons separately. This approach avoided hard-to-interpret three way
187 interactions involving season. All statistical analyses were conducted in R [49], using the lme4 [50],
188 Rethinking [51] and Rstan packages that compile GLMM models for evaluation in Stan computational
189 language [52].

190 Results

191 We obtained tracks from 72 different lizards (50 in 2009, 60 in 2010, with 38 tracked in both years)
192 with a total of 279,985 valid GPS locations that were contained within 1052 of the 1400 surveyed
193 quadrats. For each year, individual tracks started on September 10th ± 13 days (mean ± S.D.), lasted 97 ±
194 21 days, and ended on December 15th ± 16 days. Each lizard used 51.9 ± 22.9 different quadrats, using
195 about 6 more quadrats during the Early compared to the Late season (paired t-test: $t_{109}=4.1$, $P<0.001$).
196 Season did not affect the number of GPS locations per quadrat (our dependent variable) or its within-
197 individual variation. The two BTs were repeatable (see Appendix 1§1) and not strongly correlated
198 (Pearson's $\rho = 0.23$, $P=0.078$). We found no systematic differences among BTs in the ecological
199 properties of their HR or in the duration of their tracking (Appendix 1§3; Table A2).

200 **Model comparison and main effects.** We compared 27 GLMMs of lizard space-use intensity, each
201 with 7740 data points (Table 1, see Tables A4 and A5 for full ranking details). Models including
202 interactions between lizard and quadrat properties outperformed other models (including those with
203 interactions with sex but not with BTs) in both Early and Late seasons, highlighting the importance of BT-
204 dependent space use. The best model (M13 for both seasons) included all three groups of interactions
205 (BTs*DistHRc, BTs*Conspcfc and BTs*ecological factors). The second-best models included interactions
206 between BT*ecological factors and either BT* DistHRc (M18, Early) or BT*Conspcfc (M19, Late). The
207 relative ranks of models with only one interaction group further corroborated that the BT*DistHRc
208 interaction (M14) was more important than BT*Conspcfc (B15) early, but that their relative importance
209 reversed later in the season. Models with ecological factors considered at the neighborhood scale were

210 almost always ranked higher than their local scale equivalents, implying that space use by lizards is
211 better explained by neighborhood characteristics than by the local environment.

212 Effect sizes extracted from the best models (M13 for both seasons) are useful for comparing
213 seasonal variation in the effect of each predictor (Figure A3), but may be misleading when comparing
214 relative effects among predictors if those differ also in their magnitude of observed variation (e.g. Cover
215 spans over 3.5 units of S.D. while Refuge over 6.3 units) [51]. Hence, for each predictor we constructed
216 predictions across the empirically observed range of values, while using default values for all non-focal
217 predictors (Figure 2; for more information see Appendix 1§4). Both increasing distance from the HR
218 center and Conspecific use intensity had strong negative effects on lizard's space-use intensity in both
219 seasons (Figure 2A, 2B; Figure A3). During the Late season these effects were slightly stronger for
220 DistHRc and weaker for the conspecifics, corresponding with lower conspecific avoidance. The six
221 ecological factors all had weak, non-significant effects during the Early season (Figure 2C-2H; Figure A3).
222 In contrast, during the Late season, Refuge and Late-food had a strong positive effect and Cover had a
223 weak, but significant effect on lizard space use (Figure 2C-2E). Surprisingly, in this season, lizards also
224 used quadrats with higher WW&Comp (known food resources) less intensively (Figure 2F). Lizards also
225 used less intensively quadrats further from dams, especially in the Late season (Figure 2G). The opposing
226 effects of quadrat elevation on space use were both non-significant (Figure 2H). Habitat type had almost
227 no effect on lizard space use once these ecological factors were accounted for, with one exception – a
228 strong enhancement in use of anthropogenic habitat during the Early season, where road runoff
229 increase productivity and fencing prevents livestock grazing (Figure A3).

230 ***Interactions between BTs and other factors.*** Lizards with different BTs or of different sex did not
231 differ in their average number of GPS locations per quadrat (Figure A3). However, BT and sex affected
232 space use through strong interactions with quadrat properties. In general, lizard aggressiveness had a
233 stronger effect on space use (i.e., stronger interactions) than boldness or sex. Effect sizes for some of
234 the interactions are actually larger during the Early season (Figure A4); however, generating model
235 predictions by combining these interactions with the main effects shows that both BTs had stronger
236 effects in the Late season (Figure 3; see Figure A5, A6 for all interactions).

237 Aggressiveness interacted strongly with DistHRc and Conspcfc, and with most of the ecological
238 factors. Interestingly, complementary analysis showed that *HR size* was positively associated with
239 boldness, but only weakly with aggressiveness (Appendix 1§3, Table A3). This implies that the significant
240 interaction aggressiveness*DistHRc was driven by differential response to distance within the HR (and

241 was not a byproduct of overall HR size). Hence, while shy lizards had smaller HRs, both bold and shy
242 lizards showed similar patterns of decreasing use of quadrats further from their HR center. In contrast,
243 aggressiveness did not strongly affect HR size but less aggressive lizards used quadrats closer to the HR
244 center more intensively than did aggressive lizards. Similarly, these less aggressive lizards were overall
245 more responsive to the different quadrat properties, whereas aggressive lizards were less likely to use
246 quadrats used intensively by other conspecifics, or having high values of Refuge, Late food, Cover or low
247 values of WW&Comp. The sexes also differed in their space use mostly during the Late season, with
248 females more responsive to Refuge rank and less to WW&Comp and distance from the dam (Figure A7).

249 **Discussion**

250 We found four main results. First, lizard space use, in general, was explained by both distance from
251 their home range center, and by spatial variation in ecological factors including food and refuge
252 rankings, and the space-use intensity by other conspecifics. Second, measures of ecological factors at
253 the neighborhood spatial-scale explained space use by lizards better than at the local (quadrat) level.
254 Third, this response varied between seasons with many factors having stronger influences during the
255 Late season when environmental conditions were harsher. Finally, lizard BT (boldness and
256 aggressiveness), assayed independently of their movement patterns, affected their space use through
257 interactions with various quadrat properties. Models including interactions between lizard properties
258 (BTs and sex) and distance from HR center, conspecific space use and ecological factors (refuge, food
259 and cover) were better at predicting observed space-use patterns than models without these
260 interactions. Overall, aggressiveness had more influence than boldness and many of these interactions
261 were more pronounced during the Late season. Below, we discuss the implications of these results.

262 **The effect of ecological and social factors on animal space use**

263 As expected, lizards generally preferred quadrats with more food and better refuges. The
264 preferences were clearer and stronger in the Late season. Lizards also used quadrats more if they were
265 closer to their HR center or had lower levels of conspecific use. This latter finding conforms with
266 previous reports that these lizards maintain core HRs exclusive of other same sex individuals [35]. It does
267 not conflict with males following their female partners during the Early season since pairing behavior
268 accounts for only 30% of their activity time [37,38]. Also, since most quadrats were visited by multiple
269 individuals, our measure of conspecific space use is not sensitive to activity of a single conspecific.
270 Indeed, excluding paired males (13 for 2009 and 17 for 2010) from the dataset yielded the same

271 outcomes (Figure A8). One explanation for the negative effects of conspecific use intensity is that lizards
272 avoid contact with some neighboring conspecifics, a result previously reported in analyses of sleepy
273 lizard social networks [44]. An alternative (non-mutually exclusive) explanation invokes local depletion
274 of food resources by lizards, leading to apparent conspecific repulsion in heavily used quadrats. We
275 cannot distinguish between those explanations because summed space use over two months does not
276 identify social interactions, or discriminate between synchronous and asynchronous quadrat use.
277 However we speculate that food depletion is less plausible because lizards have an overall low density,
278 low metabolic rates and abundant but ephemeral food resources.

279 The observed seasonal differences in responses to ecological factors may reflect both internal or
280 social factors (pairing and mating in the Early season) and external factors (drying conditions in the Late
281 season). Teasing apart these effects would require an experimental approach. Nevertheless, many of the
282 observed seasonal trends (e.g., stronger positive responses to Refuge rank, Late food, Cover and
283 distance to the nearest dam during the Late season) agree with simple expectations based on seasonally
284 increasing heat stress and resource deterioration [42]. Resource availability at the neighborhood spatial-
285 scale was a consistently better predictor of lizard space use than at the local scale, implying spatial
286 decisions are influenced by a larger scale than our single quadrats. This finding is consistent with scale-
287 dependent foraging, where movements of animals that utilize patchy or spatially auto-correlated
288 resources match intermediate spatial scales [53–55]. Lizards may obtain relevant information on
289 resource distributions through direct detection [47] or through familiarity with their multi-year stable
290 HR [35]. Future analyses can expand our binary scale comparison to a broader range of scales [e.g., 56],
291 and explore whether BTs differ in the spatial scales they respond to.

292 **The effect of behavioral types on animal space use**

293 BT-dependent space use is probably very common in nature but empirical examples other than for
294 dispersal are rare [7,11]. Our study is novel in showing that lizards with different BTs differ in their
295 spatial response to different ecological and social factors within the same habitat. Moreover, we
296 showed that BT-dependent responses persisted across time despite seasonal changes in internal and
297 external conditions. Yet, these responses changed in their detail with season, highlighting the ecological
298 complexity of BT-dependent space-use. In contrast to other examples [19,24,26,28,57], the space-use
299 differences we observed among BTs did not result from confounding factors such as using a movement-
300 based BT definition (e.g., activity or exploration), or from any difference among BTs in the habitat or
301 niche they occupied, or from differences in their social context (e.g. different BTs in different flock sizes).

302 In general, the effects of BTs on space use were more prominent during the Late season, partially
303 because the ecological factors they interacted with had stronger effects during this season.
304 Aggressiveness was more important than boldness for most predictors. The observed
305 aggressiveness*DistHRc interaction implies that (in addition to having a slightly larger HR; Appendix 1§3)
306 aggressive individuals used their core HR *less* frequently (figure A6). Accordingly, aggressive lizards were
307 also generally less responsive to other ecological predictors (Refuge, Late food, Cover, WW&Comp and
308 elevation). We consider two (non-mutually exclusive) *a-priori* explanations for these trends. First, more
309 aggressive lizards might invest more time in territorial behavior such as patrolling their HR boundaries.
310 This would explain their HR usage patterns, lower responsiveness to Conspcfcs (discussed below) and
311 other ecological predictors. Second, as in some other species [9,11,32], more aggressive individuals may
312 forage with more superficial exploratory behavior, while less aggressive individuals may explore core
313 areas more thoroughly with stronger tendency to stay longer within patches of discovered resources
314 (using area restricted search [48]). This will also lead to the observed stronger responsiveness of less
315 aggressive individuals (who stay within a patch) to the ecological factors. Whether differential
316 investment in territorial behavior drives differential search strategies or vice versa is debatable, but
317 together, these explanations suggest insights into alternative pathways that can result in BT-dependent
318 space use and HR size (Appendix 1§3; see also [18,24]). In the future, more sophisticated HR indices
319 (e.g., LoCoH or kernel analysis [58]) should be applied to test the consistency of BT-dependent response
320 to DistHRc and HR size in different systems. Better understanding of this interaction can shed light on
321 intraspecific variation in optimal foraging, spatial ecology and response to habitat fragmentation.

322 The observed BT*Conspcfcs interactions may reflect behavior where bolder and more aggressive
323 lizards are less responsive to conspecific activity. This conforms with the well supported theoretical
324 expectation that 'proactive' (i.e., bold, aggressive, fast-exploring) individuals tend to have lower
325 sociability and weaker social network associations [9,32,21]. Alternatively, this pattern may reflect
326 either BT-dependent spatial preferences (i.e., aggressive lizards prefer different, unmeasured quadrat
327 properties, regardless of conspecifics), or stronger avoidance by other lizards of areas used by aggressive
328 individuals. Although our data cannot discriminate among these alternatives, the prevalence of
329 interactions between BTs and DistHRc, Conspcfcs and the ecological factors in our analyses support our
330 main argument that BT affects movement, space use and presumably also habitat preference of free
331 ranging animals. These effects may explain variation in the spatial distribution of BTs (e.g., why similar
332 BTs are clumped together in some cases but not in others;[19]), in their interaction rates and overall
333 social network positions [21].

334 Our study reflects a growing recognition of the importance of both animal movements and
335 consistent intraspecific behavioral variation in understanding evolutionary and ecological processes
336 [1,2,7,11,15]. Yet, surprisingly few studies have combined both approaches to examine the existence
337 and consequences of BT-dependent space use. At the proximate level, links between BTs and movement
338 patterns can be maintained by intraspecific genetic variation (e.g., in the alleles of the *DrD₄* or *for* genes)
339 [59,60]. Alternatively, BT-dependent variation in stress hormones (in particular cortisol) can influence
340 the perceived environmental risk and subsequent decisions by an individual with a particular BT about
341 space use and foraging tactics [27]. Ultimately, BT-dependent space use has the potential to act as an
342 important mechanism influencing species interactions, habitat selection and disease dynamics,
343 therefore affecting management-related issues such as reintroductions and BT-dependent use of
344 protected areas and habitat corridors [7,57,21]. Further theoretical work is needed to generate
345 additional predictions on how and why different BTs should differ in their spatial responses to
346 spatiotemporal variation in ecological and social conditions. Future empirical work should directly
347 explore BT-dependent *movement* patterns that lead to the variation in space-use patterns like those
348 reported here.

349

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362 **Data Accessibility:** The data included in the paper are available through Dryad
363 (doi:10.5061/dryad.h4dt0). Note that currently the Dryad includes 3 obsolete versions that are
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365 **Authors' contributions:** All authors conceived the study and participated in the fieldwork. OS analyzed
366 the data and drafted the manuscript. All the authors contributed to the writing of subsequent revisions.

367

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502

503

504 **Figure and table captions**

505 **Table 1.** A summary comparison of the structure and ranking of GLMMs for lizards space use. Quadrat
506 properties included its distance from HR center (DistHRc) of focal lizard, its usage intensity by
507 conspecific (Conspcfc), its habitat type and six ecological factors (Refuge, Cover, Late-food, WW&Comp,
508 Elevation and DistDam). Lizard's properties included its sex and two behavioral types (BTs) and their
509 interactions with DistHRc, Conspcfc, and Ecological factors (abbreviated to D, C and E, respectively). All
510 models included random intercepts for quadrats, lizard and lizard by year. Models were ranked using
511 Δ DIC for Early and Late seasons and M13 (in bold) was selected as the most likely model for both
512 datasets with a weight of 1. Models with Ecological factors assessed at the local spatial scale were
513 almost always outperformed by their neighborhood scale counterpart and are not presented here.
514 Tables A4 and A5 summaries the full model list and ranking details.

515

516 **Figure 1:** An aerial photo of the study site with locations of ground survey quadrats in greyscale colors
517 reflecting their refuge rank (black being the highest) and three examples of lizard tracks from the spring
518 of 2009. Note that these particular tracks are for animals with much larger than average home ranges,
519 chosen for ease of viewing.

520

521 **Figure 2.** Predicted effects of the quadrat properties included in the best models for lizard space use
522 during the Early (green) and Late (orange) seasons. A) Distance from home range center (DistHRc); B)
523 use intensity by conspecifics (Conspcfc); C) Refuge rank; D) availability of late food; E) Cover of annuals;
524 F) availability of Ward's weed and *Compositae* spp. (WW&Comp); G) ground elevation above sea level
525 and H) distance to the nearest dam. Solid lines are the predicted λ of the Poisson distribution for the
526 mean lizard, and dark shaded areas are the confidence intervals for this parameter. Light shaded areas
527 are confidence intervals for predictions while accounting for variation among lizards and years.

528

529 **Figure 3.** Selected interactions between quadrat properties and lizards' aggressiveness during the Early
530 (upper row) and Late (lower row) seasons. Predictors: Distance from HR center (DistHRc) and Z-scores of
531 use-intensity by conspecifics (Conspcfc), Refuge rank, Late food availability and cover of annuals (See
532 figure A6 for the full list). Each panel presents model predictions for non-aggressive lizards (red dashed

533 line), the average lizard (green solid line) and aggressive lizards (blue dash-dotted line) using the mean
534 value for each tercile (0-33%, 33%-66% and 67%-100%). The shaded areas are the confidence intervals
535 of the predicted λ of the Poisson distribution for each tercile. Overall, aggressiveness had stronger
536 interactions with ecological predictors during the Late season.

537

538

539

540 **Tables**

541 Table 1.

Model name	DistHRc	Conspcfc	Hab. type	Ecol. factors	Sex	BT	Intrraction sex*	Intrraction BT*	Model rank (Early)	Model rank (Late)
M2									16	16
M3	+								15	15
M4	+		+						14	14
M5	+		+	+					13	13
M6	+	+	+	+					12	10
M7	+	+	+						10	12
M8	+	+	+		+	+			11	11
M9	+	+	+	+	+		D, C, E		8	4
M10	+	+	+	+	+	+	D, C, E		7	5
M13	+	+	+	+	+	+	D, C, E	D, C, E	1	1
M14	+	+	+	+	+	+	D	D	5	9
M15	+	+	+	+	+	+	C	C	9	6
M16	+	+	+	+	+	+	E	E	6	8
M17	+	+	+	+	+	+	D, C	D, C	3	3
M18	+	+	+	+	+	+	D, E	D, E	2	7
M19	+	+	+	+	+	+	C, E	C, E	4	2

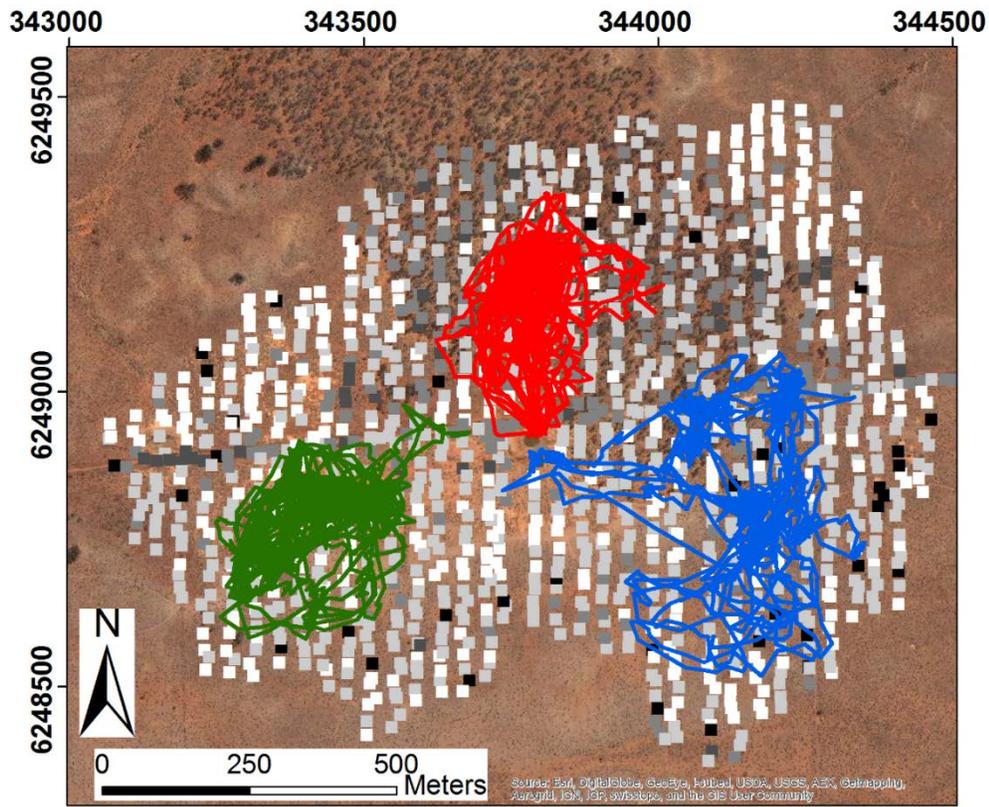
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545 **Figures**

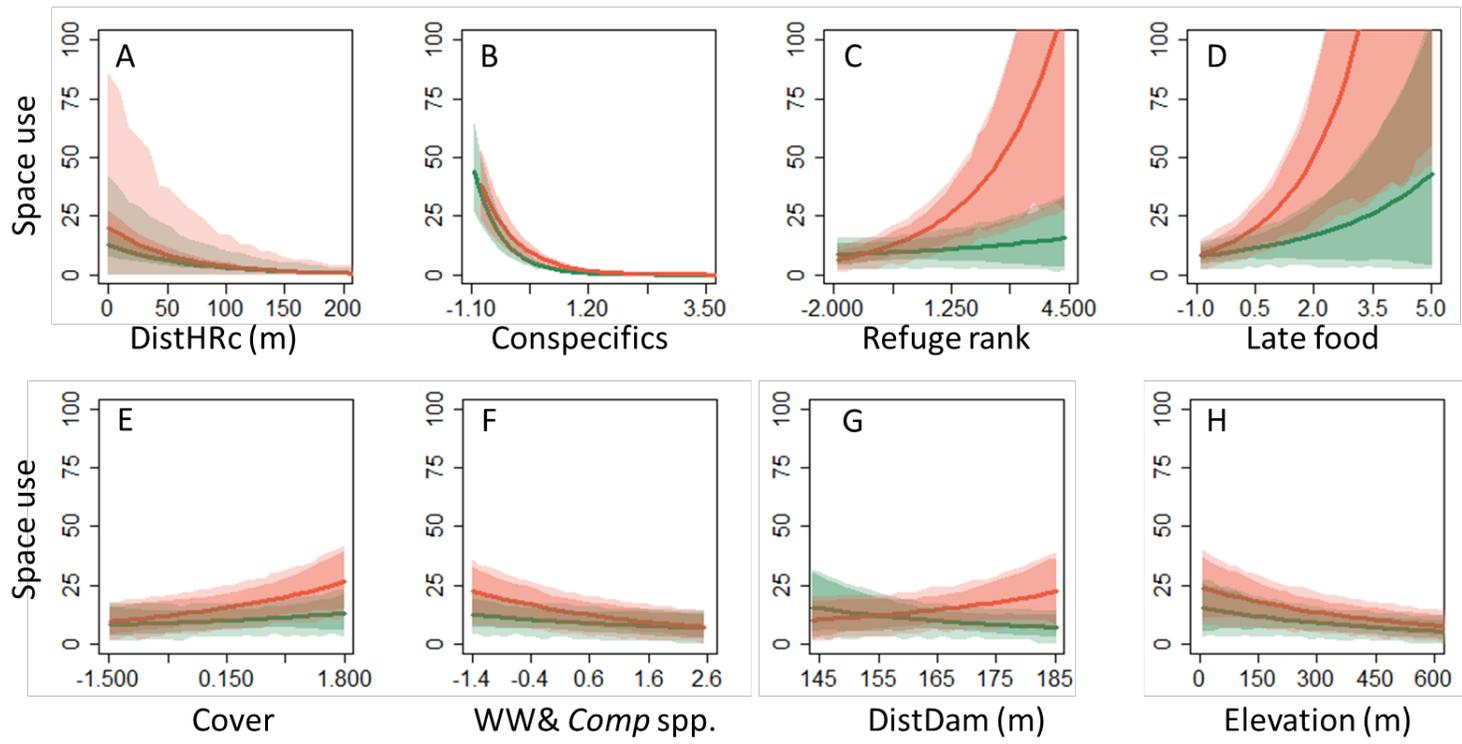
546 Figure 1.



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548

549



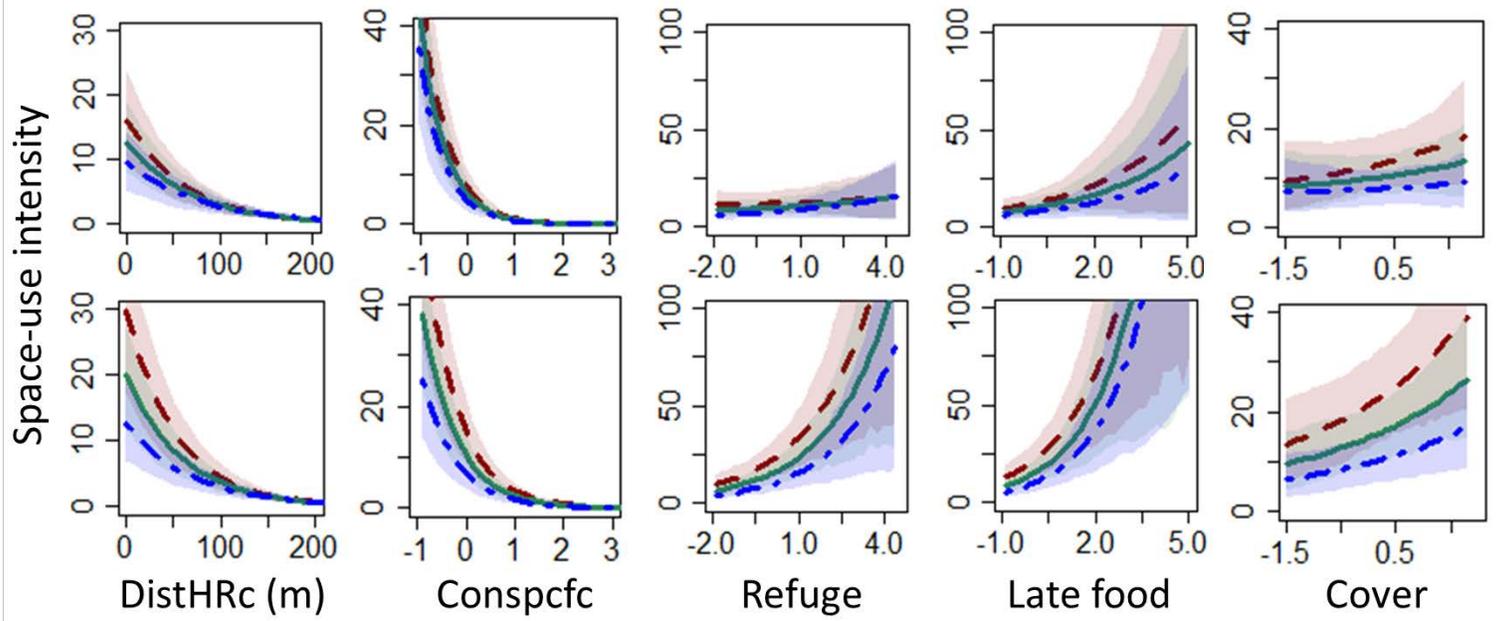
550 Figure 2.

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555 Figure 3.

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