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1   **The response of a sleepy lizard social network to altered ecological conditions**

2

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14   6192 words

Abstract

The use of social networks to describe animal social structure is increasing, yet our understanding of how social networks respond to changing ecological conditions remains limited. Animal behaviour is often constrained by temporal or spatial variation in ecological conditions; how do behaviour and social organisation respond to changing ecological conditions? We used a social network approach to ask this question in the pair-living sleepy lizard, *Tiliqua rugosa*. We attached GPS data loggers to lizards to record their movement, activity, and social interactions, during their activity period (Oct – Dec) across three years (2008 - 2010). The years varied substantially in ecological conditions; from hot and dry in 2008, to cool and wet in 2010. Our aim was not to suggest how individual climatic or ecological factors influence social organisation, but to explore the stability of social structure over varying conditions. Lizards spent less time active, and overlapped in home range area more with conspecifics in the driest year of the study (2008), than in subsequent years. Despite this variation in behaviour, the number and strength of connections in the social network was stable across years. Intra-sexual associations were similar across years, but there was a lower incidence of inter-sexual associations in 2008 compared with the other two years. Among male-female dyads, pairing intensity was lower in 2008, while for males, extra-pair strength was higher in 2008. These results suggest that although the overall social network is tolerant to changes in ecological conditions, the nature of contacts within the network shifts in response to ecological conditions.

Keywords: social network, ecological variation, resource availability, pair bond, extra-pair associations, temporal network dynamics, lizard, skink

Introduction

As interest continues to grow in describing how animal populations form social networks

(Wey & Blumstein 2012; Zohdy et al. 2012), we still lack a fundamental understanding of

how animal social networks respond to ecological perturbations (Sih et al. 2009; Wong

2012). Social networks describe the direct and indirect connections between all members of a

population as a series of nodes (representing individuals) connected together by edges

(representing associations), and provide a quantitative framework to analyse social structure

(Krause et al. 2007; Sih et al. 2009). Networks represent pathways for the transmission of

information and pathogens, so that individuals in a population that do not directly interact

with each other may still influence each other through indirect connections (Liu et al. 2011).

Empirically derived social networks are often presented as static structures based on a snap-

shot study of relationships among individuals over a short time period (Croft et al. 2004; Pike

et al. 2008), or aggregated across a longer time period (Lusseau 2003; Lusseau et al. 2006).

Critical questions that cannot be answered from those studies concern network dynamics, the

extent of temporal stability, and the robustness of the network structure against change

(Blonder et al. 2012). Environmental and ecological processes have the potential to influence

the behaviour and subsequent network position of individuals, causing changes in network

structure (Wey et al. 2008; Sih et al. 2009; Tanner & Jackson 2012).

Animal societies can vary widely in the stability of their structure, and the

associations maintained within them. Social structure can be dynamic, with fission-fusion

societies characterised by short-term associations of groups of individuals followed by some

mixing and the formation of new groups (Lusseau et al. 2006; Aureli & Schaffner 2007; de

Silva et al. 2011). In contrast, some societies show long-term stability in group membership

(Lusseau et al. 2003) or monogamous partnerships (Getz et al. 1981; Mock & Fujioka 1990).

One way of examining the stability (consistency) of direct social associations between dyads

looks at lagged association rates, which quantify how the probability of association between two individuals changes with time between interactions (Baird & Whitehead 2000; Whitehead 2008; Parra et al. 2011). These studies provide insights into the temporal nature of direct social associations within defined social units (dyads or groups). However, a social network approach provides a framework for examining stability under changing environmental conditions, of the whole social organisation, including both direct and indirect social associations. This is particularly useful for species with more ambiguous and loosely structured social units.

The impacts of altered ecological conditions on social network structure have normally been explored through comparing network structure of populations across an ecological gradient of interest. For example, Stanley and Dunbar (2013) found clique size within feral goat networks was stable among three populations that varied in climate and vegetation. In contrast, Chaverri (2010) found that network clustering and betweenness of bat networks was lower in sites with a higher density of roost sites, across three populations. Populations with different levels of predation risk may also differ in network structure. Edenbrow et al. (2011) reported that guppies from low-predation risk populations showed more even social associations among individuals and more social mixing than did guppies from high-predation risk populations. While these studies provide insights into how social structure varies with different ecological conditions, only comparisons that track changes in social structure over time can provide insights into how a population responds to ecological perturbations. For example, Edenbrow et al. (2011) did not detect social network change within guppy populations when the habitat complexity and the perceived risk of predation were experimentally adjusted. If the structure of a social network is flexible then the population can rapidly adjust its social organisation to respond to changes in the degree of clustering of resources, or to changes in the intensity of predation.

87   However, social network flexibility is not always beneficial. A more robust social

88   network that retains a stable structure in the face of altered ecological circumstances may

89   protect the population against rapid social structural change that may be inappropriate in the

90   longer term. Social stability can be important for individual fitness. For instance Barocas et

91   al. (2011) suggested that rock hyrax individuals lived longer if they were members of stable

92   social groups with more equal within-group associations. While the number of empirical

93   studies about the temporal stability of social network structure in natural populations is

94   growing (Wiszniewski et al. 2010; Drewe et al. 2011; Kerth et al. 2011; Cantor et al. 2012;

95   Jeanson 2012), we lack an understanding of social network stability in the context of

96   changing ecological conditions. Foster et al. (2012) showed that the connectivity of a killer

97   whale network changed in response to food availability, becoming more connected in years

98   with high salmon abundance. Thus, studies of network dynamics over a period that includes

99   temporal variation in ecological conditions can provide deeper insights into the resilience of

100   social networks to ecological changes.

101   Overlaid upon this, networks can be composed of several types of interactions.

102   Interactions may be aggressive or affiliative (Madden et al. 2011; Hirsch et al. 2012), and

103   may be inter- or intra-sexual (Hamede et al. 2009; Edenbrow et al. 2011). We do not yet

104   understand how variation in ecological conditions influences the stability of these different

105   types of interactions within social networks. In the current study, we studied both the overall

106   network stability, and the stability of different forms of associations, within a social network

107   of an Australian lizard over three consecutive years that varied substantially in ecological

108   conditions.

109   The sleepy lizard, *Tiliqua rugosa*, is a large, long-lived, Australian scincid lizard that

110   occupies stable, overlapping home ranges (Bull 1994; Kerr & Bull 2006a). Each spring, adult

111   lizards form monogamous pair-bonds for up to 10 weeks before they mate, and individual

pairs of lizards often re-establish those partnerships in subsequent years (Bull 1988; 1994; Bull et al. 1998; Bull 2000; Bull & Burzacott 2006; Leu et al. 2010a). The development of on-board activity loggers, which count the number of steps taken by lizards (Kerr et al. 2004a), combined with GPS units (Leu et al. 2010a) has allowed deeper insights into more cryptic aspects of their social system beyond pair associations. Leu et al. (2010a) described a social network based on frequency of contacts among active lizards, and reported specific associations and avoidances among neighbouring individuals. They also explored the temporal stability in associations among sleepy lizards within an activity season, and found no difference in the mean network degree (a measure of the number of connections in the network) between the pre-mating and post-mating activity period (Leu et al. 2010a). Our current study builds upon this previous research to explore the temporal stability of the social network of sleepy lizards across three years. In particular, we asked how resilient were sleepy lizard social networks to changes in climate and climate driven behaviour.

Previous studies have shown that climatic conditions drive ecology and behaviour of this species, mainly through the influence of winter and spring rainfall on the abundance and persistence of the annual flowering plants that the lizards feed on. However, those studies lead to divergent predictions for network structure. On the one hand, in years of lower rainfall when food is scarce, lizards are less active, home ranges are smaller and overlap less with individuals of the opposite sex, and lizards form fewer pairs, or retain partnerships with lower frequency of contact (Kerr & Bull 2006a; 2006b). Thus, we predict that inter-sexual pairing associations in the network will have lower strength in response to drier conditions. On the other hand, in those drier years, the scarcer food resources become clustered around dams and depressions where the soil retains some moisture. This may increase the overall frequency of social interaction as lizards are forced to aggregate more as they come to the same few places to feed. A prediction is that some associations, particularly non-pairing associations, will

137 increase in response to drier conditions. Overall, these considerations may lead to predictions

138 of little net change in the number and strength of associations within the network as a result

139 of contrasting climatic conditions, with reduced pairing associations countered by increased

140 feeding aggregations. But underlying that stability we would predict changes in the types of

141 associations within the network from one year to the next.

142   We asked whether changes in rainfall and climate among the three years affected

143 lizard body condition and behaviour (activity and home range use), and whether those

144 changes influenced social structure in the population. Because this study only covered three

145 years, we did not expect to provide rigorous evidence for the effects of specific climate

146 factors. Our aim was to explore overall network stability, and the balance among different

147 types of interactions within the network, in response to ecological and climatic variation

148 across years.

149

150 **Methods**

151 The study was conducted in a 1.0 x 1.5 km area of chenopod shrubland near Bundey Bore

152 Station (33° 54' S, 139° 20' E) in South Australia, over three years (2008 – 2010) during the

153 austral spring and early summer of each year (Aug- Dec). Most of the annual activity of

154 sleepy lizards is confined to this period (Kerr & Bull 2006b; Kerr et al. 2008). We measured

155 annual rainfall and maximum daily temperature (during the study period only) using records

156 from a rain gauge and thermal datalogger, located less than 4km from our study site. The

157 long-term average annual rainfall in the study area is about 250 mm. The rainfall was

158 substantially below this average in 2008, about average in 2009, and above average in 2010

159 (Fig. 1a).

160   In late August-early September of each year, we captured all resident adult lizards

161 within the study area (2008, n=47 (27 males: 20 females); 2009, n=58 (31 males: 27

162   females); 2010, n=60 (30 males: 30 females)). These were part of a larger continuous

163   population inhabiting similar habitat surrounding the study area. Using surgical tape, we

164   attached a combined activity and GPS logger to the dorsal surface of the tail of each lizard

165   (Kerr et al. 2004a; Leu et al. 2010a; Godfrey et al. 2012), which stored data on the number of

166   steps taken by the lizard every 2 minutes, plus the GPS location every 10 minutes, when the

167   lizard was active, over the following four months of each year. Steps were recorded using a

168   magnet glued to the hind leg of the lizard, which activated a reed switch positioned on the

169   torso of the lizard each time the leg passed the torso, counting each step taken by the lizard

170   (Kerr et al. 2004a). This technology has been extensively used on sleepy lizards to provide

171   accurate step counts (Kerr et al. 2004a; 2004b; 2006b; 2006c; 2008; Leu et al. 2010a; 2010b;

172   Godfrey et al. 2012). The time when GPS locations were recorded was synchronised across

173   all lizards. GPS loggers were manufactured at Flinders University (Adelaide, Australia) (Kerr

174   et al. 2004a). A radio transmitter (Sirtrack, Havelock North, NZ) with unique frequency

175   allowed us to identify and locate each lizard every 12 days to download data, change batteries

176   and measure body mass (to nearest 5g) and snout-to-vent length (SVL). Lizards were

177   captured by hand. Each data logger plus radio unit weighed 37 g, or 4.5% of the average body

178   weight of an adult lizard, and 5.6% of the body weight of the lightest lizard in our study. Data

179   downloads were conducted at times before or after the diurnal period of lizard activity, to

180   avoid interfering with normal behaviours and to reduce the impact of handling on lizard

181   behaviour (Kerr et al. 2004b). In all comparisons, we used a period of 81 days from Oct 1 –

182   Dec 20 that was common to all three years of the study. The number of GPS locations

183   recorded in that period varied among lizards and years because locations were only taken

184   when lizards had been actively moving in the last 10 minutes. Some units malfunctioned, and

185   some lizards were only effectively tagged for a short period of time. Those individuals that

186 were observed relatively infrequently (< 600 GPS locations) were removed from all further

187 analyses (2008: 5 removed; 2009: 3 removed; 2010: none removed).

188   To measure lizard body condition in each year, we calculated the average SVL and

189 mass of each lizard over all captures in that year, and performed a mixed model regression of

190 SVL against body mass (both log-transformed), with individuals as subjects, and using

191 repeated measures on individuals among years. The regression was significant ($F_{1,87.04} =$

192 48.29, $P < 0.001$), and we used the residuals from the regression as an index of lizard body

193 condition.

194   The lizards were treated using procedures formally approved by the Flinders

195 University Animal Welfare Committee in compliance with the Australian Code of Practice

196 for the Use of Animals for Scientific Purposes and conducted under permits from the South

197 Australian Department of Environment and Heritage to Undertake Scientific Research. We

198 observed no adverse effects of the loggers on the lizards, which is consistent with other

199 studies using the same loggers on these lizards (Leu et al. 2010a; Godfrey et al. 2012). At the

200 end of each year of the study, we removed the units and released the lizards. These lizards

201 normally shed their skins sometime during December to January, after the units had been

202 removed, and we did not detect any damage or irritation where the units had been attached.

203

204 *Effect on behaviour: Comparing home range and activity patterns among years*

205 Our first set of analyses considered whether there were detectable changes in space use and

206 activity patterns among the three years. We used the home range analysis software package

207 Ranges 6 (Kenward et al. 2003) to estimate the home range areas for each lizard in each year.

208 Home range area was estimated from the 95% minimum convex polygons (MCPs) derived

209 from the GPS locations each 10 minutes while the lizard was active (mean 1904 locations per

210 lizard per year over the 81 day period; range 641 - 4548). We then calculated the proportion

211   of home range overlap between each pair of lizards in each year, and derived an index of

212   home range overlap for each individual in that year as the sum of the proportions of overlap

213   with all other lizards.

214   We derived two measures of activity for each lizard in each year. We considered a

215   lizard active within a 2 minute period when it took more than 10 steps in that period. One

216   activity measure was the percentage of all 2 minute time periods when the lizard was active.

217   The other was the mean number of steps per 2 minutes when the lizard was active.

218   We tested whether the home range area or either of the two measures of activity level

219   varied among years for the 30 individuals that were observed in all 3 years, using separate

220   repeated measures ANOVA in the statistical software package PASW 18. Year was the

221   repeated effect, and lizards were subjects. The Greenhouse-Geisser correction was used when

222   the data violated the assumption of sphericity.

223   The derived index of home range overlap was not independent among individual

224   lizards. We used a two-sample randomisation test for differences in mean home range overlap

225   among paired samples, between each pair of years. In this procedure, we calculated the mean

226   of the home range overlap index among individuals in each year, and then calculated the

227   absolute difference in means (Δ Mn) between years. We then randomised the measures

228   between years (by keeping the indices of home range overlap recorded for each individual

229   constant, but randomly swapping the measures between years) to test whether the observed

230   difference in means was greater than expected by chance. We used 10,000 randomisation

231   permutations, and derived the p-value as the number of times the randomised difference in

232   means exceeded the observed difference in means, divided by the number of permutations.

233

234   *Social networks*

235   We constructed social networks based on the frequency of times that two active lizards were

236   recorded in spatial proximity to each other. This was derived from the synchronous GPS

237   locations of each lizard. Following Leu et al. (2010a), we considered that lizards that were

238   within 2 m of each other at any recorded time had made recent social contact or were going to

239   make social contact soon. We allowed for a median GPS precision of 6 m, and included each

240   pair of GPS derived locations within 14 m of each other as a record of social contact (Leu et

241   al. 2010a). To construct the social network we calculated the Simple Ratio Index (SRI) for

242   each pair of lizards, as the number of recorded contacts divided by the total number of

243   observations when both lizards were active. The SRI is not driven by the level of activity.

244   Lizards may have interacted less often in a year when they were less active, but could have

245   retained the same SRI because it was measured relative to the period when lizards were

246   active. An undirected edge in the network was included for each pair of lizards in contact at

247   least once over the study period, and the weight of that edge was determined by the SRI. This

248   meant there was a higher weighting for the edge between two lizards that had a higher

249   proportion of their active times in contact over the study period. The networks were assumed

250   to be symmetrical, with contacting lizards having equal roles in a contact interaction.

251   Separate networks were developed for each year. For each network we derived a number of

252   metrics that are defined in Table 1.

253   We first determined whether our observed networks were different from random

254   associations, based on their home range use patterns and activity levels, following Leu et al.

255   (2010a). We developed random networks using the ideal gas model (Hutchinson & Waser

256   2007), which estimated expected association rates if individual lizards moved randomly

257   within their home ranges. For each dyad in each year, we calculated f, the expected encounter

258   rate per day, using the formula [1] derived from Leu et al. (2010a):

$$[1]\ f = \frac{8v(14)o}{\pi hr_i hr_j}$$

259

260 where v is the mean velocity of the two lizards (average distance (m) travelled/day), o is the

261 area of home range overlap between the two lizards, and hr_i and hr_j are the home range areas

262 of individual i and individual j, respectively. We used the estimated f as encounter rates to

263 determine edge weights in random association networks, developed separately for each year.

264 We compared the mean degree (K = mean number of other individuals each individual is

265 connected to in the network) in the observed networks and the random association networks

266 in each year, using a two-sample randomisation test.

267

268 *Effect on social structure: Comparing social network structure among years*

269 We defined network stability as lack of change and analysed the stability of the networks

270 among years in four ways. First, we examined the stability of the network as a whole, by

271 estimating network density, a parameter which integrates both the number and weighting of

272 associations (Table 1). Our analyses compared network density between pairs of networks in

273 three combinations of the three years. Each analysis was a paired samples t-test, using

274 bootstrapping with 10,000 permutations (Snijders & Borgatti 1999) in UCINET 6.343

275 (Borgatti et al. 2002).

276   Second, we determined the stability of associations in the network by testing for

277 correlations between associations among lizards (relative to each other) across years. For

278 each pair of years we conducted a Mantel test (Mantel 1967), which calculated the correlation

279 between each pair of social network matrices, using 10,000 permutations in PopTools for

280 Excel (Hood 2010). We first examined associations using all individuals, and then separately

281 we looked at the stability of male-male associations, female-female associations, and male-

282 female associations.

283   Third, we examined year to year variation in the mean degree, strength, clustering

284 coefficient and mean edge weight (including all edges, and excluding pair bonds) (defined in

285   Table 1) of individual nodes in the network. These parameters describe the connections of

286   nodes to the rest of the network. To describe the structure of the network in each year, we

287   calculated the average for each of the network parameters in each network. We then

288   compared each pair of networks over the three years, using a two-sample randomisation test

289   with 10,000 permutations. For comparisons of mean degree (the number of connections an

290   individual has in the network (Table 1)), we ran the analyses first on unfiltered networks, and

291   then on networks where edges were only allowed where pairs of lizards had an SRI greater

292   than 0.001 (they spent $> 0.1\%$ of their active time together), an SRI greater than 0.01 (they

293   spent $> 1\%$ of their active time together), and an SRI greater than 0.1 (they spent $> 10\%$ of

294   their active time together).

295   Fourth, we examined the consistency across years of intra-sexual and inter-sexual

296   associations within the networks. We defined (Table 1) and calculated intra-sexual strength

297   and inter-sexual strength separately for males and females in each year. We further

298   subdivided inter-sexual strength into the strength of the one main male-female association

299   resulting from the prolonged monogamous partnerships displayed by this lizard (pair

300   strength), and the summed strength of all other contacts with opposite sex individuals (extra-

301   pair strength) (Table 1). For each of these four parameters of network strength we compared

302   mean values among pairs of years as in previous analyses. Because pair-strength is calculated

303   as the maximum edge weight to an individual of the opposite sex, it is not necessarily equal

304   among sexes. For lizards that had no recorded partner, their pair-strength score will be

305   derived from a more brief interaction with an individual of the opposite sex, who might have

306   a different lizard as its main partner. Thus, males and females can have unreciprocated pair-

307   strength scores. For all of these analyses we focussed on network properties of individuals

308   within the network, rather than overall network parameters such as small-world-ness

309   (Humphries & Gurney 2008) for which we would only have had a single measure for each

310 year, and, without spatial replication, no rigorous comparative test. We recognise that our

311 parameter estimates will be subject to errors, resulting from differences in numbers of

312 locations per individual, from exclusion of interactions between individuals on the edges of

313 our study site and adjacent untagged individuals, and inclusion of non-contacts in the

314 derivation of weighted edges (James et al. 2009). However, those biases would have affected

315 the data similarly in each year of sampling. For each pair-wise comparison, we only analysed

316 the subset of lizards that were present in both years that were being compared.

317   We are aware that comparisons between networks of different sizes could affect

318 network metrics. Therefore, we conducted an additional set of analyses to test how varying

319 the number of lizards we sampled influenced our conclusions. We developed networks for a

320 subset of 40 individuals in each year, selected from those that were located most central to

321 the study site. Thus, networks in this comparison were constructed from the same number of

322 individuals. While this may have eliminated one possible source of bias, the smaller number

323 of nodes (individual lizards) reduced the power of the analyses. Any discrepancies between

324 these and the original analyses are highlighted in the results.

325

326 **Results**

327 *Climate and lizard body condition*

328 The three years of the study were characterised by substantially different climatic conditions.

329 Rainfall was lowest (and below average) in 2008, and highest (and above average) in 2010

330 (Fig. 1a). Mean maximum temperature varied among years, being lowest in 2010, and highest

331 in 2009 (Fig. 1b). Lizard body condition varied significantly among years ($F_{2, 58} = 39.12$, $P <$

332 0.001), with lowest values in 2008, the year of lowest rainfall (Fig. 1c).

333

334 *Effect on behaviour: Comparing home range and activity patterns among years*

335 Mean home range area for the 30 lizards common to all three years did not vary significantly

336 among years ($F_{2,56} = 2.08$, $P = 0.133$, Fig. 2a). Sex influenced home range area ($F_{1,28} = 6.30$,

337 $P = 0.018$), with males having larger home ranges (7.81 ha ± 0.55 SE) than females (5.82 ha

338 ± 0.48 SE), but there was no significant interaction between lizard sex and year ($F_{2,56} = 0.14$,

339 $P = 0.868$). Conditions in each year affected each sex equally. The extent of home range

340 overlap was significantly higher in 2008, than in either 2009 (two-sample randomisation test:

341 $\Delta Mn = 0.86$, $\Delta Mn_{(rand)} = 0.18$ (0.007 – 0.491, 95% CI), $P < 0.0001$) or 2010 ($\Delta Mn = 0.72$,

342 $\Delta Mn_{(rand)} = 0.17$ (0.006 – 0.457, 95% CI), $P = 0.0002$) (Fig. 2a). There was no difference in

343 home range overlap between 2009 and 2010 ($\Delta Mn = 0.14$, $\Delta Mn_{(rand)} = 0.11$ (0.004 – 0.307,

344 95% CI), $P = 0.3179$).

345   The mean percentage of time lizards spent active varied significantly among years ($F_{2, 56} = 60.51$, $P < 0.001$), with lizards spending less time active in 2008 than 2009, and less time

346 active in 2009 than 2010 (Fig. 2b). However, the mean number of steps taken by lizards

347 active in 2009 than 2010 (Fig. 2b). However, the mean number of steps taken by lizards

348 while they were active was similar among years ($F_{2, 56} = 0.14$, $P = 0.714$) (Fig. 2b). That is,

349 lizards moved at the same 'speed' when they were active, but varied in the amount of time

350 they were active among years. Specifically, as annual rainfall increased so did the amount of

351 time that lizards were active.

352

353 *Social networks vs random association networks*

354 The mean degree (K) was significantly lower in the observed social network than in the

355 random association network for all years (2008: $K_{obs} = 9.90 \pm 0.78$ SE, $K_{rand} = 20.16 \pm 0.93$

356 SE, mean diff. $= 10.26$ (0.07 – 3.83, 95% CI), $P < 0.0001$; 2009: $K_{obs} = 8.23 \pm 0.59$ SE, K_{rand}

357 $= 15.07 \pm 0.84$ SE, mean diff. $= 6.84$ (0.04 – 2.29, 95% CI), $P < 0.0001$; 2010: $K_{obs} = 6.78 \pm$

358 0.39 SE, $K_{rand} = 17.23 \pm 0.81$ SE, mean diff. $= 10.45$ (0.05 – 3.28, 95% CI), $P < 0.0001$).

359 Thus, lizards normally associated with less than half of the individuals they would be

360   expected to contact by chance, and this avoidance of conspecifics was consistent across

361   years.

362

363   *Effect on social structure: Comparing social network structure among years*

364   *Network density and Mantel tests of association*

365   Paired t-tests showed no significant difference in network density in any pair-wise

366   comparison of networks among years (Table 2). The network matrices were strongly and

367   significantly correlated, and thus consistent, across all pairs of years (Table 3). Male-female

368   associations remained significantly correlated among all years, reflecting the stability of

369   pairing associations (Table 3). However, male-male associations were only significantly

370   correlated between 2009 and 2010 (the two wetter years), and not significantly correlated

371   between 2008 (the dry year) and either of the two wetter years (Table 3). Female-female

372   associations were significantly correlated between adjacent years (that did not differ as much

373   in rainfall), but not significantly correlated between 2008 and 2010 (Table 3).

374

375   *Degree, strength, clustering coefficient and mean edge weight*

376   Measures of mean degree diminished as the SRI based filter was increased, as expected. The

377   patterns of differences among years varied according to the level of filtering. With no filters

378   or with edges recognised if encounters occurred at a frequency of greater than 0.001, there

379   were no significant differences in degree among years ($P > 0.05$). In both of the more heavily

380   filtered social networks, the mean degree in 2008 differed significantly from 2009 (Table 4,

381   SRI > 0.01: difference in means = 1.48 (0 – 1.36, 95% CI), $P = 0.0114$), and for SRI > 0.1, it

382   also differed from 2010 (Table 4). After correcting for differences in sample size between

383   years, the result for SRI > 0.01 was no longer significant ($P > 0.05$).With the filter set at

384   SRI> 0.1, the network in 2008 retained a lower mean degree (0.22 ± 0.08 SE) than in the

385   other two years (2009: 0.67 ± 0.09 SE; 2010: 0.78 ± 0.11 SE) after correcting for differences

386   in sample size (Table 4).

387   Mean strength did not differ significantly between 2009 and 2010, but was

388   significantly lower in 2008 than 2009 and 2010 (Table 4, Fig. 3a). The clustering coefficient

389   was not significantly different among years (Table 4; Fig. 3b). Both measures of mean edge

390   weight varied significantly among years (Table 4). Mean edge weight when all edges were

391   considered (including pair bonds) was significantly lower in 2008 than both 2009 and 2010

392   (Table 4, Fig. 3c). In contrast, mean edge weight when pair bonds were excluded ($0 < SRI <$

393   0.1) was significantly higher in 2008 than 2009, but only marginally higher than 2010 (Table

394   4, Fig. 3c). Strength, clustering coefficient and mean edge weight results were robust when

395   analysed on subsets of networks of the same size.

396

397   *Intra-sexual and inter-sexual associations*

398   In all years, and for both sexes, male-female intersexual interactions had higher network

399   strength than intrasexual interactions (Fig. 4). Indeed, in wet years (2009 and 2010), far and

400   away the strongest interaction was between the male and female in a primary pair (Fig. 5a).

401   In the dry year, 2008, the interaction strengths of the primary pairs were substantially and

402   significantly lower than in the wet years (Table 5, Fig. 5a). As a result, the overall strength of

403   intersexual interactions was also significantly lower in 2008 than in the other years (Table 5,

404   Fig. 4b). In contrast, the strengths of interaction among males and among females (Fig. 4a),

405   and between extra-pair males and females (Fig. 5b) were either not significantly different

406   among years, or for male extra-pair interactions with females, were even stronger in 2008

407   than in 2009 (Table 5).

408

409   **Discussion**

410   Our study covered three years with substantially different rainfall patterns. Those climatic

411   differences generated significant variation in lizard behaviour, but the basic social network

412   structure was retained. Overlaid upon this underlying stability however, were changes from

413   year to year in the nature of the associations among individual lizards. The influence of

414   changing ecological conditions on these patterns is discussed below.

415

416   *Behavioural effects*

417   Previous studies of this system have reported that, within a year, lizard activity is stimulated

418   by spring rainfall (Kerr et al. 2008), and in years of low rainfall, when spring growth of

419   annual plants is reduced, there are earlier declines in feeding opportunities, and many lizards

420   choose to reduce foraging time, presumably to conserve energy (Kerr & Bull 2006b). Our

421   observations in the current study reflected those trends. In 2008, a year of exceptionally low

422   rainfall, lizards achieved significantly lower body condition and spent less time active than in

423   2009 and 2010. Although home range size remained the same across the three years, the

424   extent of home range overlap was significantly greater in the drier year. This suggests that

425   lizards were aggregating more, perhaps around a few sites where some soil moisture allowed

426   persistence of their food plants, or perhaps more frequently using a few deeper and cooler

427   refuges to reduce metabolic costs and water loss (Kerr & Bull 2006c).

428

429   *Social network effect*

430   Despite significant changes in body condition, activity levels, and space use patterns across

431   the three years, the basic social network structure remained intact. The overall network

432   density, which is defined by the number and weighting of edges as a proportion of the total

433   possible edges, remained unchanged, and networks were correlated across years, with lizards

434   generally remained in the same network positions relative to each other from year to year.

18

435   Similarly, the clustering coefficient and the mean degree in all but the most heavily filtered

436   networks (SRI > 0.1) did not vary among years. Note that the consistent structure from year

437   to year is not simply a result of lizards retaining the same spatial organisation (reported

438   previously by Bull & Freake (1999)). Random association networks had a higher mean

439   degree than observed social networks for all years, reflecting an apparently deliberate

440   avoidance by individual lizards of more than half of their close neighbours. This was also

441   observed by Leu et al. (2010a) in a smaller group of sleepy lizards in a one year study. The

442   current study suggests that the active choice of which neighbours to associate with, and

443   which neighbours to avoid was retained over our three year study.

444   Within this overall stability of network structure, there was inter-annual variation in

445   the types of interactions, and their strength. In particular, strong linkages between lizards

446   were less prevalent in the dry year of 2008, despite the increased overlap among home ranges

447   (and consequently, increased opportunities for contact among lizards) in that year, and

448   despite the fact that rarer rainfall events might have increased the synchronisation of activity

449   patterns in that year. Thus mean strength of nodes and mean edge weights (when pair bonds

450   were included) within the network were significantly lower in the dry year, and most of that

451   decrease resulted from the reduced strength of male-female associations. Excluding pair-

452   bonds revealed that the mean weight of all other edges was significantly higher in 2008 than

453   in the other two years, suggesting that other forms of contact were higher in the drier year.

454   For networks derived from SRI > 0.1 (only considering links when pairs of lizards were in

455   contact for more than 10% of active observations), mean degree, defined as the number of

456   links from each lizard to other lizards, was significantly lower in 2008.

457   Although male-female associations were strongly correlated among years (that is, the

458   same individuals interacted with each other in each year), the intensity of these associations

459   was lower in the dry year. Lizards invested less time in pairing in that year, with a

significantly lower intersexual-strength and pair-strength in 2008. We suspect that, in these

long-lived lizards, females can forgo reproduction in dry years. They can choose to spend less

time with their monogamous partner during the spring of years when there are inadequate

food resources to provide nutrients for successful embryonic development (Bull et al. 1993;

Bull & Burzacott 2002; Kerr & Bull 2006b). In the current study, males and females showed

a similar trend, although females displayed a more marked change in inter-sexual

associations between years than males. In the driest year, males appeared to compensate for

lower pairing strength by associating with more females outside the pair-bond. We have

previously suggested that female lizards control the prolonged male-female partnerships

before mating in late spring (Bull & Pamula 1998). If, in dry years, females are less likely to

be reproductive, that control may be reduced and males might seek alternative females more

frequently.

Although the overall strength of male-male interactions remained consistent across

the three years, the position of males in the network relative to each other differed between

2008 and the other two years. We cannot explain this response without more detailed

observations of how males interact with each other, but we note that it suggests that changes

in climate can have some subtle impacts on overall network structure. Female-female

interactions remained stable over the study period.

Our major aim was not to attribute changes in network structure to specific climatic

conditions. Instead we asked whether networks retained their structure over ecologically

variable conditions. Although all changes we detected were apparent responses to the very

dry year in 2008 our study was inadequately replicated to make rigorous conclusions. There

were also substantial climatic changes in both rainfall and mean temperature between 2009

and 2010, but in each of those years rainfall was sufficient to provide adequate germination

and growth of the annual plants that the lizards feed on, and to promote normal behaviour

485 patterns in lizards, with few differences in any of the parameters we measured. Dry years

486 with low food supplies may be the trigger for major behavioural shifts in this species. But

487 despite the more subtle changes in network structure that we have discussed above, the

488 overall structure remained remarkably stable over a range of climatic conditions that

489 generated contrasting ecological challenges.

490   What can explain the broad persistence of this network structure? Perhaps the main

491 reason is the inherent stability resulting from high longevity and low mortality of adult lizards

492 (Bull 1995). When this is coupled with long-term stability of home range occupancy (Bull &

493 Freake 1999), it results in generally stable spatial organisation in these lizard populations, and

494 that would allow time for individuals to become familiar with their neighbours and to learn

495 who to associate with. Associations might involve sharing patches of food or shelter sites

496 with compatible individuals, while lizards may avoid aggressive neighbours (Kerr & Bull

497 2002; Godfrey et al. 2012). A mechanism to avoid neighbours may be through the detection

498 and response to conspecific chemical trails (Bull et al. 1993; Bull & Lindle 2002).

499 Advantages of a stable social network could be reduced stress from fewer (potentially

500 aggressive) encounters with unfamiliar individuals, and more reliable and uncontested access

501 to resources. Although the mechanisms behind this apparent network stability are still

502 unclear, our current study is among the first to report social network stability across changing

503 ecological conditions, and lays a foundation for future probing of social structures in species

504 that do not form natural aggregations.

505

506 **Acknowledgements**

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677   **Table 1** – Definitions of the network metrics used in this study.

678

Term	Definition
Density	The sum of edge weights in the network, divided by the number of possible edges (Hanneman & Riddle 2005).
Degree	Number of connections an individual has in the network (Freeman 1977).
Strength	Sum of edge weights connected to an individual in the network (Newman 2004).
Clustering coefficient	An index that measures the proportion of an individual's neighbours that are also connected to each other, and the weighting of those connections. Calculated in R using the weighted local clustering function in tnet (Opsahl & Panzarasa 2009).
Mean edge weight (all edges)	Average of edge weights connected to an individual in the network, for edges SRI > 0
Mean edge weight (edges SRI < 0.1)	Average of edge weights connected to an individual in the network, excluding pair bonds (0 < SRI < 0.1)
Intra-sexual strength	Sum of edge weights connected to an individual of the same sex
Inter-sexual strength	Sum of edge weights connected to an individual of the opposite sex
Pair strength	Maximum edge weight to an individual of the opposite sex
Extra-pair strength	Sum of edge weights connected to individuals of the opposite sex, excluding the main pair bond (maximum edge weight)

679
680
681

682   **Table 2** – Paired samples t-test, comparing the density of networks (sum of edge weights in

683   the network, divided by the number of possible ties) between years, using bootstrapping with

684   10 000 permutations in UCINET 6.343. *N* is the number of individuals compared in the test

685   (ie, number of lizards present in the network in both years), Δ Density is the difference in

686   density between years, Δ Density SE_{BS} is the bootstrapped standard error of the difference in

687   density between years. P-values were corrected for multiple comparisons using the

688   Bonferroni correction.

689

Pair of years	*N*	Δ **Density**	Δ **Density SE_{BS}**	95% CI	*P*
2008 – 2009	31	-0.003	0.002	-0.007 - 0.007	0.2937
2009 – 2010	41	0.0009	0.001	-0.001 - 0.002	1.0000
2008 – 2010	28	-0.002	0.002	-0.006 - 0.001	0.5142

690 **Table 3 –** Results from Mantel tests, testing correlations between the position of individuals

691 in the network, relative to each other, among pair-wise combination of years, using 10 000

692 permutations in PopTools for Excel (Hood 2010). P-values were corrected for multiple

693 comparisons using the Bonferroni correction, and p-values in bold are significant ($P < 0.05$).

694

Overall	r	$r_{(rand)}$	95% CI	P
2008 - 2009	0.331	0.000	-0.040 - 0.120	**0.0036**
2009 - 2010	0.789	-0.001	-0.021 - 0.109	**0.0003**
2008 - 2010	0.295	0.000	-0.045 - 0.147	**0.0015**
Male-male associations				
2008 - 2009	0.072	0.000	-0.106 - 0.200	0.4983
2009 - 2010	0.529	-0.001	-0.082 - 0.165	**0.0003**
2008 - 2010	0.246	0.000	-0.091 - 0.227	0.0612
Female-female associations				
2008 - 2009	0.627	0.001	-0.097 - 0.471	**0.0069**
2009 - 2010	0.401	0.000	-0.060 - 0.238	**0.0057**
2008 - 2010	0.001	0.000	-0.083 - 0.539	0.6888
Male-female associations				
2008 - 2009	0.511	0.000	-0.129 - 0.139	**0.0003**
2009 - 2010	0.675	-0.001	-0.094 - 0.098	**0.0003**
2008 - 2010	0.462	0.000	-0.142 - 0.152	**0.0003**

695

696

698 **Table 4** – Results from two-sample randomisation tests, comparing the mean degree (for

699 edges with SRI > 0.1), mean strength, clustering coefficient and mean edge weight

700 (considering all edges, and excluding pairing associations (SRI > 0.1) of individuals in the

701 network between each pair-wise combination of years. P-values were corrected for multiple

702 comparisons using the Bonferroni correction, and p-values in bold are significant (P < 0.05).

Degree (SRI > 0.1)	Difference in means	95% Confidence Intervals	*P*
2008 - 2009	0.387	0.000 - 0.258	**0.0120**
2009 - 2010	0.119	0.024 - 0.214	1.0000
2008 - 2010	0.500	0.000 - 0.357	**0.0084**
Strength			
2008 - 2009	0.111	0.001 - 0.097	**0.0249**
2009 - 2010	0.027	0.001 - 0.065	1.0000
2008 - 2010	0.124	0.001 - 0.089	**0.0033**
Clustering coefficient			
2008 - 2009	0.018	0.001 - 0.095	1.0000
2009 - 2010	0.018	0.001 - 0.068	1.0000
2008 - 2010	0.075	0.001 - 0.081	0.1215
Mean edge weight (all edges)			
2008 - 2009	0.014	0 – 0.012	**0.0180**
2009 - 2010	0.012	0 – 0.012	0.0537
2008 - 2010	0.009	0 – 0.008	**0.0336**
Mean edge weight (edges SRI < 0.1)			
2008 - 2009	0.006	0 – 0.003	**0.0003**
2009 - 2010	0.000	0 – 0.002	1.0000
2008 - 2010	0.012	0 – 0.012	0.0537

703

704 **Table 5 –** Results of two-sample randomisation tests comparing the intrasexual and

705 intersexual associations among individuals in the networks, between pair-wise combinations

706 of years, using 10 000 permutations. P-values were corrected for multiple comparisons using

707 the Bonferroni correction, and p-values in bold are significant (P < 0.05). [NS] P-values became

708 non-significant in comparisons of subset networks of equal size and after Bonferroni

709 correction. *P-values were originally non-significant, but became significant in comparisons

710 of subset networks of equal size and after Bonferroni correction.

Intrasexual strength	Males			Females		
	Δ Means	95% CI	*P*	Δ Means	95% CI	*P*
2008 – 2009	0.029	0.001 - 0.033	0.1866	0.035	0.000 - 0.038	0.1974[*]
2009 – 2010	0.012	0.000 - 0.016	0.3288	0.021	0.020 - 0.045	1.0000
2008 – 2010	0.034	0.000 - 0.027	**0.0024**[NS]	0.014	0.001 - 0.044	1.0000
Intersexual strength						
2008 – 2009	0.091	0.002 - 0.104	0.1644	0.250	0.003 - 0.201	**0.0003**
2009 – 2010	0.019	0.001 - 0.078	1.0000	0.046	0.001 - 0.090	0.8802
2008 – 2010	0.115	0.001 - 0.100	**0.0234**	0.215	0.003 - 0.187	**0.0207**
Pair strength						
2008 – 2009	0.116	0.002 - 0.102	**0.0249**	0.251	0.002 - 0.197	**0.0003**
2009 – 2010	0.009	0.001 - 0.073	1.0000	0.047	0.001 - 0.094	0.8790
2008 – 2010	0.108	0.001 - 0.087	**0.0075**	0.217	0.002 - 0.200	**0.0330**
Extra-pair strength						
2008 – 2009	0.041	0.001 - 0.037	**0.0231**	0.033	0.001 - 0.056	0.7281
2009 – 2010	0.013	0.000 - 0.020	0.5349[*]	0.002	0.000 - 0.018	1.0000
2008 – 2010	0.024	0.001 - 0.042	0.8691	0.029	0.001 - 0.062	1.0000

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Figures

Figure 1 – (a) Annual rainfall at the study site (mm), (b) the mean daily maximum
temperature ($^{\circ}$C $\pm$ 1 SE) during the observation period, and (c) the mean condition of lizards
in each year.

Figure 2 – (a) The mean extent of home range overlap among lizard home ranges (grey bars,
left y-axis), and the mean home range size of lizards among years (lines, right y-axis) and (b)
the mean percentage of time lizards were active (grey bars, left y-axis), and the mean number
of steps taken per 2 minutes when lizards were active (lines, right y-axis) among years.

Figure 3 – Variation in (a) mean strength, (b) clustering coefficient, and (c) mean edge
weight, for all edges (grey bars) and excluding pair bonds (SRI > 0.1) (white bars), of sleepy
lizard social networks among years.

Figure 4 – Variation in (a) mean intra-sexual strength and (b) mean inter-sexual strength,
among years, for males (white bars) and females (grey bars). Note the different scales on the
y-axes.

Figure 5 – Variation in (a) mean pair strength, and (b) mean extra-pair strength, among years,
for males (white bars) and females (grey bars). Note the different scales on the y-axes.
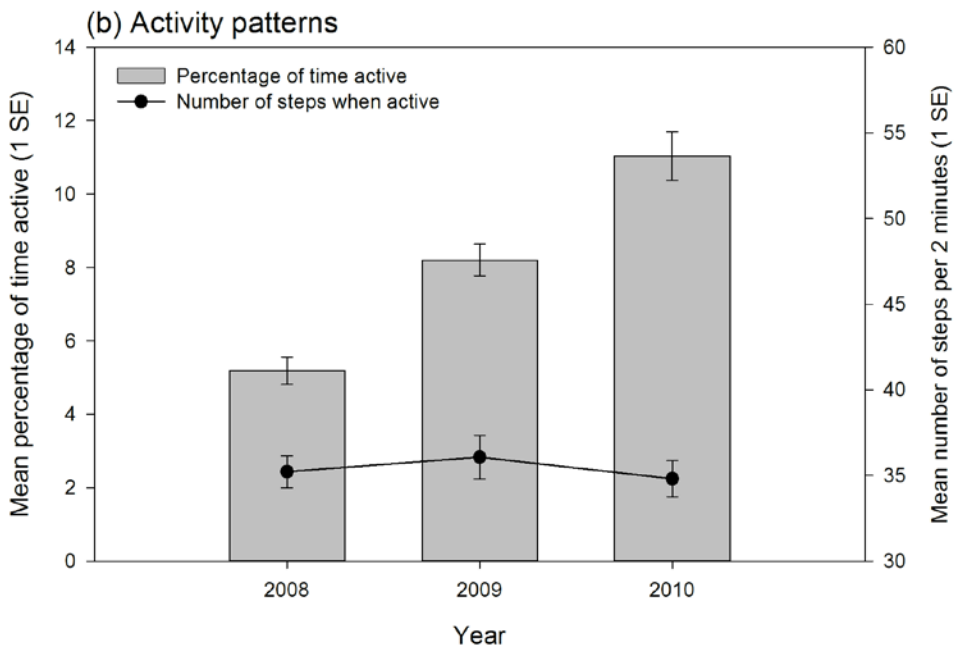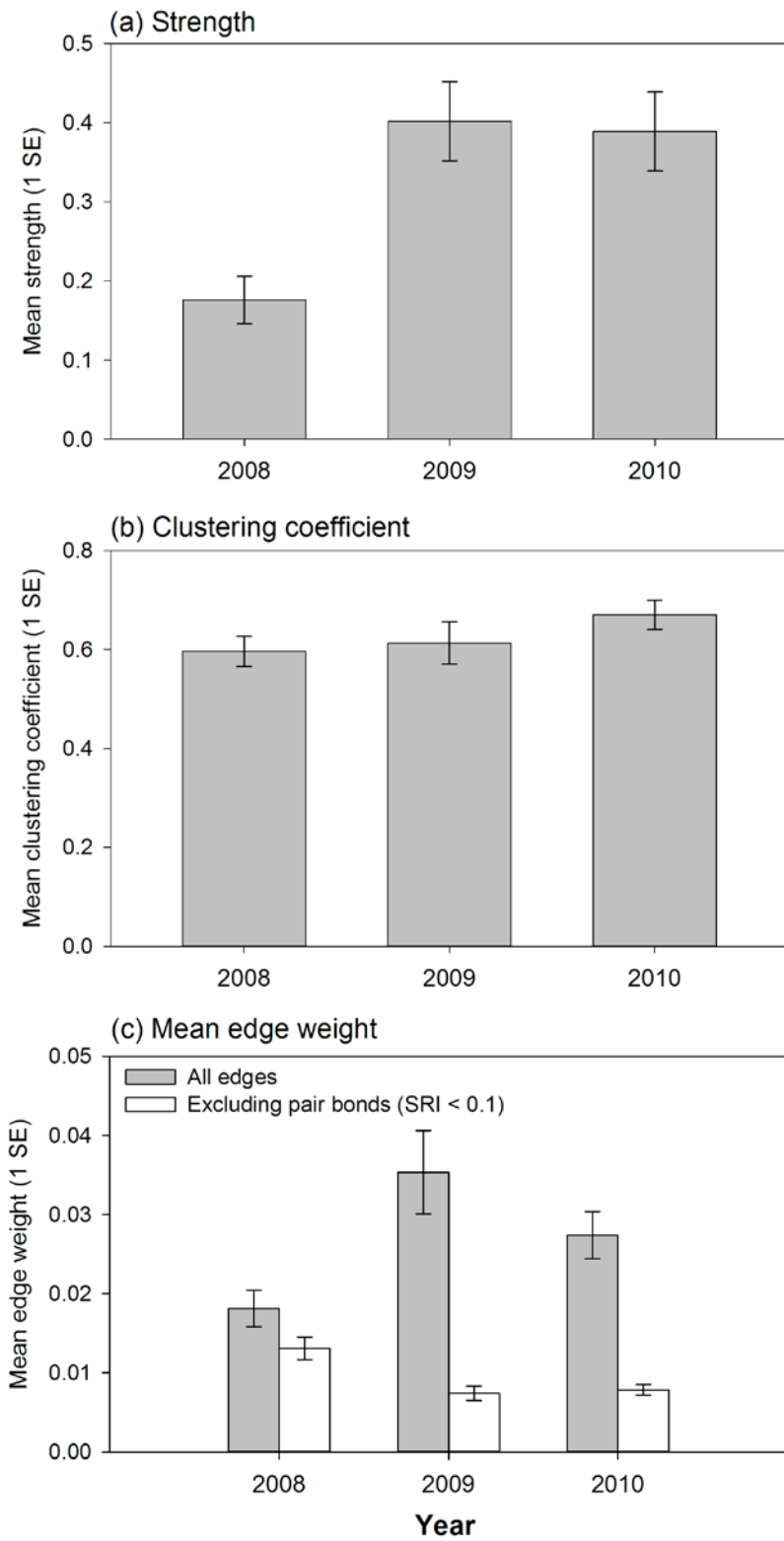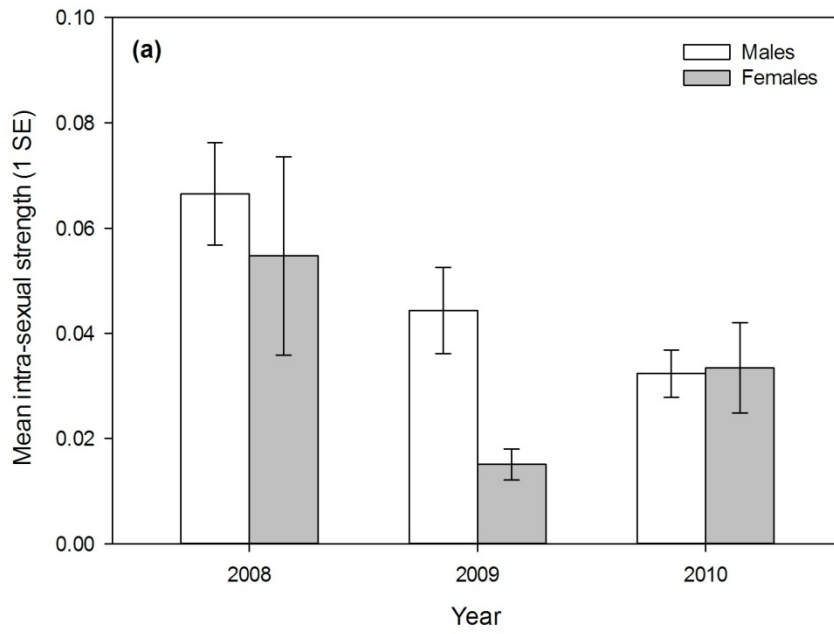
734   **Figure 1**

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738 **Figure 2**

(a) Home ranges

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(b) Activity patterns
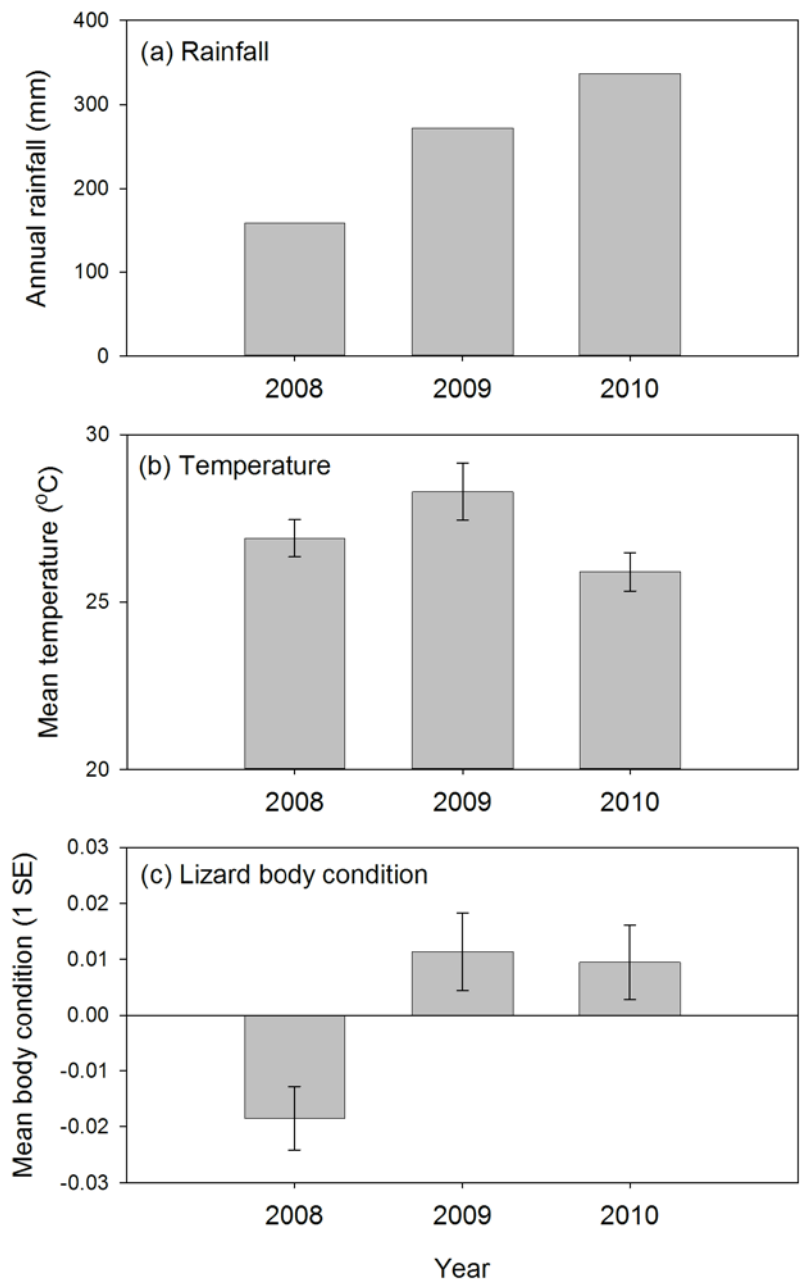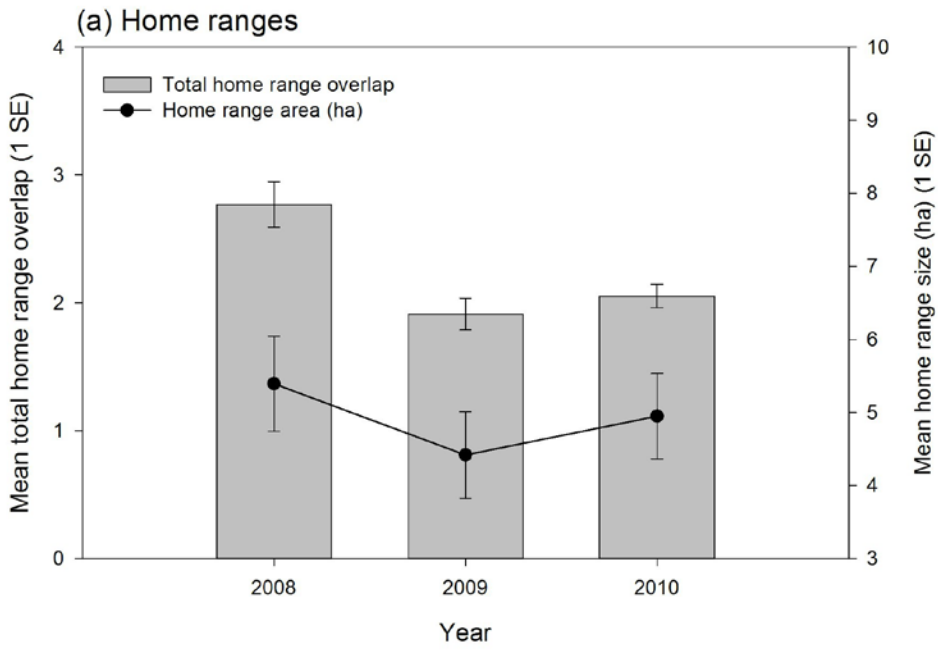
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741   **Figure 3**

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Figure 4

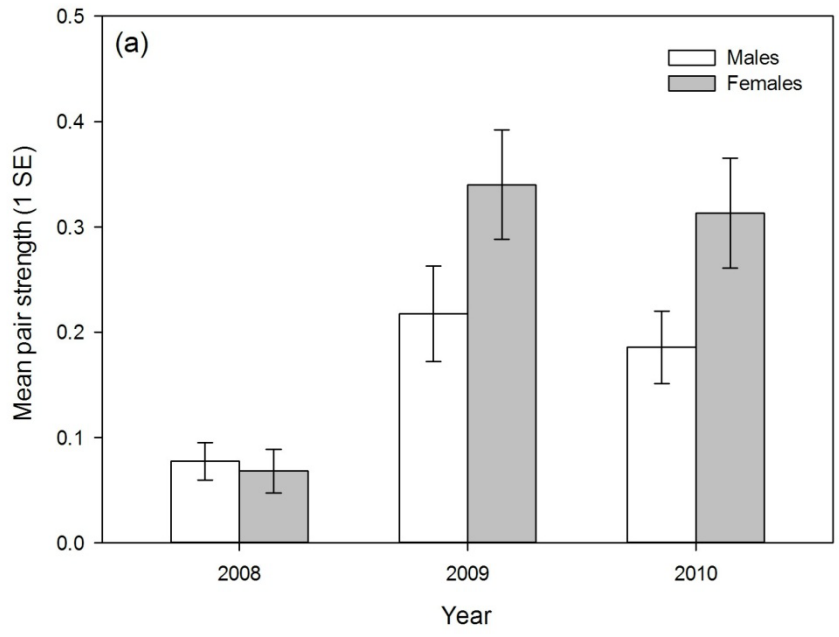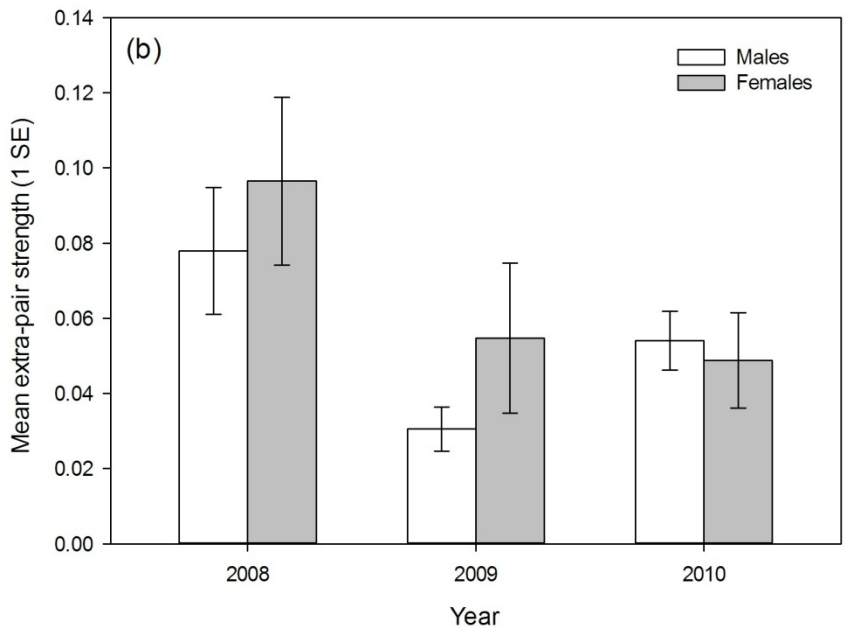751 **Figure 5**

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