A test of desert shrub facilitation via radiotelemetric monitoring of a diurnal lizard

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2   **A test of desert shrub facilitation via radiotelemetric monitoring of a diurnal lizard**

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12   **Summary**

13   1.   Preservation of desert ecosystems is a worldwide conservation priority. Shrubs can play a key

14   role in the structure of desert communities, and can function as foundation species.

15   Understanding desert shrub ecology is therefore an important task in desert conservation. A

16   useful model for the function of shrubs in deserts is ecological facilitation, which explores

17   benefits that shrubs confer on their community. Facilitation has been well developed in the

18   context of shrub-plant interactions but less well studied for plant-animal interactions.

19   2.   We used radiotelemetry to test the hypothesis that a dominant desert shrub facilitates one species

20   of diurnal lizard. We hypothesized that the blunt-nosed leopard lizard *Gambelia sila* would spend

21   some part of its daily activity cycle associated with California jointfir *Ephedra californica*, and

22   that lizard association with shrubs would increase during the afternoon peak temperature period.

23   We relocated lizards three times daily for 24 days and scored whether lizards were within 0.5

24   meters of a shrub, which we used as an indicator of shrub association. For each relocation we also

25   scored lizard association with a set of predefined microhabitat features. We also scored lizard

26   behavior according to a set of predefined behavioral traits. We constructed home ranges

27   following the minimum convex polygon method and generated estimates of shrub density and

28   relative shrub area within each home range polygon.

29   3.   We obtained 1190 datapoints from a sample of 27 lizards. We found that lizards were associated

30   with open sites significantly more often than with shrubs but were associated with shrubs more

31   than predicted by percent shrub area within their home ranges. Lizards were associated

32   significantly more often under shrubs during the afternoon peak temperature period, and lizards

33   were observed cooling under shrubs significantly more often. The frequency of association of

34   individual lizards with shrubs was not correlated with the density of shrubs within their home

35   range.

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36   4. *Synthesis and Applications*. Shrubs can be considered as a component of high-quality habitat for

37   ectothermic desert vertebrates for the purposes of restoration and management. Furthermore,

38   radiotelemetry provides a novel methodological approach for assessing shrub-animal facilitative

39   interactions within desert communities.

40   Keywords: *Gambelia sila*, *Ephedra californica*, San Joaquin Desert, plant-animal interactions,

41   endangered species, thermoregulatory behavior, ectotherm

42

43   **Introduction**

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45   Deserts are highly distinct ecosystems that contribute significantly to global biodiversity and

46   global ecosystem function. The conversion and loss of desert habitat is therefore a global biodiversity

47   crisis requiring immediate intervention, including conservation of remaining undisturbed habitat and

48   restoration of degraded desert (Hannah et al. 1995, Cook et al. 2004, Hoekstra et al. 2005, Kéfi et al.

49   2007, Mouat et al. 2008, Bachelet et al. 2016, Westphal et al. 2016). Identifying the drivers of ecological

50   health in desert communities will be a crucial component of such interventions. Shrubs can maintain the

51   diversity of desert plant communities (Flores & Jurado 2003) and are predicted to play significant roles in

52   the thermal ecology of desert ectotherms (Sears et al 2016, Basson et al. 2017). Shrubs can also facilitate

53   ectotherm populations in the face of climate change (Adolph 1990, Kearney, Shine and Porter 2009,

54   Sinervo et al 2010, Sears and Angilletta 2015, Sears et al 2016).

55   Ecological facilitation theory provides a roadmap for describing and predicting the beneficial

56   interactions of shrubs with other organisms within their communities (Bruno et al. 2003, Mcintire &

57   Fajardo 2014, Filazzola and Lortie 2014, Bulleri et al 2016, Filazzola et al. 2017). Using facilitation

58   theory, Filazzola et al (2017) extended the exploration of the beneficial interactions between desert shrubs

59   and vertebrates, and found that one species of shrub provided facilitative benefits to a target species of

60   lizard. We sought to confirm and add depth to their findings using radiotelemetry tracking of the same

61   target species. . Radio telemetry is a well-tested and powerful tool that allows the longitudinal tracking

62   of individual animals throughout their daily behavioral cycles (McGowan et al 2017) and enables the

63   direct observation of habitat interactions and behaviors. We used radio telemetry study to test and refine

64   our understanding of the beneficial interaction of shrubs with lizards. To our knowledge, incorporating

65   radiotelemetry into a facilitation study is a novel use of the method.

66   We sought to test the hypothesis that shrubs facilitated lizards by providing thermoregulatory

67   opportunity. We predicted that lizards would associate with shrubs for a meaningful proportion of their

68   daily activity cycle; that shrub association would increase in the afternoon when daytime temperatures

69   peak (Filazzola, Sotomayor, and Lortie, 2017); and that lizard association with shrubs would be

70   correlated with thermoregulatory behaviors. The results of our study confirm the application of

71   radiotelemetry to ecological facilitation studies and the application of such studies to the description of

72   beneficial interactions between shrubs and vertebrate ectotherms.

73   **Materials and Methods**

74   *Study site*.-- The study was conducted on the Elkhorn Plain within Carrizo Plain National

75   Monument (San Luis Obispo County, California, USA, 35.1914° N, 119.7929° W) (Fig, 1) within the San

76   Joaquin Desert ecosystem (Germano et al 2011). Average annual precipitation within the Monument

77   ranges from 15 cm in the southeast to 25 cm in the northwest (Hijmans et al. 2005). The Elkhorn Plain is

78   located within the Monument on an elevated plain separated from the main valley floor of the Carrizo

79   Plain by the San Andreas Fault (Germano et al. 1994). The area has been heavily invaded by non-native

80   annual grasses including *Bromus madritensis, Erodium cicutarium*, and *Hordeum murinum* (Schiffman

81   1994, Stout et al. 2014, Gurney et al. 2015) but still provides habitat for endemic keystone species such as

82   the giant kangaroo rat *Dipodomys ingens* (Bean et al. 2014). California jointfir, *Ephedra californica* was

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83   the dominant shrub at our study site. The blunt-nosed leopard lizard, *Gambelia sila*, was well documented

84   on the study (Germano, Smith and Tabor, 2007).

85   *Study species* .— *E. californica*, a basal gymnosperm in the Gnetophyta division, is a large, slow-

86   growing woody shrub restricted to arid environments in western North America (Sawyer, Keeler-Wolf &

87   Evens 2009). Although the genus has a worldwide distribution and is represented by over a dozen species

88   in the desert southwest of North America, *E. californica* is the only species that occurs in the San Joaquin

89   Valley, where it is locally considered rare and sensitive (Sawyer, Keeler-Wolf & Evens 2009) and has

90   been documented to be a foundation species in the San Joaquin desert community (Hawbecker 1951,

91   Lortie et al. 2017, Lortie, Filazzola & Westphal 2017). *Gambelia sila* is a state and federally listed

92   endangered species endemic to the San Joaquin Valley and restricted to San Joaquin Desert habitat

93   (Germano & Williams 1992, U.S. Fish and Wildlife Service 1998, Warrick, Kato, & Rose 1998,

94   Germano et al. 2011, Germano & Rathbun 2016). *Gambelia sila* are diurnal and mainly insectivorous

95   though they may eat smaller lizard species on occasion (Warrick et al. 1998, Germano, Smith & Tabor,

96   2007). Though *G. sila* can bury themselves and will occasionally dig primitive burrows, they mostly

97   utilize abandoned burrows of other animals such as *D. ingens* (Fields, Coffin & Gosz 1999, Prugh et al.

98   2012). Adult *G. sila* are inactive in burrows for much of the year, emerging only from late March or April

99   through July (U.S. Fish and Wildlife Service 1998, Warrick, Kato, & Rose 1998, Germano et al. 2016).

100   During the active season, *G. sila* will also spend the night underground in burrows and may return to a

101   burrow during the day if the temperature becomes too hot or cold (Warrick, Kato, and Rose 1998,

102   Germano and Rathbun 2016).

103   *Experimental design*.-- *Gambelia sila* individuals were located during foot and vehicle surveys

104   and captured using a pole and noose. Individuals were collared following the method of Germano &

105   Rathbun (2016). VHF radio transmitters (Holohil model BD-2, frequency 151-152 MHz, battery life 8-16

106   weeks, Holohil Systems Ltd., Carp, ON, Canada) were attached to a small beaded chain collar using

107   jewelry wire and epoxy, and the collars were then fastened around the lizard's neck. *Gambelia sila* were

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108   kept overnight to ensure the collar was fitted correctly and did not irritate or harm the animal, and then

109   were then released at their capture site. Collars weighed 1.6-2.2 grams (depending on the size of chain

110   needed for the lizard's neck), and we ensured that the weight of the collar did not exceed between 5% and

111   10% of the body mass of the individual.

112   In the first two days following release, all captured *G. sila* individuals were relocated (i.e.

113   repeatedly sighted using radio telemetry) several times between to ensure that the lizards were

114   successfully adjusting to the collars and that impacts to their behavior and survival were minimal. We

115   looked for any negative effects the collar had on the lizards, such as impacts on movement or any other

116   deviation from normal lizard behaviors. *Gambelia sila* were then formally surveyed for 24 consecutive

117   days. Surveys were conducted on each lizard 3 times a day. Two of these daily surveys were conducted

118   during daylight hours, when lizards were typically active above ground. One survey was conducted before

119   noon and one was conducted after noon. The third survey was conducted during the night when lizards

120   are inactive below ground. The 'night survey' was conducted before 7:30 AM or after 7:30 PM on each

121   day.

122   *Gambelia sila* were relocated using a 3-element Yagi antenna and Model R-100 telemetry

123   receiver (Communications Specialists, Inc., Orange, CA, USA). Once found, a location was taken for

124   each lizard using a Garmin 64st GPS unit (Garmin Ltd., Olathe, KS, USA) and a laser range-finder

125   (Bushnell Outdoor Products, Overland Park, KS, USA). Habitat was categorized as whether a lizard was

126   within 0.5 meters of a shrub (shrub) or not (open) (henceforth, the "shrub association zone"), and

127   behavior was scored from a suite of predetermined behavioral syndromes (Table S1). Disturbance from

128   the observer to the lizard was kept to a minimum for each observation to avoid influencing behavior and

129   habitat selection.   At the completion of the study all collars were removed from the lizards.

130   *Analyses*.-- Analyses were conducted in R (version 3.3.2). Habitat association was analyzed using

131   a generalized linear model (Bolker et al. 2009) with the multcomp package (Hothorn, Bretz & Westfall

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132   2008). Behavioral data were analyzed with a multinomial logistic regression using the nnet package that

133   accounts for the multiple levels of nominal outcomes of the observations (Venables and Ripley 2002).

134   Home range size was calculated using a 95% Minimum Convex Polygon (MCP) estimation (Mohr 1947)

135   using the adehabitatHR package (Calenge 2006). MCPs were visualized in two dimensions in R.

136   Shrub density was calculated by visually counting individual shrubs within each lizard's MCP

137   using aerial photographs (**Google Earth**, image taken December 20, 2016, accessed November 2017) and

138   dividing that number by the area in square meters of the MCP. We calculated a standardized measure of

139   shrub association zone area using on-the-ground measurements of a large number of randomly chosen

140   shrubs in the study area, from which we calculated an average radius for each shrub following the method

141   of Filazzola et al. (2017) and to which we added the 0.5m association criterion described above. We

142   calculated the area of each shrub association zone using the formula πr^2 and then took the average across

143   the sample. We multiplied this standardized shrub association zone area by the number of shrubs counted

144   in each MCP to obtain an estimate of the percent area of an MCP subsumed by shrub association zones.

145   R code used for this project can be found at https://cjlortie.github.io/Carrizo.telemetry.

146

147   **Results**

148   A total of 27 lizards were relocated more than 5 instances cumulatively either in the AM or the

149   PM across the sampling period. On a given day, the median total number of relocations was 22 with a

150   maximum of 27 and a minimum of 1 relocation. There were a total of 1190 relocations and MCPs

151   generally did not overlap (Fig 1). Mean female MCP area was 1.87 ha +/- 0.53 se. Mean male MCP area

152   was 5.14 ha +/- 2.15 se.   The difference in MCP area between males and females was not significant (Pr

153   < Chi 0.095920). Gender was initially included as a factor in all other analyses but no relevant effects

154   were significant (not reported), therefore gender was subsequently removed from the remaining analyses.

7

155   *Habitat:*-- The frequency of lizard observation differed significantly between habitat types (Fig.

156   2, Table 1, p < 0.01). Lizards were observed in the open on an average of 18.8 days and in shrubs an

157   average of 10.5 days. Shrub association frequencies of individual lizards ranged from 0 to 0.63 with a

158   mean of 0.23 +/- 0.035 se (Table S2). Observations of lizards within open habitat did not differ between

159   different times of day, but observations of lizards associating with shrubs differed significantly between

160   morning and afternoon with lizards being found more frequently at shrubs in the afternoon (Table 1, p =

161   0.0252).

162   *Behavior:*—Behavior differed significantly between habitat types (Fig. 2, Table 2, p < 0.0001).

163   Lizards were observed cooling under shrubs significantly more than other habitat types (Fig. 2, Table 2, p

164   < 0.0001). Lizards were also observed avoiding predators under shrubs more frequently than at other

165   microhabitat types (Table 3, p < 0.0001). The predators that lizards were observed avoiding in this study

166   were all aerial predators (either ravens or raptor species). Burrowing and interacting occurred

167   significantly less often under shrubs (p < 0.,0001). Other types of behavior such as sunning, hunting, or

168   active observation did not differ significantly between habitat types. Observed behavior also differed

169   significantly between different times of day e.g. lizards were more frequently observed sunning in the

170   morning in both habitat types compared to the afternoon and more often burrowing and avoiding

171   predators in the afternoon (Fig. 2, Table 2, p < 0.001).

172   *Shrub use as a function of shrub density and area.*-- Shrub use by individual lizards did not vary

173   significantly as a function of shrub density within that lizard's home range (Fig 3.) Percent of MCP areas

174   subsumed by shrub association zones ranged from 1% to 15% with an average of 5% of total surface area,

175   and frequency of shrub use by lizards was significantly higher than predicted by the percent of MCP area

176   subsumed by shrubs (Z = -4.714 from a Wilcoxon Signed ranks test, *p* < 0.001).

177

178   **Discussion**

179   Shrubs are foundation species in many ecosystems due to the facilitative benefits that they

180   provide to both plant and animal species (Filazzola & Lortie 2014, Lortie, Filazzola & Sotomayor 2015).

181   We hypothesized that *E. californica* facilitates *G. sila* by providing thermoregulatory benefits. Our

182   finding that *G. sila* was associated with *E. california* an average of 10 out of 24 days, and that individual

183   lizards were associated with shrubs more than predicted by shrub area within their home ranges, support

184   our hypothesis. Our hypothesis is also supported by the observed significant shift towards shrub

185   association in the afternoon during peak daytime temperatures. Our observation that shrub use was not

186   correlated with shrub desnity suggests that lizards are actively choosing shrubs over open habitats rather

187   than as a consequence of shrubs being more densely distributed in their home ranges. The observed

188   association of *G. sila* with shrubs is consistent with results of studies of thermoregulatory behavior of

189   lizards (Sears et al. 2016, Vickers et al 2016, Basson et al. 2017) and suggest that shrubs facilitate *G. sila*

190   by providing shade. Shrubs can buffer the extremes of multiple environmental conditions such as

191   temperature, wind, and solar radiation, creating a moderate microclimate under their canopy (Kerr et al.

192   2004, Pugnaire 2010). At the landscape scale, the presence of shrubs and their pattern of distribution (i.e.

193   clumped vs. dispersed) will affect lizard thermoregulatory behavior and can be crucial to an ectotherm's

194   thermoregulatory efficiency (Sears et al 2016, Basson et al 2017). Sources of shade are particularly

195   important for ectotherms, which must maintain body temperature through behavior (Huey 1974, Huey

196   and Slatkin 1976, Díaz and Cabezas-Díaz 2004, Kerr et al. 2004). Visual concealment from predators and

197   physical protection is also important (Fields et al. 1999, Anderson et al. 2010, Filazzola et al. 2017).

198   Shrubs may therefore provide important mechanisms of facilitation for *G. sila*. Our results suggest an

199   important mechanism (shrub restoration) for the management of desert ectotherms such as *G. sila*, and

200   provide support for radiotelemetry as a viable method for studying ecological facilitation.

201   Shrub use by *G. sila* was addressed in one previous paper that also used radiotelemetry. Germano

202   & Rathbun (2016) employed *post hoc* tests to answer the question of whether shrubs are important

203   components of *G. sila* habitat. One test depended on an assumption based on Schoepf et al 2015 that

204   home ranges were resource-based (ie shrub-limited) and would thus be smaller in the presence of high

205   quality habitat (= shrubs), while another test sought to bound the amount of shrub habitat present in

206   lizard home ranges away from a null expectation. The authors found no effect of shrubs on home range

207   size but did find more shrubs present within lizard home ranges than predicted. Our *a priori* approach (ie

208   taking direct observations of association with shrubs) provided evidence that lizards actively seek out

209   shrubs rather than randomly encountering them during their daily activity. The lack of a correlation

210   between individual shrub use and shrub density suggests that a threshold presence of shrubs may be

211   sufficient to provide thermoregulatory opportunity, therefore a strong correlation between absolute

212   number of shrubs within a home range and home range size would not be predicted. This conclusion is

213   further supported by the Germano and Rathbun's (2106) result that home ranges tended to include more

214   shrub habitat than predicted by the study-site wide prediction, i.e. it is likely beneficial that SOME shrubs

215   be available within the daily activity theater of individual lizards. Our results therefore confirm and are

216   consistent with the results from Germano & Rathbun (2016). Germano and Rathbun (2016) also provide

217   a caveat against overestimating the importance of shrubs to *G. sila* by noting that *G. sila* occurs in places

218   that lack shrubs. Given the variation that we observed in lizard shrub association within one population,

219   is not surprising that entire populations can persist in relatively shrubless areas. Although heritability of

220   thermoregulatory response in lizards is still undescribed, heritable variation in propensity to use shrubs

221   would predispose a population to adapt either to the presence of shrubs or the absence of shrubs (Logan,

222   Cox & Calsbeek 2014). More to the point, where population-scale variation exists in the predisposition to

223   use shrubs, such as we found in this study, it would be reasonable to propose that shrubs be made

224   available to those lizards that are predisposed to associated with shrubs. The net effect would be to

225   optimize the habitat available for that population. Such optimization may be crucial to impart population

226   resilience to climate change (Sinervo et al 2010, Sears et al 2016). Additionally, structured and/or

227   heterogeneous habitats are becoming increasingly recognized as important to achieve individual-scale

228   thermoregulatory optimization for lizards (Clusella-Trullas & Chown 2014, Basson et al 2016, Sears et

229   al 2016).

10

Conclusions

231   Our results document the benefits of shrubs to vertebrate ectotherms in desert communities,

232 including endangered species such as *G. sila*, thus providing guidance for land managers evaluating

233 habitat preservation and restoration designs.   We also advance methodology by demonstrating the utility

234 of combining ecological facilitation theory with radiotelemetry. It should be noted that our study was not

235 intended to test the hypothesis that *G. sila* require shrubs per se. Rather, we designed our study to ask

236 whether shrubs provide benefits to *G. sila,* and found evidence to support our hypothesis. In our view this

237 subtle divergence in focus and outcome demonstrates the power of taking an ecological facilitation

238 approach to community interactions.

Author's Contributions

240 MFW, CL and CB acquired funding for the project; MW, CJL, SB and TN conceived the study; TN and

241 MW collected the data; CL, TN and MW analysed the data; MW and TN led the writing of the

242 manuscript. Noble participated in design, fieldwork and writing. All authors contributed critically to

243 the drafts and gave final approval for publication.

Data Accessibility

245 Data are available at https://cjlortie.github.io/Carrizo.telemetry

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References

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253   Adolph, S. C. (1990) 'Influence of behavioral thermoregulation on microhabitat use by two

254   Sceloporus lizards', Ecology, pp. 315–327. doi: 10.2307/1940271.

255   Bachelet, D. et al. (2016) 'Climate change effects on southern California deserts', Journal of

256   Arid Environments, 127, pp. 17–29. doi: 10.1016/j.jaridenv.2015.10.003.

257   Basson, C. H. et al. (2017) 'Lizards paid a greater opportunity cost to thermoregulate in a less

258   heterogeneous environment', Functional Ecology, 31(4), pp. 856–865. doi:

259   10.1111/1365-2435.12795.

260   Bean, W. T. et al. (2014) 'Species distribution models of an endangered rodent offer conflicting

261   measures of habitat quality at multiple scales', Journal of Applied Ecology, 51(4), pp.

262   1116–1125. doi: 10.1111/1365-2664.12281.

263   Bolker, B. M. et al. (2009) 'Generalized linear mixed models: a practical guide for ecology and

264   evolution', Trends in ecology & evolution, 24(3), pp. 127–35. doi:

265   10.1016/j.tree.2008.10.008.

266   Bruno, J. F., Stachowicz, J. J. and Bertness, M. D. (2003) 'Inclusion of facilitation into

267   ecological theory', Trends in Ecology and Evolution, pp. 119–125. doi: 10.1016/S0169-

268   5347(02)00045-9.

269   Bulleri, F. et al. (2016) 'Facilitation and the niche: Implications for coexistence, range shifts and

270   ecosystem functioning', Functional Ecology, 30(1), pp. 70–78. doi: 10.1111/1365-

271   2435.12528.

272   Calenge, C. (2006) 'The package adehabitat for the R software: a tool for the analysis of space

273   and habitat use by animals' Ecological modelling, 197, 516–519

274   Clusella-Trullas, S. and Chown, S. L. (2014) 'Lizard thermal trait variation at multiple scales: A

275   review', Journal of Comparative Physiology B: Biochemical, Systemic, and

276   Environmental Physiology, pp. 5–21. doi: 10.1007/s00360-013-0776-x.

277   Cook, E. R. et al. (2004) 'Long-term aridity changes in the western United States.', Science

278   (New York, N.Y.), 306(5698), pp. 1015–8. doi: 10.1126/science.1102586.

279   Díaz, J. A. and Cabezas-Díaz, S. (2004) 'Seasonal variation in the contribution of different

280   behavioural mechanisms to lizard thermoregulation', Functional Ecology, 18(6), pp. 867–

281   875. doi: 10.1111/j.0269-8463.2004.00916.x.

282   Fields, M., Coffin, D. and Gosz, J. (1999) 'Burrowing activities of kangaroo rats and patterns in

283   plant species dominance at a shortgrass steppe-desert grassland ecotone', Journal of

284   Vegetation Science, 10(1), pp. 123–130. doi: 10.2307/3237167.

285   Filazzola, A. and Lortie, C. J. (2014) 'A systematic review and conceptual framework for the

286   mechanistic pathways of nurse plants', Global Ecology and Biogeography, pp. 1335–

287   1345. doi: 10.1111/geb.12202.

288   Filazzola, A. et al. (2017) 'Non-trophic interactions in deserts: Facilitation, interference, and an

289   endangered lizard species', Basic and Applied Ecology, 20, pp. 51–61. doi:

290   10.1016/j.baae.2017.01.002.

291   Filazzola, A., Sotomayor, D. A. and Lortie, C. J. (2017) 'Modelling the niche space of desert

292   annuals needs to include positive interactions', Oikos. doi: 10.1111/oik.04688.

293   Flores, J., & Jurado, E. (2003). Are nurse-protégé interactions more common among plants from

294   arid environments? Journal of Vegetation Science, 14, 911–916.

295   Germano, D. J. and Williams, D. F. (1992) 'Recovery of the blunt-nosed leopard lizard: past

296   efforts, present knowledge, and future opportunities', Transactions of the Western

297   Section of the Wildlife Society, 28, pp. 38–47.

298   Germano D.J., Smith P.T., Tabor S.P. 2007. Food habits of the blunt-nosed leopard lizard

299   (*Gambelia sila*). The Southwestern Naturalist. 52(2):318-323.

300   Germano, D. J. and Williams, D. F. (2005) 'Population ecology of blunt-nosed leopard lizards in

301   high elevation foothill habitat', Journal of Herpetology, 39(1), pp. 1–18. doi:

302   10.1670/0022-1511(2005)039[0001:PEOBLL]2.0.CO;2.

303   Germano, D. J. et al. (2011) 'The San Joaquin Desert of California: ecologically misunderstood

304   and overlooked', Natural Areas Journal, 31(2), pp. 138–147. doi: 10.3375/043.031.0206.

305   Germano D.J., Rathbun G.B. (2016). 'Home range and habitat use by blunt-nosed leopard lizards

306   in the southern San Joaquin Desert of California.', Journal of Herpetology. 50(3):429-

307   434.

308   Gurney, C. M., Prugh, L. R. and Brashares, J. S. (2015) 'Restoration of native plants is reduced

309   by rodent-caused soil disturbance and seed removal', Rangeland Ecology and

310   Management, 68(4), pp. 359–366. doi: 10.1016/j.rama.2015.05.001.

311   Hannah, L., Carr, J. L. and Lankerani, A. (1995) 'Human disturbance and natural habitat: a

312   biome level analysis of a global data set', Biodiversity and Conservation, 4, pp. 128–155.

313   doi: 10.1007/BF00137781.

314   Hawbecker A.C. (1951). 'Small mammal relationships in an *Ephedra* community', Journal of

315   Mammalogy. 32(1), pp. 50-60.

316   Hijmans, R. J. et al. (2005) 'Very high resolution interpolated climate surfaces for global land

317   areas', International Journal of Climatology, 25(15), pp. 1965–1978. doi:

318   10.1002/joc.1276.

319   Hoekstra, J. M. et al. (2005) 'Confronting a biome crisis: Global disparities of habitat loss and

320   protection', Ecology Letters, 8(1), pp. 23–29. doi: 10.1111/j.1461-0248.2004.00686.x.

321   Hothorn, T., Bretz, F. and Westfall, P. (2008) 'Simultaneous inference in general parametric

322   models', Biometrical Journal, pp. 346–363. doi: 10.1002/bimj.200810425.

323   Huey, R. B. (1974) 'Behavioral thermoregulation in lizards: importance of associated costs',

324   Science, 184(140), pp. 1001–1003. doi: 10.1126/science.184.4140.1001.

325   Huey, R. B. and Slatkin, M. (1976) 'Cost and benefits of lizard thermoregulation', The Quarterly

326   Review of Biology, 51(3), pp. 363–384. doi: 10.1086/409470.

327   Kearney, M., Shine, R. and Porter, W. P. (2009) 'The potential for behavioral thermoregulation

328   to buffer "cold-blooded" animals against climate warming', Proceedings of the National

329   Academy of Sciences, 106(10), pp. 3835–3840. doi: 10.1073/pnas.0808913106.

330   Kéfi, S. et al. (2007) 'Spatial vegetation patterns and imminent desertification in Mediterranean

331   arid ecosystems', Nature, 449(7159), pp. 213–217. doi: 10.1038/nature06111.

332   Kerr, G. D. and Bull, C. M. (2004) 'Microhabitat use by the scincid lizard *Tiliqua rugosa*:

333   Exploiting natural temperature gradients beneath plant canopies', Journal of Herpetology,

334   38(4), pp. 536–545. doi: 10.1670/82-04A.

335 Logan, M. L., Cox, R. M. and Calsbeek, R. (2014) 'Natural selection on thermal performance in

336   a novel thermal environment', Proceedings of the National Academy of Sciences of the

337   United States of America, (19), pp. 1–5. doi: 10.1073/pnas.1404885111.

338 Lortie, C. J., Filazzola, A. and Sotomayor, D. A. (2016) 'Functional assessment of animal

339   interactions with shrub-facilitation complexes: A formal synthesis and conceptual

340   framework', Functional Ecology, 30(1), pp. 41–51. doi: 10.1111/1365-2435.12530.

341 Lortie C.J., Liczner A., Filazzola A., Noble T., Gruber E., Westphal M.F. 2017. 'The Groot

342   Effect: plant facilitation and desert shrub regrowth following extensive damage' *Ecology*

343   *and Evolution* 2017:1–10 doi: 10.1002/ece3.3671

344 Lortie C, Filazzola A, Westphal M. (2017): 'The foundation species effect of *Ephedra*

345   *californica*.' Knowledge Network for Biocomplexity. doi:10.5063/F1VM49D1.

346 McGowan, J. et al. (2017) 'Integrating research using animal-borne telemetry with the needs of

347   conservation management', Journal of Applied Ecology. doi: 10.1111/1365-2664.12755.

348 Mcintire, E. J. B. and Fajardo, A. (2014) 'Facilitation as a ubiquitous driver of biodiversity',

349   New Phytologist, 201(2), pp. 403–416. doi: 10.1111/nph.12478.

350 Mouat D.A., Lancaster J.M. 2008. Drylands in Crisis. Environmental Change and Human

351   Security. 67-80.

352 Mohr, C. O. (1947) 'Table of Equivalent Populations of North American Small Mammals',

353   American Midland Naturalist, 37(1), p. 223. doi: 10.2307/2421652.

354   Prugh, L.R. and Brashares, J. S. (2012) 'Partitioning the effects of an ecosystem engineer:

355   Kangaroo rats control community structure via multiple pathways', Journal of Animal

356   Ecology, 81(3), pp. 667–678. doi: 10.1111/j.1365-2656.2011.01930.x.

357   Pugnaire F.I. (ed.) (2010). 'Positive Plant Interactions and Community Dynamics.' CRC Press,

358   Boca Raton, FL, USA.

359   Sawyer J., Keeler-Wolf T and Evens J. 2009. A manual of California vegetation, 2nd ed.

360   California Native Plant Society. Sacramento. 1300 p.

361   Schiffman, P.M. (1994) 'Promotion of exotic weed establishment by endangered giant kangaroo

362   rats (Dipodomys ingens) in a California grassland', Biodiversity and Conservation, 3(6),

363   pp. 524–537. doi: 10.1007/BF00115158.

364   Schoepf, I., Schmol, G., Keonig, B., Pillay, N., Schradin, C. (2015). 'Manipulation of

365   population density and food availability affects home range sizes of African Striped

366   Mouse females', Animal Behaviour 99:53–60.

367   Sears, M.W. and Angilletta, M. J. (2015) 'Costs and benefits of thermoregulation revisited: Both

368   the heterogeneity and spatial Structure of temperature drive energetic costs', The

369   American Naturalist, 185(4), pp. E94–E102. doi: 10.1086/680008.

370   Sears, M.W. et al. (2016) 'Configuration of the thermal landscape determines thermoregulatory

371   performance of ectotherms', Proceedings of the National Academy of Sciences, 113(38),

372   pp. 10595–10600. doi: 10.1073/pnas.1604824113.

373   Sinervo, B. et al. (2010) 'Erosion of lizard diversity by climate change and altered thermal

374   niches', Science, 328(5980), pp. 894–899. doi: 10.1126/science.1184695.

17

375 Stout D., Buck-Diaz J., Taylor S., Evens J. (2014). Vegetation mapping and accuracy assessment

376   report for Carrizo Plain National Monument. California Native Plants Society. Available:

377   https://www.cnps.org/cnps/vegetation/pdf/carrizo-mapping_rpt2013.pdf. Accessed Jan.

378   21th, 2017.

379 U.S. Fish and Wildlife Service. 1998. Recovery plan for upland species of the San Joaquin

380   Valley, California. Portland, OR. 1998; 1-319.

381 Venables W. N., Ripley B. D. 2002. Modern Applied Statistics with S. Fourth Edition. Springer,

382   New York. ISBN 0-387-95457-0

383 Vickers, M., Manicom, C. and Schwarzkopf, L. (2011) 'Extending the cost-benefit model of

384   thermoregulation: high-yemperature environments', The American Naturalist, 177(4), pp.

385   452–461. doi: 10.1086/658150.

386 Warrick, G. D., Kato, T. T. and Rose, B. R. (1998) 'Microhabitat Use and Home Range

387   Characteristics of Blunt-Nosed Leopard Lizards', Journal of Herpetology, 32(2), pp. 183–

388   191. doi: 10.2307/1565295.

389 Westphal, M. F. et al. (2016) 'Contemporary drought and future effects of climate change on the

390   endangered blunt-nosed leopard lizard, Gambelia sila', PLoS ONE, 11(5). doi:

391   10.1371/journal.pone.0154838.

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397   **Tables**

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399   **Table 1**: Generalized linear model for habitat associated with relocated *G. sila*, with degrees of freedom,
400   deviance, and p-values.

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Generalized linear model					
Factor	Df	Deviance	P-value		
habitat	1	88.33	< 0.0001		
Time class	1	2.901	0.1		
habitat:time.class	1	5.281	0.01		
Post Hoc, least squared means					
contrast	estimate	SE	df	z.ratio	p.value
open,AM-shrub,AM	0.769229	0.102934	NA	7.473	<.0001
open,AM-open,PM	-0.01848	0.067966	NA	-0.272	0.993
open,AM-shrub,PM	0.44597	0.085189	NA	5.235	<.0001
shrub,AM-open,PM	-0.78771	0.102727	NA	-7.668	<.0001
shrub,AM-shrub,PM	-0.32326	0.11485	NA	-2.815	0.0252
open,PM-shrub,PM	0.464446	0.084938	NA	5.468	<.0001

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414 **Table 2**: Multinomial logistic regression for observations of *G. sila* behaviors associated with shrubs.

Factor	shrub		Time.class	
	z	P-value	z	P-value
avoiding.predators	6.61E+01	<0.0001	4.60E+07	<0.0001
burrowing	-1.88E+07	<0.0001	2.71E+01	<0.0001
cooling	8.80E+00	<0.0001	1.65E+00	9.91E-02
hunting	8.27E-01	0.4084232	-1.94E+00	5.23E-02
interacting	-1.74E+01	<0.0001	-8.19E-01	4.13E-01
observing	1.14E+00	0.2534383	-8.04E-01	4.21E-01
sunning	6.02E-01	0.5468632	-6.51E+00	7.67E-11

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Figures

Figure 1: Left: location of *G. sila* radiotelemetry study. Top left: Location of study area within California. Top right: aerial photograph of study site overlain with sample home ranges calculated using a 95% minimum convex polygon (MCP) estimate, for each individual. Bottom: Aerial image depicting all home ranges of lizards in the study. Different individuals are indicated by different colors.
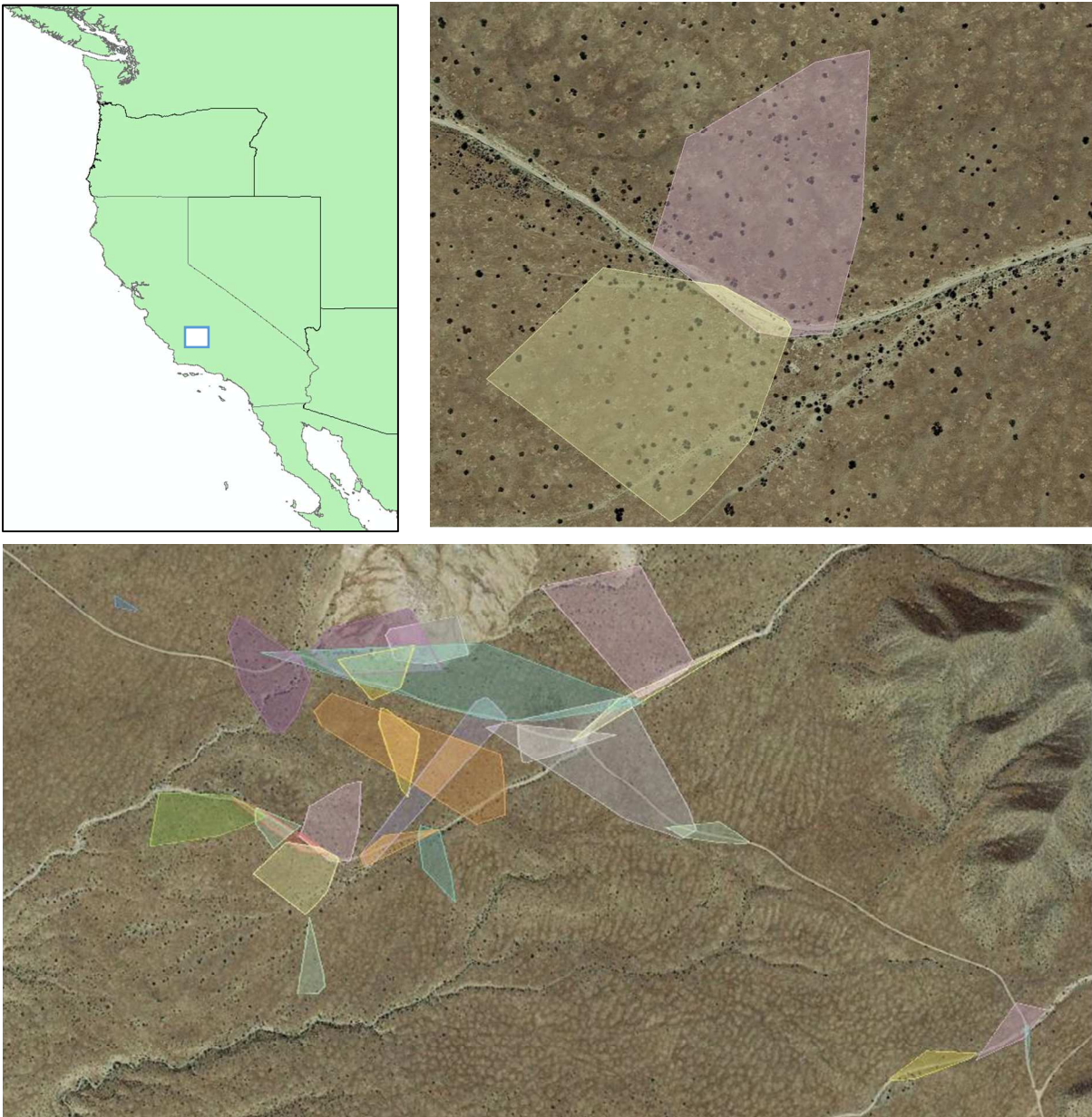
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459 **Figure 2:** Plot of *G. sila* behaviors with respect to habitat and time. Lizards engaged significantly more
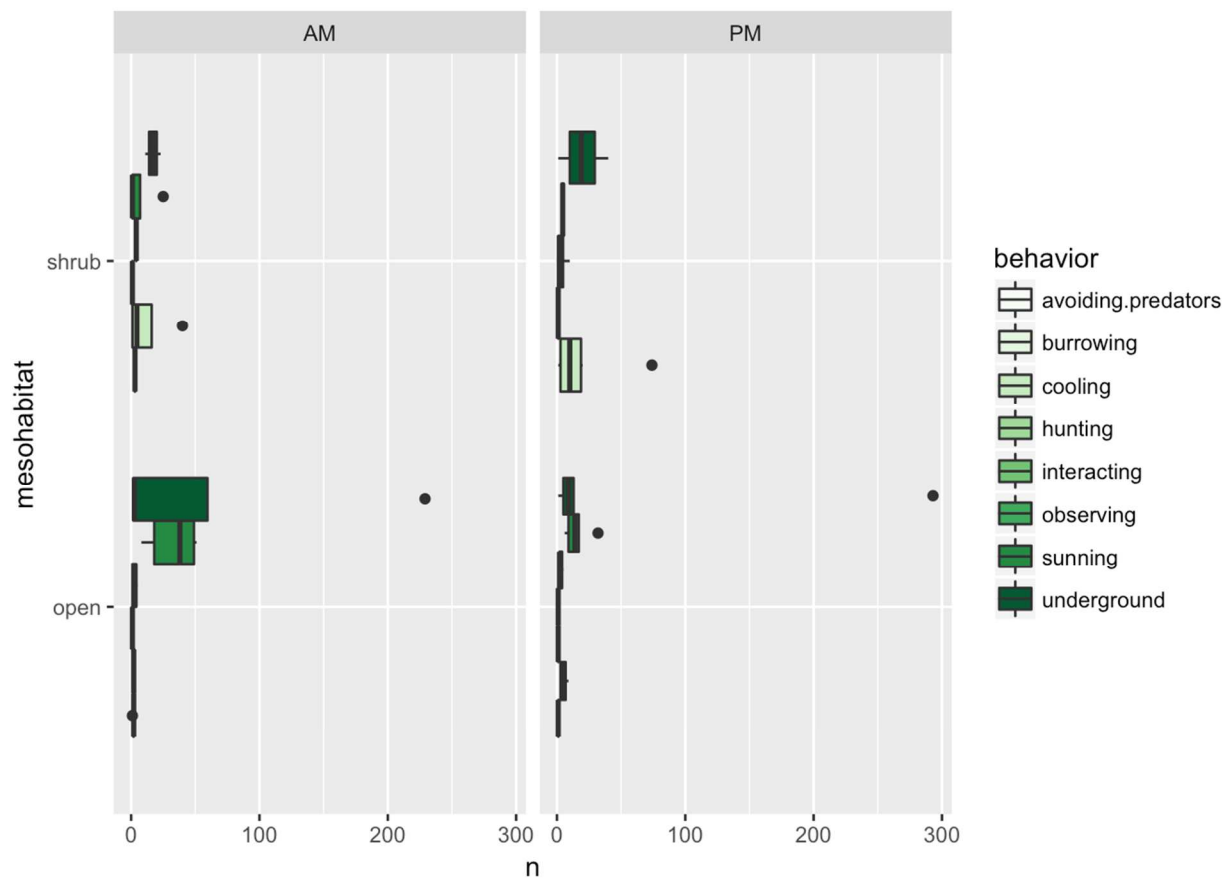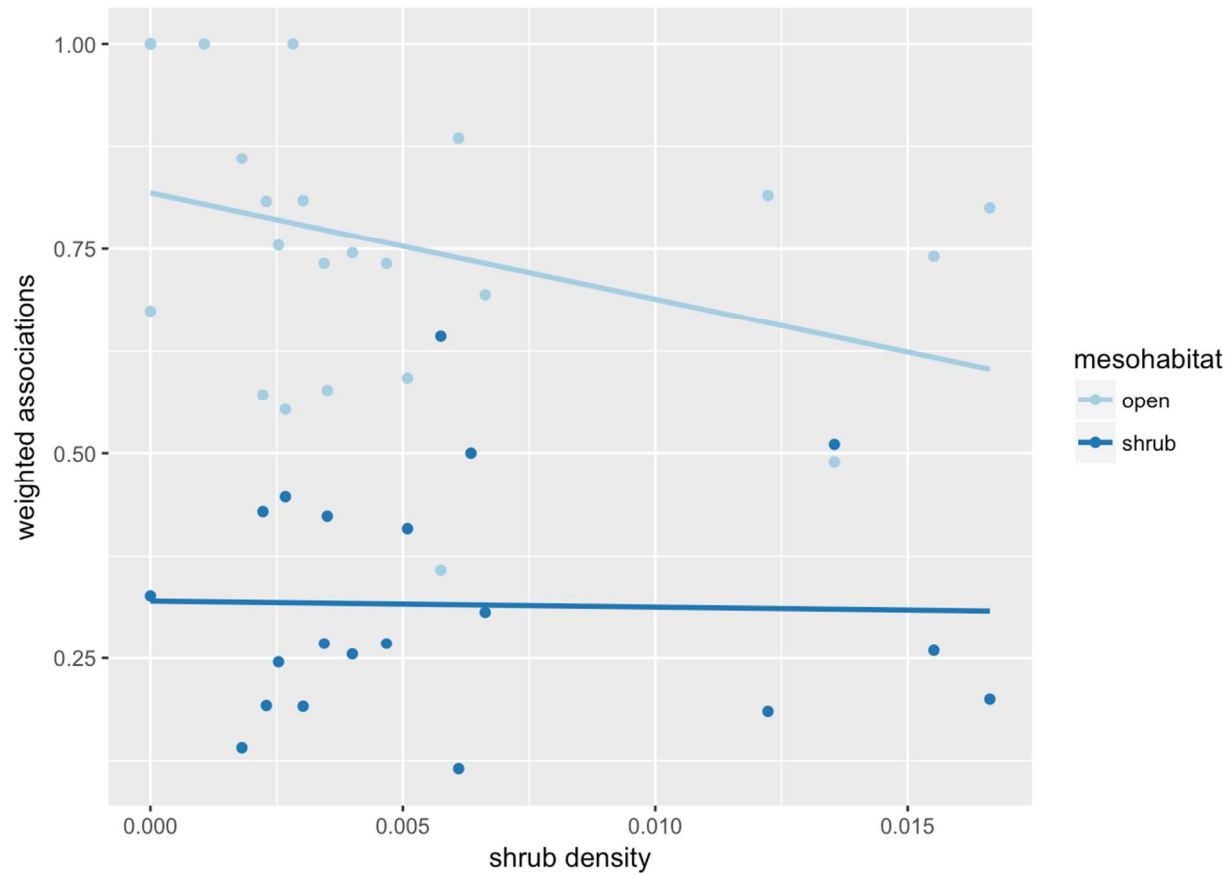460 often in cooling behaviors when under shrubs during afternoon temperature peak.

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467   **Figure 3:** Plots of shrub density on the weighted *G. sila* associations with shrubs.

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479 **Supporting Information**

480 **Table S1**: Behavior classification table for lizard observations.

Classification	Observed behavior
avoiding predators	Moving (most often running) away from predators
burrowing	Actively digging a burrow, or burying itself. This classification was only used if the lizards was actively creating its own burrow, it was not used if a pre-existing burrow was utilized.
cooling	Lizard moving into, or remaining still in shade. Lizard would typically sit upright in shade with front legs extended and rear toes pointed up and off the ground. Occasionally the tail would be lifted off the ground as well.
hunting	Actively stalking or attempting to catch prey. Usually comprised of a slow stalking of an insect and then a sudden burst of speed.
interacting	Interacting with another lizard including either genders of the same species as well as members of other lizard species such as whiptail lizards (*Aspidocelis tigrinum*).
observing	Actively observing environment (eg moving head or body to track motion).
underground	Lizard underground, behavior could not be otherwise be determined.
sunning	Lizard in sun, not moving. Most often either low to ground, with lower body touching ground or sitting upright with head and shoulders up and rear toes pointed out. Eyes often closed or squinted.

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485   **Table S2**. Frequencies of shrub association of individual lizard, density of shrubs within individual home ranges, and percent of area of individual
486   Minimum Convex Polygons (MCP) subsumed by shrub association zones for radiotracked *Gambelia sila* on Elkhorn Plain in 2016.

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Lizard ID	Total obs.	Shrub obs.	Shrub association frequency	MCP area m^2	Number of shrubs	Shrub density	Shrub assoc area m^2	% Shrub assoc area within MCP
180	59	0	0.000	7509	8	0.001	73.491	0.010
320	5	0	0.000	2	0	0.000	0.000	0.000
360	5	0	0.000	8	0	0.000	0.000	0.000
500	50	0	0.000	803	0	0.000	0.000	0.000
900	9	0	0.000	354	1	0.003	9.186	0.026
939	12	0	0.000	9	0	0.000	0.000	0.000
780	55	5	0.091	8190	50	0.006	459.318	0.056
220	56	7	0.125	57400	104	0.002	955.381	0.017
740	31	4	0.129	5636	7	0.001	64.304	0.011
919	47	8	0.170	40998	124	0.003	1139.108	0.028
381	17	3	0.176	5533	92	0.017	845.144	0.153
439	55	10	0.182	3597	44	0.012	404.200	0.112
760	52	10	0.192	4356	10	0.002	91.864	0.021
660	50	11	0.220	5500	22	0.004	202.100	0.037
960	54	12	0.222	18920	48	0.003	440.945	0.023
520	53	12	0.226	4120	5	0.001	45.932	0.011
820	55	14	0.255	3802	59	0.016	541.995	0.143
840	55	14	0.255	10693	50	0.005	459.318	0.043
240	57	15	0.263	21786	75	0.003	688.976	0.032
979	50	16	0.320	13723	91	0.007	835.958	0.061
0	46	15	0.326	20331	88	0.004	808.399	0.040
800	28	11	0.393	7136	25	0.004	229.659	0.032
540	50	20	0.400	15908	81	0.005	744.095	0.047
420	50	21	0.420	4488	10	0.002	91.864	0.020
680	56	24	0.429	51618	138	0.003	1267.717	0.025
860	51	25	0.490	12759	81	0.006	744.095	0.058
460	50	26	0.520	3838	52	0.014	477.690	0.124
717	56	36	0.643	39292	226	0.006	2076.116	0.053

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