1 TITLE: Elucidating dispersal ecology of reclusive species through genetic analyses of parentage

2 and relatedness: the island night lizard (*Xantusia riversiana*) as a case study.

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21 **ABSTRACT**

22   Characterizing dispersal and movement patterns are vital to understanding the

23 evolutionary ecology of species. For many reclusive species, such as reptiles, the observation of

24 direct dispersal may be difficult or intractable. However, dispersal distances and patterns may be

25 characterized through indirect genetic methods. We used genetic and capture data from the island

26 night lizard (*Xantusia riversiana*) to estimate natal dispersal distances through indirect genetic

27 methods, characterize movement and space use patterns, and compare these distances to previous

28 estimates made from more traditional ecological approaches. We found that indirect estimates of

29 natal dispersal were greater than previous field-based estimates of individual displacement of 3-5

30 m. Parent-offspring differences had a mean of approximately 14 m on Santa Barbara Island

31 (SBI) and 41 m on San Clemente Island (SCI) whereas Wright's σ was estimated at 16 m on SBI

32 and 20 m for SCI. Spatial autocorrelation with correlograms of Moran's I revealed large

33 differences in the scale of autocorrelation between islands (SBI=375 m, SCI=1,813 m).

34 Interpretation of these distances as average per generation distance of gene flow was incongruent

35 with parentage analyses and σ. We also used variograms to evaluate the range of spatial

36 autocorrelation among two inter-individual genetic differences. The range of spatial

37 autocorrelation again identified different scales on the two islands (102 - 169 m on SBI and 955 -

38 1,424 m on SCI). No evidence of sex-biased dispersal was found on either island. However, a

39 permutation logistic regression revealed that related individuals >0.8 years old were more likely

40 to be captured together on both islands. Overall, our findings suggest that field-based estimates

41 of individual displacement within this species may underestimate genetic dispersal. We suggest

42 indirect inferences of natal dispersal distances should focus on parentage analyses and Wright's

43 σ for parameter estimation of individual movement, whereas the ranges identified by spatial

44 autocorrelation and variograms are likely to be relevant at the metapopulation or patch scales.

45 Furthermore, characterization of capture patterns and relatedness revealed kin-affiliative

46 behavior in *X. riversiana*, which may be indicative of delayed dispersal and cryptic sociality.

47 These results highlight the power of parentage- and relatedness-based analyses for characterizing

48   aspects of the movement ecology of reclusive species that may be difficult to observe directly.

49   These data can then be leveraged to support future conservation and population modeling efforts

50   and assess extinction risks and management strategies.

51

52   **INTRODUCTION**

53   The dispersal and movement of organisms is a fundamental process in population

54   biology, yet may be difficult to characterize even in abundant species. Dispersal studies provide

55   insight into the evolutionary ecology of focal species and inform conservation planning and

56   management (e.g. Bowler & Benton 2005; Dussex et al. 2016; Hawkes 2009). Dispersal, defined

57   here as the movement of individuals away from their natal sites, may be quantified directly

58   through long-term capture-mark-recapture (CMR) studies and spatial monitoring, or indirectly

59   through genetic inference methods.

60   Both approaches to characterizing dispersal have limitations. Direct observations of

61   dispersal are labor intensive and time consuming, resulting in reduced sample sizes that may

62   underestimate typical dispersal rates and distances (e.g. Dussex et al. 2016), whereas genetic

63   inference may be complicated through modeling assumptions and challenges in study design and

64   sample collection (Broquet & Petit 2009). While few studies use both direct and indirect

65   inference methods, the proliferation of genetic methods has led to a variety of analytical

66   approaches for detecting dispersed individuals (Manel et al. 2005), categorize age and sex biases

67   in dispersal patterns, and characterize dispersal distances (Broquet & Petit 2009; Goudet et al.

68   2002). The processes and potential confounds of these methods are important to understand, as

69   incorporating unrealistic assumptions or parameters within spatial models of dispersal may yield

70   inaccurate results and directly impact management actions and efficacy (Bowler & Benton 2005;

71   Hawkes 2009). However, for reclusive species the characterization of dispersal from field data

72   may be especially problematic due to low probabilities of recapture (e.g. Pimm et al. 2015); thus

73   indirect methods present a compelling tool for characterizing dispersal patterns and distances.

74   Genetic methods are an increasingly common tool for elucidating species dispersal

75   ecology. Recently, Moore et al (2014) used parentage analyses with pairwise distances between

76   dyad members to characterize condition-dependent dispersal patterns in American black bears.

77   Dussex et al (2016) found that assignment methods were generally inconsistent with CMR and

78   parentage analyses inferences. Furthermore, they found that parentage analyses were the most

79   powerful approach at fine scales for elucidating dispersal ecology of the greater white-toothed

80   shrew. In addition to understanding dispersal, managers often need to determine the spatial

81   extent over which landscape influences a focal species (Jackson & Fahrig 2014). Jackson and

82   Fahrig (2014) found that the scale at which landscape structure affects species varies with the

83   population outcome measured. The simulation study conducted by Jackson and Fahrig (2014)

84   suggested that the scale of landscape structure for population persistence should be a lower

85   bound for conservation as the scale needed for supporting genetic diversity is much larger. Taken

86   together, statistical methods that help characterize the dispersal of species and the scale at which

87   landscape affects genetic structure can provide vital information in the context of conservation.

88   The island night lizard (*Xantusia riversiana*) was recently delisted from the Endangered

89   Species Act and provides a unique opportunity to evaluate the utility of indirect methods to

90   elucidate dispersal ecology. This species has been well studied, has few documented predators,

91   and exists in discrete insular populations with high regional abundances of 3,200 individuals/ha

92   in prime habitat. Even with long-term study, direct observations of individual movement suggest

93   very small individual displacement distances of 3 to 6 m over multiple years (Fellers & Drost

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94   1991; Mautz 1993). The dearth of information on island night lizard dispersal ecology is a direct

95   obstacle to modelling metapopulation dynamics and potential threats due to climatic change.

96   We applied genetic inference methods to characterize dispersal ecology and infer natal

97   dispersal distances in *X. r. reticulata*. We used genetic and capture data from our landscape

98   genetics analysis (Rice & Clark 2016) to characterize dispersal ecology and space use on two of

99   the three California Channel Islands this species is known to occupy. The goal of this study was

100   to leverage existing data to assess different techniques for estimating dispersal from genetic data

101   and compare these patterns to values derived from ecological studies.

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103   **METHODS**

104   *Study System and Data*

105   Island night lizards are endemic to three California Channel Islands, two of which were

106   evaluated by Rice and Clark (2016): Santa Barbara Island (SBI) and San Clemente Island (SCI).

107   In brief, we captured 917 island night lizards across both islands utilizing a clustered sampling

108   approach. Individuals were genotyped at 23 microsatellite loci (Rice et al 2016) and first-order

109   relatives, defined as parent-offspring and full siblings, were identified using a consensus

110   approach between three methods: COLONY vers 2.0.5.9 (Jones & Wang 2010), CERVUS vers 3.07

111   (Kalinowsi et al 2007), and the DyadML estimator (Milligan 2003) as calculated in COANCESTRY

112   vers 1.0.1.5 (Wang 2011). The current study draws on the capture data, individual genetic

113   profiles, relatedness and relationship analyses of Rice and Clark (2016).

114   *Statistical Approaches*

115   We used 4 approaches to quantify dispersal distances in the island night lizard: pairwise

116   distances between inferred relationships in Rice and Clark (2016), estimation of Wright's gene-

117   dispersal distance (Wright 1946), correlogram of Moran's I (reviewed in Hardy & Vekemans

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118   1999), and range estimates from variograms (reviewed in Wagner et al. 2005). We characterized

119   sex-biases in dispersal using the approach of Goudet et al. (2002). We evaluated predictors of co-

120   capture among individuals with a permutation based logistic regression on distance matrices

121   (LRDM, Prunier et al. 2015). Statistical analyses were carried out in R (R Core Team 2016)

122   using the packages *adegenet* (Jombart 2008), *hierfstat* (Goudet & Jombart 2015), *coin* (Hothorn

123   et al. 2006), *phylin* (Tarroso et al. 2015), and *fmsb* (Nakazawa 2015). We estimated Wright's

124   gene dispersal distance, σ, and Moran's I using the program SPAGEDI vers 1.5 (Hardy &

125   Vekemans 2002).

126   *Distances Between First-Order Relatives*

127   The pairwise distances between parents and offspring have been demonstrated to be a

128   powerful tool in the characterization of dispersal ecology (e.g. Dussex et al. 2016; Moore et al.

129   2014). We utilized the data of Rice and Clark (2016) to characterize distances between inferred

130   relationship classes. First-order relatives consisted of individuals identified through the

131   consensus method in Rice and Clark (2016) wherein dyads were considered first-order relatives

132   when the inferred relationship was parent-offspring, full sibling, or the relatedness coefficient,

133   DyadML, was greater than 0.35. Relationship classes of parent-offspring, full sibling, and half

134   sibling were inferred by COLONY. Unrelated samples were all relationships not detected by

135   COLONY.

136   We used an approximate general independent test of distances between ordered

137   relationship groups in the package *coin* to test whether pairwise geographic distances differed

138   between relationship groups within and between islands. To correct for the presence of neonates

139   captured in close proximity to adults, we present analyses based on the full data sets and data sets

140   consisting only of individuals greater than 40 mm snout-to-vent length (SVL) which equates to

141   approximately 0.8 years old (Fellers & Drost 1991).

142   *Wright's* σ

143   Wright (1946) described an isolation by distance model in which the genetic

144   neighborhood is a 2-dimensional area in which most mating events occur. This model can be

145   used to estimate σ from a regression of the inter-individual genetic distance, Rousset's a

146   (Rousset 2000), on the logarithm of the inter-individual distance (Hardy et al. 2006; Rousset

147   2000). We assumed drift-migration equilibrium and estimated σ, interpreted as mean natal

148   dispersal distance, for each island across 3 distance classes and 5 density estimates (Table 1).

149   Density estimates were based on the average effective population size per sample site as

150   estimated by the linkage-disequilibrium method (Hill 1981) and confidence intervals from the

151   program NEESTIMATOR vers 2.01 (Do et al. 2014). Additional estimates of density were derived

152   from the census population size over the entire area of each island and the prime-habitat area

153   listed in the United States Fish and Wildlife Service post-delistment monitoring plan (USFWS

154   2014).

155   *Moran's I*

156   Moran's I is a common measure of spatial autocorrelation of individual allele frequencies

157   (Hardy & Vekemans 1999). Moran's I was calculated for each pairwise distance bin, set at

158   increments of 150 m for SBI and 500 m for SCI, and significance was tested with 1000

159   permutations. The increments for distance bins were assigned based on the smallest distance at

160   which all bins had observations. For each island, we produced a correlogram of Moran's I at

161   each distance class. The distance at which the value of Moran's I became ≤ 0 was interpreted as

162   the point at which individual allele frequencies were no longer spatially autocorrelated. We

163   interpreted this point as the average maximum dispersal distance of island night lizards (e.g.

164   Yaegashi et al. 2014).

165   *Variograms*

166   Variograms assess the spatial autocorrelation of a variable by depicting the semivariance

167   (defined as half the variance of all pairwise differences) against distance, and may identify the

168   spatial scale of dispersal processes (Dutech et al. 2008; Le Corre et al 1998). The empirical data

169   is used to generate a variogram which is then fit with a theoretical variogram with parameters for

170   nugget (semivariance associated with non-spatial effects), sill (the value at which semivariance

171   stabilizes), and range (the scale of effect or threshold of spatial independence) (Wagner et al.

172   2005). There are few guidelines for determining the increment or maximum distances considered

173   in empirical variograms; therefore, we followed the conventions of using the minimum lag

174   distances which produced a minimum of 30 observations per bin and limited variograms to one-

175   half the maximum pairwise distance compared (Rossi et al. 1992). Lag distances differed

176   between Moran's I and variogram analyses, due to variogram constraint to a smaller maximum

177   distance.

178   We used the package *phylin* to produce empirical and theoretical variograms. For

179   theoretical variograms, exponential models were fit to all data sets with the nugget set to the

180   semivariance of the first distance bin and the remaining parameters estimated within the package.

181   The variogram approach implemented in *phylin* requires pairwise distance variables; therefore

182   we evaluated DPS, an inter-individual genetic distance calculated as 1 – proportion of shared

183   alleles in *adegenet*, and a measure of (un)relatedness by subtracting DyadML values from 1, the

184   theoretical maximum probability under identity by descent (Milligan 2003).

185   *Sex-Biased Dispersal*

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186   The methods of Goudet et al (2002) identify a permutation t-test approach to test for sex-

187   biases in dispersal based on four metrics derived from genetic data of each sex: mean and

188   variance of the corrected assignment index (mAIc and vAIc, respectively), Fst, and Fis.

189   However, these methods have been reported to perform well only in the presence of strong sex-

190   biased dispersal (Goudet et al. 2002). Statistical tests to detect sex bias were conducted in the

191   package *hierfstat* with the metrics mAIc, vAIc, Fst, and Fis (Goudet et al. 2002). Significance for

192   comparisons based on mAIc and vAIc were ran with 10,000 permutations whereas tests based on

193   Fst and Fis were based on 1,000 permutations due to computational constraints.

194   *LRDM*

195   We used an extension of permutation-based LRDM (Prunier et al. 2015) to assess

196   whether the probability of capturing individuals together could be attributed to the predictors of

197   pairwise sex, sexual maturity, relatedness, or relationship. We used a binary response variable

198   with success defined as being captured together. Predictors were pairwise distance matrices with

199   sex and sexual maturity coded as categorical comparisons.

200   Models were constructed from single variable up to full models; due to the highly

201   collinear nature of DyadML and COLONY -inferred relationships (data not shown) these

202   predictors were not included in the same models. Logistic regression models were constructed

203   with the glm function and a binomial 'logit' link. Nagelkerke's R^2 (Prunier et al. 2015; Smith &

204   McKenna 2013) was calculated for each model using the NagelkerkeR2 function in the package

205   *fmsb* and served as the reference distribution statistic for determining significance by permuting

206   the binary response matrix 10,000 times and recalculating Nagelkekre's R^2 for each permutation.

207   Semi-standardized beta weights for the full models were calculated as in Prunier et al. (2015)

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208   with the odd's ratios calculated as the exponentiated semi-standardized beta weights following

209   King (2007).

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211   **RESULTS**

212   Mean pairwise distances (Table 2) were significantly different for each relationship group

213   within both islands ($p < 2.2 \times 10^{-16}$). Mean pairwise distances for full siblings and parent

214   offspring were not significantly different within either island (SBI p=0.1017, SCI p=0.7566); all

215   other comparisons were significant at the p<0.005 level. When controlling for young of year

216   (SVL < 40 mm), mean pairwise distances were significantly different between islands for first-

217   order relationship (p=0.0062) and parent-offspring dyads (p=0.0228). When young of year were

218   included there were no significant differences. When controlling for young of year, mean parent-

219   offspring distance for SBI was 13.93 m and 40.68 m on SCI.

220   The gene dispersal estimate, σ, ranged between approximately 7 m and 31 m for SBI and

221   approximately 7 m to 23 m for SCI. Estimates of σ were sensitive to density estimates. However,

222   estimates of σ were consistent across different distance classes when density was constant and

223   robust to the inclusion of young of year (Table 1). Constraining density estimates to average

224   effective density (Ne/km^2) across sample locations resulted in estimates of 16 m for SBI and 19

225   m for SCI for full data sets and 16 m for SBI and 18 m for SCI when young of year were

226   removed.

227   Spatial autocorrelation on SBI, as represented by Moran I, was significantly positive

228   (p≤0.005) at distances less than 375 m at which Moran's I became negative but not significant

229   (Figure 1). On SCI, spatial autocorrelation was significantly positive (p≤0.001) up to distances of

230   1,395 m and had standard errors overlapping 0 at a distance of 1,813 m (Figure 2). Variograms

231   based on relatedness had higher support, as indicated by R^2, than those based on DPS for both

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232   islands (Figures 3,4). On SBI, the range for the DyadML variogram was approximately 102 m

233   whereas SCI had a range estimate of 955 m. The genetic distance measure, DPS, resulted in

234   greater range estimates on SBI at 169 m and SCI at 1424 m.

235   We found no statistical support for sex-biased dispersal on either island. We utilized

236   LRDM in both exploratory and predictive contexts. Exploratory analyses revealed that

237   relatedness and relationship were the only significant predictors of co-capture when controlling

238   for young of year on each island (Table 3). Pairs of individuals were 1.067 times more likely to

239   be captured at the same point with a one standard deviation change in DyadML relatedness

240   estimates on SBI and 1.031 times more likely on SCI. To examine the predictive ability of these

241   patterns we utilized a traditional logistic regression with SBI as the training dataset and SCI as

242   the test dataset. This predictive analysis DyadML and COLONY -inferred relationships had high

243   accuracy (0.9996) and low misclassification (0.0004) rates when predicting capture success

244   trained on SBI and tested on SCI.

245

246   **DISCUSSION**

247   We found inferred parent-offspring distances were between 2 and 13 times greater than

248   the individual displacement distances of long-term CMR studies of 3 to 6 m (Fellers & Drost

249   1991; Mautz 1993). We provide the first quantitative estimates of dispersal distances in the

250   species (14 m on SBI and 41 m on SCI) and found spatial autocorrelation of allele frequencies,

251   genetic distance, and relatedness at previously unrecorded scales. The LRDM approach of

252   Prunier et al. (2015) resulted in relatedness and relationships being the strongest predictors of

253   island night lizard co-captures, suggesting a social structure with kin-affiliative behavior.

254   *Distances Between First-Order Relatives*

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255   Fellers and Drost (1991) found 12 juveniles on SBI 30 to 40 m from prime habitat over a

256   6 year study and surmised these represented juvenile dispersal, whereas individual recapture data

257   suggested average displacements of 5.6 m. While there is no indication of juvenile dispersal

258   distances for SCI, Mautz (1993) found that individual relocations to be only an average of 3 m

259   apart, with the longest recorded displacement at 18.5 m. Our findings provide the first

260   quantitative estimates of juvenile dispersal distances, although the distance between parent-

261   offspring pairs is approximately 3 times shorter than the estimates of Fellers and Drost (1991).

262   However, our estimates of dispersal distance are approximately 2.5 times greater than the

263   individual movement distances on SBI and 13 times greater than those on SCI.

264   Moore et al. (2014) and Dussex et al. (2016) both found parentage analyses more

265   accurate in describing dispersal ecology than alternate genetic methods. Our results support the

266   utility of parentage and kinship analyses in characterizing natal movement, especially when

267   focused on parent-offspring pairs. Estimation of first-order relationships as described in Rice and

268   Clark (2016) and their pairwise differences may be informative in the characterization of

269   dispersal when few parent-offspring comparisons are available. Comparisons of mean pairwise

270   distance for COLONY -inferred relationships were not significantly different between parent-

271   offspring or full sibling groups for either island. The mean distances inferred for first-order

272   relationships differed between islands, potentially due to differences in island scale and

273   population densities. It is notable that the maximum distance between first-order relatives is very

274   close (SBI=158.63 m, SCI=156.75 m) between both islands, although these maximums belong to

275   different relationship groups (full sibling and parent-offspring respectively) for each island.

276   *Gene Dispersal Distances*

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277   Estimates of gene dispersal were also remarkably close between each island at the same

278 lag distances and density estimate methods. Comparing these two metrics, distances from

279 inferred parentage and sigma estimated distances were within 3 m on SBI and SCI when

280 evaluating distances with young of year included, and remained consistent when young of year

281 were excluded. The discrepancy between parent-offspring distance and σ for SCI when

282 controlling for young of year may be attributable to changes in sample size and analytical

283 method. Future research should consider simulation-based approaches to evaluate the accuracy

284 of these metrics compared to the known simulation parameters; however, in the context of

285 estimating parameters for natural populations characterized by an isolation by distance pattern,

286 parentage analyses and σ both appear to yield consistent results.

287 *Spatial Autocorrelation*

288   Spatial autocorrelation analyses, such as Moran's I, have been used to understand the

289 scale of autocorrelation for individual allele frequencies and interpret this scale as a measure of

290 dispersal (e.g. Epperson & Li 1997; Yaegashi et al. 2014). The interpretation of the

291 correlogram's x-intercept as average maximum dispersal distance is uncommon in the literature,

292 and generally noted as the scale at which allele frequencies are become spatially independent.

293 This method returned notable differences between islands, with SBI reaching this point at 375 m

294 and SCI at 1,813 m. These scales are much larger than the displacement estimates from long-

295 term field studies and are also much larger than our dispersal estimates from parentage analyses

296 and σ. Thus, we recommend that studies focused on estimating dispersal distances should favor

297 parentage analyses or gene dispersal distances over spatial autocorrelation analyses.

298 *Variograms*

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299   Estimates using variograms were also incongruent with parentage analyses, but provided

300   smaller estimates of the scale of spatial autocorrelation than Moran's I. The use of variograms to

301   estimate dispersal has not been formally studied. These estimates could denote the scale of

302   spatial genetic structure (Wagner et al. 2005), connectivity among localized groups (Le Corre et

303   al. 1998), or the "patch size" of the process evaluated (Legendre & Fortin 1989). Because we

304   generated distance measures from the proportion of shared alleles and relatedness our estimates

305   may denote the "patch size" of relatedness, or may indicate familial territories. More meaningful

306   biological interpretation of these field studies using long-term telemetry paired with parentage

307   analyses would provide data on individual movement necessary for more thorough interpretation

308   of genetic patterns. However, simulation-based approaches may offer a more tractable solution to

309   determine whether range estimates produced from spatial autocorrelation and variogram analyses

310   are congruent with known or simulated dispersal patterns.

311   *LRDM*

312   The results of LRDM indicate that pairwise relatedness and relationships are the best

313   predictors of capturing individuals together. Due to the late spring and summer sampling on SBI

314   the removal of young of year individuals had little effect on the pseudo-R^2 or odds ratio.

315   However, extensive sampling on SCI during the autumn to capture neonates and associated

316   adults impacted both the pseudo-R^2 and odds ratio for relatedness, but this remained a significant

317   predictor even after removal of young of year. The continued association of relatives after the ca.

318   0.8 year mark suggests a level of previously undocumented sociality within the system, which

319   may explain the strong signals of isolation by distance reported by Rice and Clark (2016).

320   Cryptic sociality and kin affiliation has been noted for the sister species (*X. vagilis*) on

321   the mainland, in which fostering was demonstrated to effect philopatry and kin-affiliative

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322   behaviors through delayed dispersal (Davis 2011; Davis et al. 2010). The studies of Davis et al.

323   (2010) highlight several similarities shared between the two species, including dense

324   populations, low dispersal, and small home range sizes. Thus, our findings suggest island night

325   lizards may also form kin groups through delayed juvenile dispersal and prolonged parent-

326   offspring interactions as noted by Davis et al. (2010). Some reclusive reptiles that are social also

327   exhibit parental care, such as attendance of neonates in egg-guarding lizards (e.g. Huang 2006;

328   Mateo & Cuadrado 2012) or maternal attendance of pre-ecdysis neonates in pit-vipers (e.g.

329   Greene et al. 2002; Hoss et al. 2015). Given the frequent and prolonged association between

330   adults and neonates, it is possible *X. riversiana* also exhibits parental care. Although predators on

331   both islands are limited, attending parents could protect neonates from intra-specific aggression.

332   Unsurprisingly, samples collected in autumn most frequently included neonates and associated

333   adults as parturition occurs seasonally (Fellers & Drost 1991; Mautz 1993). However, the

334   association of related island night lizards extending beyond this parturition period warrant further

335   investigation into the extent of their social structure and affiliative behaviors.

336   *Conservation Implications*

337   Our characterization of dispersal ecology of the island night lizard suggests scale

338   dependent effects and supports the independent management of each island. On SBI, we found

339   parent-offspring distances of approximately 14 m and spatial autocorrelation up to 375 m

340   whereas dispersal distances on SCI were 41 m with spatial autocorrelation up to 1,813 m. These

341   distance estimates will be useful for the management and post-delistment monitoring of

342   populations on both islands (USFWS 2014). We suggest management actions should maintain

343   population sizes and meta-population connectivity, and that the spatial scales derived from our

344   spatial autocorrelation analyses be used to guide those actions. On SBI, a scale of 100 m to 375

345   m should be used as a focus for remediation efforts, such as direct-line connectivity between

346   habitat patches. On SCI, management should focus at the scales of 1-2 km in efforts to connect

347   remote patches through corridors of prime habitat, as opposed to replanting isolated or remote

348   patches. Furthermore, these findings can inform the design and mitigation of increased

349   infrastructure by identifying patches that would become disconnected at these scales under

350   increased development.

351   *Conclusions*

352   Dispersal is a key factor in the life history of a species, and a key parameter affecting

353   conservation and management decisions (Bowler & Benton 2005; Hawkes 2009). Although

354   dispersal can be directly observed, it is often labor and time intensive. Indirect inference of

355   dispersal based on genetic evidence is gaining in application but lacks a framework for consistent

356   and reliable inference. Studies utilizing both CMR and genetic inference methods have found

357   that CMR methods generally underestimate dispersal distances, while assignment methods on

358   genetic data can often overestimate dispersal and conflict with direct observations (e.g. Dussex et

359   al. 2016). The application of genetic inference methods to estimate dispersal is likely to be a

360   valuable tool for conservation management in understanding the scale of dispersal processes and

361   the potential effects of management actions on connectivity. However, we have demonstrated

362   that different inference methods may yield very different results which may lead to incorrect

363   inferences and misspecification of parameters, rendering management actions ineffectual

364   (Bowler & Benton 2005; Jackson & Fahrig 2014). Recent studies found parentage analyses to be

365   the most accurate method for characterizing dispersal ecology, and our analyses of the island

366   night lizard support this usage. Furthermore, our findings suggest that natal dispersal parameters

367   should not be derived from spatial autocorrelation or variogram analyses as the parameters

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368   inferred are highly variable and likely overestimate dispersal in the context of individual

369   movement. However, these approaches may yield insight into the scale of fine-scale patterns

370   relevant to conservation and suggest a minimum scale below which individuals are likely to be

371   related and thus management actions may be confounded (e.g. Jackson & Fahrig 2014).

372

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TABLES

Table 1: **Isolation by Distance Model Results**. Results from the program SPAGEDI for estimation of Wright's σ. Islands were estimated independently (SBI=Santa Barbara Island, SCI=San Clemente Island). Density (De) was estimated as individuals/km^2 by considering the census population size (Nc) and island area, average for effective density across sampling locations (Ne) with 95% confidence intervals (Ne-LCI=lower, Ne-UCI=upper), and census population size over prime habitat area (Ncp). Lag distance refers to the increment of distance bins (m). SPAGEDI estimated the number of breeders (Nb) and σ (m); standard errors in parentheses for each parameter were estimated by jackknifing over loci. Two data sets were ran for each island, the full data set (All Individuals) and a data set in which the young of year were removed (>40 SVL Individuals).

Island	Density Method	De	Lag	All Individuals		>40 SVL Individuals	
				Nb	σ	Nb	σ
SBI	Nc	6795.37	25	79.52 (7.69)	30.5 (1.5)	79.44 (7.70)	30.5 (1.5)
	Ncp	167619.00	25	96.33 (48.17)	6.8 (1.7)	104.63 (44.95)	7.0 (1.5)
	Ne – LCI	19157.91	25	77.22 (14.06)	17.9 (1.6)	79.90 (12.04)	18.2 (1.4)
	Ne – UCI	33679.07	25	81.58 (12.24)	13.9 (1.0)	84.23 (16.04)	14.1 (1.3)
	Ne	24291.60	25	75.58 (11.87)	15.7 (1.2)	78.57 (16.44)	16.0 (1.7)
	Ne	24291.60	50	75.58 (11.87)	15.7 (1.2)	78.57 (16.44)	16.0 (1.7)
	Ne	24291.60	200	75.58 (11.87)	15.7 (1.2)	78.57 (16.44)	16.0 (1.7)
SCI	Nc	141490.60	50	151.03 (26.84)	9.2 (0.8)	142.58 (17.30)	9.0 (0.5)
	Ncp	267991.90	50	163.56 (37.09)	7.0 (0.8)	140.68 (23.15)	6.5 (0.5)
	Ne – LCI	23016.35	50	159.12 (54.55)	23.5 (4.0)	140.85 (61.86)	22.1 (4.8)
	Ne – UCI	182711.40	50	159.00 (22.51)	8.3 (0.6)	152.20 (26.53)	8.1 (0.7)
	Ne	34631.00	50	160.18 (44.80)	19.2 (2.7)	133.94 (44.96)	17.5 (2.9)
	Ne	34631.00	100	160.18 (44.80)	19.2 (2.7)	133.94 (44.96)	17.5 (2.9)
	Ne	34631.00	200	160.18 (44.80)	19.2 (2.7)	133.94 (44.96)	17.5 (2.9)

Table 2: Pairwise Distances among Relatives. Islands are indicated as Santa Barbara Island (SBI) or San Clemente Island (SCI). Relationship were first-order (FO, based on Rice and Clark (2016)), COLONY inferred relationships of parent-offspring (PO), full sibling (FS), half sibling (HS) or unrelated (U). For each relationship, the number of pairwise comparisons (N), mean (Mean), standard deviation (Sd), median (Median), and maximum (Max) distance values (m). The P column is the approximated p-value comparing the same Relationships between islands. The lower half of the table displays values for each island with young of year samples (>40mm SVL) removed.

	SBI					SCI					
Relationship	**N**	**Mean**	**Sd**	**Median**	**Max**	**N**	**Mean**	**Sd**	**Median**	**Max**	**P**
FO	44	16.55	25.25	10.14	158.63	74	21.82	36.61	2.91	156.75	0.4109
PO	20	13.93	13.24	9.50	42.49	52	20.64	40.44	1.00	156.75	0.4815
FS	14	24.90	39.70	12.93	158.63	33	22.42	30.00	4.55	95.29	0.8244
HS	418	243.25	404.76	38.86	1862.69	686	3480.46	5961.83	132.95	26465.22	<2.2e-16
U	48064	831.05	502.81	778.79	2368.02	171220	11285.37	8175.89	9670.69	28258.99	
	SBI > 40 mm SVL					**SCI > 40 mm SVL**					
Relationship	**N**	**Mean**	**Sd**	**Median**	**Max**	**N**	**Mean**	**Sd**	**Median**	**Max**	**P**
FO	44	16.55	25.25	10.14	158.63	43	37.18	41.86	16.90	156.75	0.0062
PO	20	13.93	13.24	9.50	42.49	26	40.68	49.99	12.79	156.75	0.0228
FS	14	24.90	39.70	12.93	158.63	19	38.01	31.51	25.61	95.29	0.3005
HS	391	236.72	402.38	37.31	1862.69	613	3447.68	5994.7	136.08	26465.22	<2.2e-16
U	45631	836.88	502.73	783.46	2368.02	141120	11193.78	7949.20	9667.75	28258.99	

Table 3: Logistic Regression on Distance Matrices Results. LRDM was conducted separately for each island (SBI=Santa Barbara Island, SCI=San Clemente Island) and for each data set with all individuals (All Samples) or controlled by removal of young of year (>40mm SVL). LRDM was conducted on each predictor variable (Model) independently to determine significance (p-value) through permutation and model support by Nagerkerke's R^2 (R^2). Odds-ratios (Odds-ratio) were computed from 3-variable models in which either the DyadML estimator (Dyad) or COLONY-inferred relationships were used (COLONY) due to the collinear nature of relatedness and relationship. Since the predictors of sex and maturity were used in 2 3-variable models both odds ratios are listed with the forward slash separating the DyadML model from the COLONY relationship model. The predictors of sex and maturity were categorical matches between male and female (sex) and sexually mature and immature individuals (Maturity).

| | SBI | | | | | | SCI | | | | | |
| | All Samples | | | >40mm SVL | | | All Samples | | | >40mm SVL | | |
Model	**p-value**	**Odds-ratio**	R^2	**p-value**	**Odds-ratio**	R^2	**p-value**	**Odds-ratio**	R^2	**p-value**	**Odds-ratio**	R^2
Dyad	*0.0001*	*1.0644*	*0.112*	*0.0001*	*1.0659*	*0.112*	*0.0001*	*1.4373*	*0.339*	*0.0001*	*1.0307*	*0.081*
COLONY	*0.0001*	*1.7004*	*0.089*	*0.0001*	*1.7316*	*0.089*	*0.0001*	*0.9969*	*0.392*	*0.0001*	*0.9990*	*0.073*
Sex	0.6845	1.3120/ 2.4283	0.008	0.7005	1.3265/ 2.4386	0.008	*0.0001*	1.0006/ 1.0003	0.018	0.3911	1.0003/ 1.0002	0.005
Maturity	0.9356	1.3259/ 1.2964	0.001	0.8512	1.3409/ 1.3139	0.001	0.0033	1.0005/ 0.9799	0.009	0.6900	1.0003/ 0.9959	0.001

FIGURES
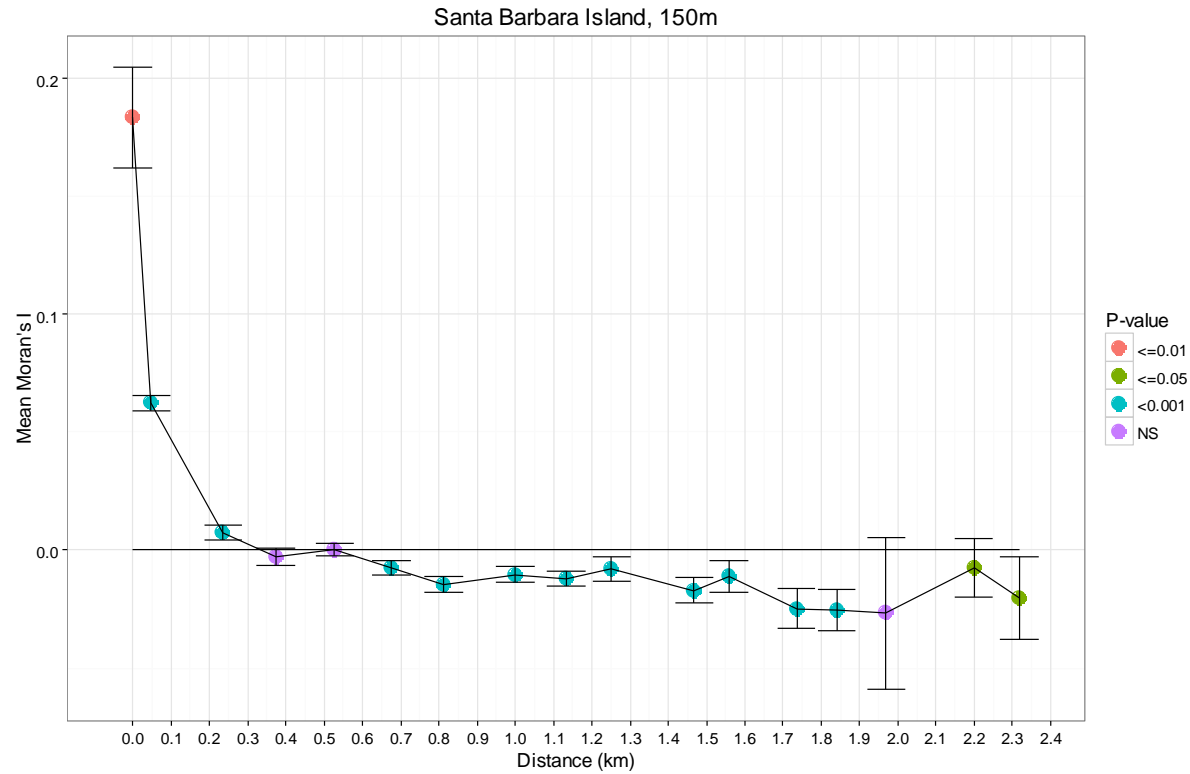
Figure 1: Correlogram of Moran's I on Santa Barbara Island. Moran's I was calculated for each distance bin and significance

assess through permutation. Points represent the value of Moran's I for the mean distance within each 150 m distance interval. Bars

indicate standard error around the mean while each point color indicates significance of correlation within each point.
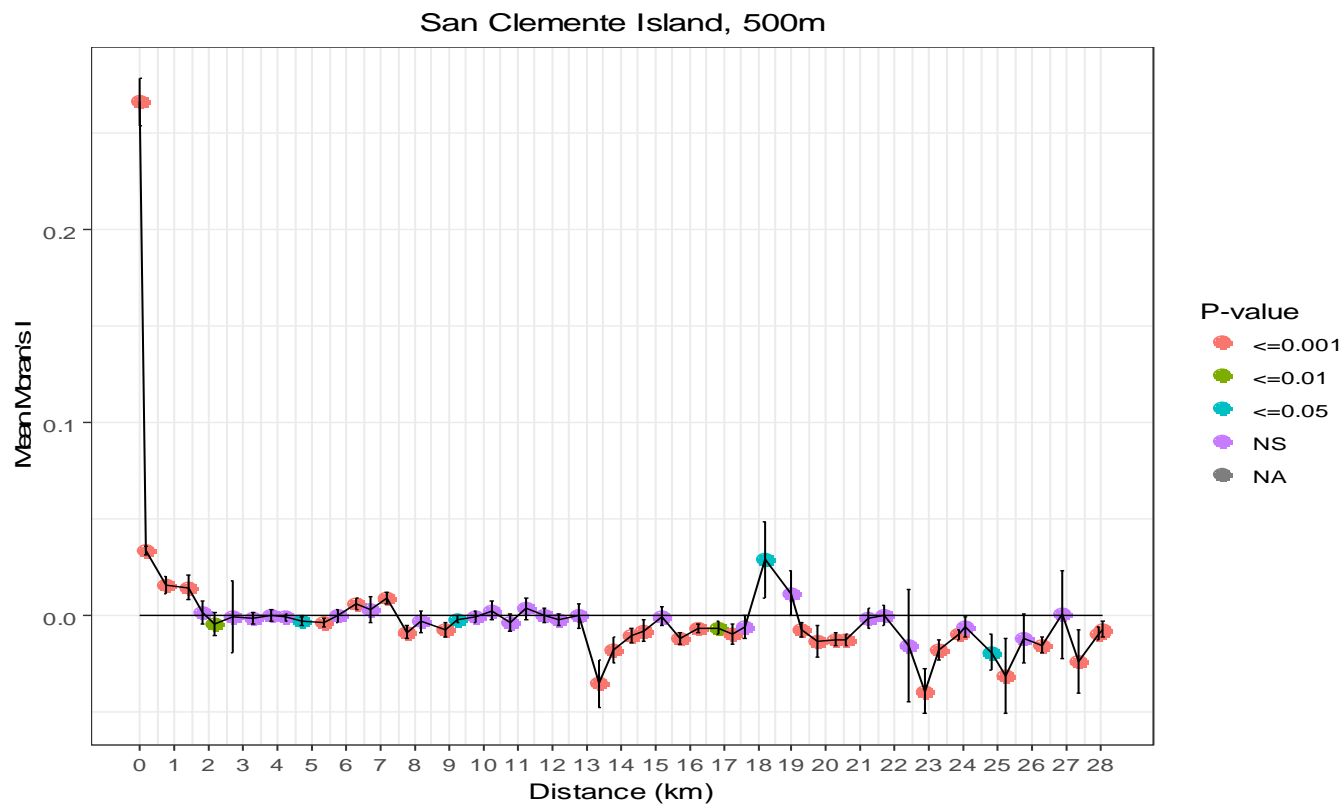
Figure 2: Correlogram of Moran's I on San Clemente Island. Moran's I was calculated for each distance bin and significance assess through permutation. Points represent the value of Moran's I for the mean distance within each 500 m distance interval. Bars indicate standard error around the mean while each point color indicates significance of correlation within each point.
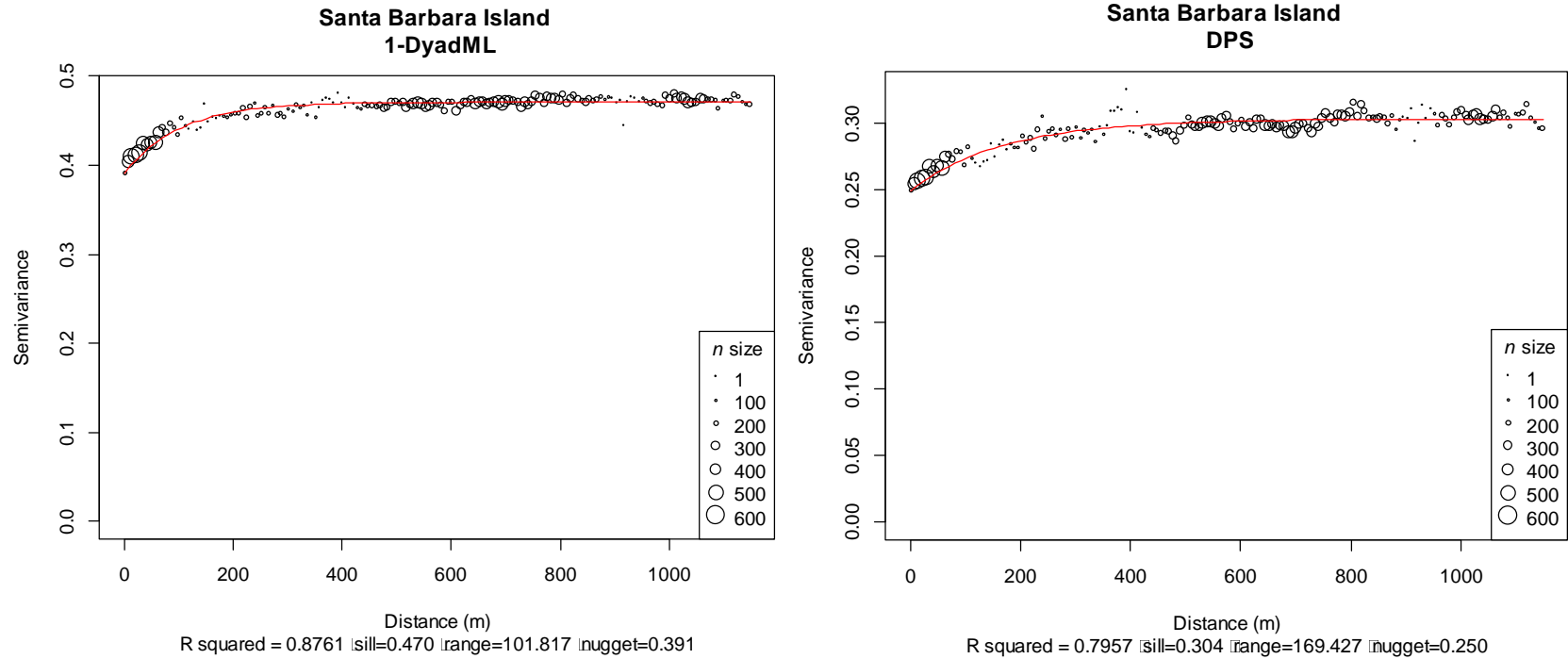
Figure 3: Variogram Analyses for Santa Barbara Island. Empirical variograms (circles) were generated from two distance measures: left) 1-DyadML relatedness estimates, right) Inter-individual genetic distance DPS. Circle size denotes the number of pairwise comparisons within each distance class. Maximum distance evaluated was 1,100 m with a lag distance of 7 m for both variables. Theoretical variograms (red line) were fit as fixed-nugget models. Model R^2 values were used as a measure of model support and the point of spatial independence is denoted by the range.
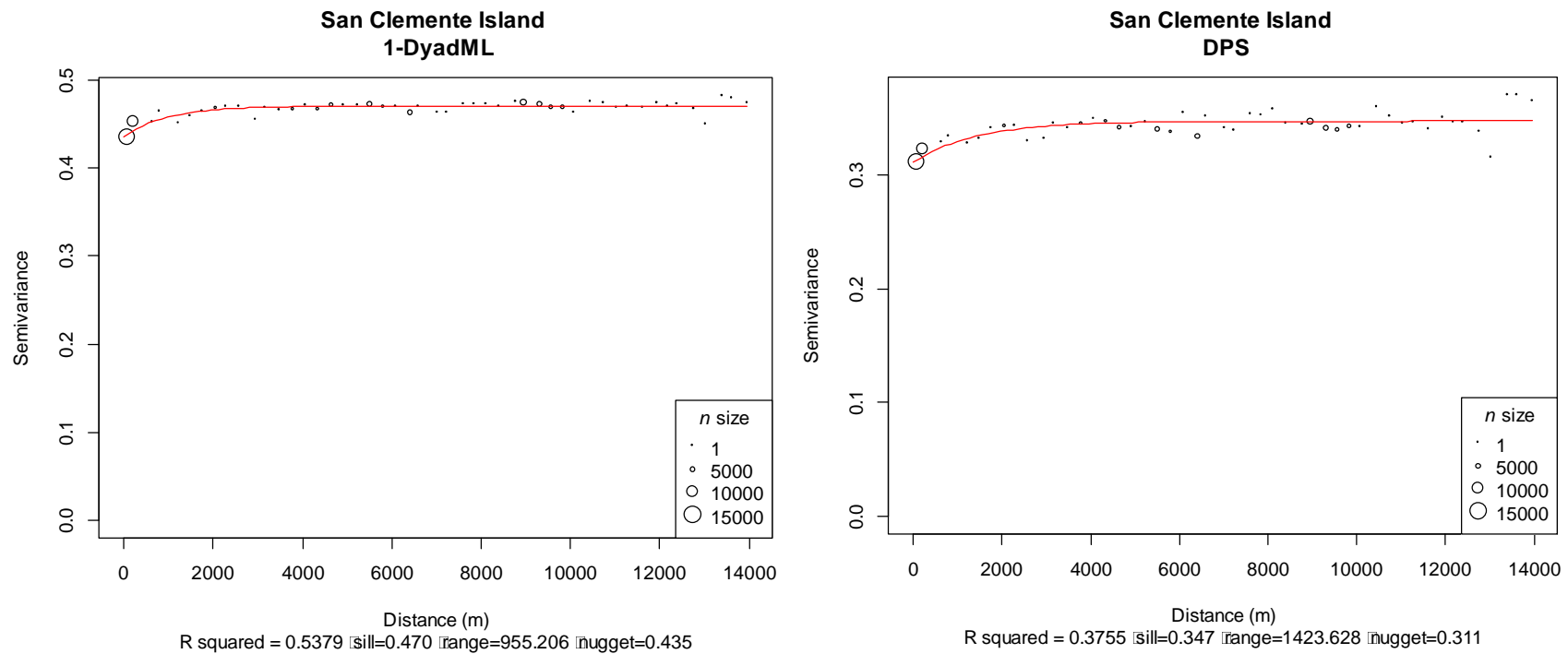
Figure 4: Variogram Analyses for San Clemente Island. Empirical variograms (circles) were generated from two distance

measures: left) 1-DyadML relatedness estimates, right) Inter-individual genetic distance DPS. Circle size denotes the number of

pairwise comparisons within each distance class. Maximum distance evaluated was 14,000 m with a lag distance of 290 m for both

variables. Theoretical variograms (red line) were fit as fixed-nugget models. Model R^2 values were used as a measure of model

support and the point of spatial independence is denoted by the range.

SUPPLEMENTALS: RAW DATA GRAPHS

Santa Barbara Island
1-DyadML (raw)

x-axis: Pairwise Distance (m)

y-axis: 1-DyadML relatedness

Santa Barbara Island
DPS (raw)

San Clemente Island
1-DyadML (raw)

San Clemente Island
DPS (raw)

DPS

Pairwise Distance (m)