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1 **Understanding dispersal patterns can inform future translocation strategies: a case**
2 **study of the threatened greater stick-nest rat (*Leporillus conditor*)**

3

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5

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13

14 **Short title: Understanding dispersal informs translocation**

15

16 **Abstract**

17

18 Dispersal behaviour and sociality are significant factors influencing survival at both the
19 individual and population level. In translocation and breeding programs, social structure and
20 sex-biased philopatry and dispersal should be considered in order to maximise population
21 viability and conservation outcomes. Here we use the greater stick-nest rat (*Leporillus*
22 *conditor*), a native Australian rodent, as a case study to understand how knowledge of social
23 structure and dispersal can inform conservation and translocation programs. We combine
24 high-throughput DNA sequencing with field trapping data from a translocated population of
25 greater stick-nest rats at Arid Recovery Reserve, South Australia to provide the first
26 empirical evidence of female philopatry and male biased dispersal in this species. Males were

27 found to disperse, on average, 1.5 km from the natal nest, while females typically did not
28 disperse beyond 500 m. Further, recapture data showed that females demonstrated a higher
29 degree of nest fidelity than males over time. Based on these findings, we make two key
30 recommendations for future translocations of the species. Firstly, founders should be
31 harvested in small groups at adjacent nest sites with groups separated by a minimum of 1.5
32 km allowing family group structure to be retained during translocation while simultaneously
33 maximising genetic diversity. Secondly, translocated individuals should be released in family
34 cohorts into patches of optimal habitat that contain adequate shelter substrates interspersed
35 over short distances (~300-500 m, the maximum dispersal distance of females found in this
36 study), thereby facilitating nest establishment and maintenance of family groups. The results
37 of this study have implications for conservation and reintroduction biology as a whole; we
38 highlight the importance of considering spatial genetic structure during all stages of
39 translocations to improve outcomes, and the value of combining genetic and field data to
40 better understand species' social and spatial preferences.

41

42 **Key words**

43

44 Reintroduction biology, conservation genetics, spatial genetics, ecology

45

46 **Declarations**

47

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56 Adelaide, Bush Heritage Australia and the South Australian Department for Environment and
57 Water.

58

59 *Conflicts of interest*

60 The authors declare no conflicts of interest.

61

62 *Ethics approval*

63 Live animal trapping and sampling at Arid Recovery Reserve was conducted under South
64 Australian Wildlife Ethics Committee permit numbers 27/98, 4/99, 22/99, 2/2000, 19/2000,
65 and 18/2000.

66

67 *Availability of data and material*

68 SNP data set and trapping metadata used in the kinship analysis can be found on Isabelle
69 Onley's GitHub repository < <https://github.com/ionley/sticknestratdispersal>>.

70

71 *Code availability*

72 Code used in sex assignment can be found on Dr Graham Gower's GitHub repository <
73 <https://github.com/grahamgower/sexassign>>. Code used in the kinship analysis can be found
74 on Isabelle Onley's GitHub repository < <https://github.com/ionley/sticknestratdispersal>>.

75

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80 constructive feedback on the final draft, and Amy Slender for assistance in the use of
81 COLONY software. We thank four anonymous reviewers for their constructive feedback on
82 the manuscript.

83

84 **Introduction**

85

86 Sociality in mammals has many benefits at both the individual and population level,
87 particularly in regards to female fitness (Silk 2007). A common observation in mammalian
88 social systems is that males will disperse from their natal territory, while females will
89 demonstrate philopatric behaviour and remain close to their place of birth (Greenwood 1980).
90 This pattern typically results in distinct local matriline, with daughters inheriting territories,
91 warrens, or nests from their mothers or other female relatives (Holekamp and Sawdy 2019).
92 Female philopatry can have a number of benefits, including sharing of knowledge about food
93 distribution and landscape cover for predator avoidance, as well as kin-selected social
94 behaviours such as cooperative care of young (Hamilton 1964; Clutton-Brock and Lukas
95 2012). Female philopatry may also be advantageous when shelter sites are limited or require
96 considerable investment, as female offspring can inherit a shelter site from their mother.
97 There are genetic consequences of female kin clustering, wherein female offspring remain
98 close to their natal territory (Peakall et al. 2003; Matocq 2004; Banks and Peakall 2012);
99 potential outcomes of limited female dispersal include mitochondrial DNA-specific
100 population structure, wherein reduced movement of females results in genetic differentiation
101 visible only in the mitochondrial genome (Ruppell et al. 2003), and increased pairwise

102 relatedness between females within territories (Hazlitt et al. 2004). Male-biased dispersal,
103 meanwhile, aids in inbreeding avoidance (Dobson et al. 1997; Liebgold et al. 2011).

104

105 In translocation and breeding programs, social structure and sex-biased philopatry and
106 dispersal should be considered in order to maximise population viability and conservation
107 outcomes (Kleiman 1989; Gouar et al. 2012; Garnier et al. 2021). For example, a study on
108 near-threatened brush-tailed rock-wallabies (*Petrogale penicillata*) in Australia revealed
109 evidence of female philopatry and male-biased dispersal, suggesting that females were less
110 likely to disperse between colonies (Hazlitt et al. 2004). On the basis of these results, Hazlitt
111 et al. (2004) cautioned that a geographically restricted collection of source animals for
112 relocation would likely include highly related females, which could have adverse
113 consequences for the translocated brush-tailed rock-wallaby population, such as inbreeding
114 depression and reduced genetic diversity. However, several studies have noted that the
115 harvesting of social groups during translocation is vital for population establishment in
116 several species, including the black-tailed prairie dog (*Cynomys ludovicianus*) (Shier 2006),
117 as it allows individuals to continue cooperative behaviour such as nest building and
118 allogrooming with neighbours and relatives following translocation (Goldenberg et al., 2019;
119 Shier and Swaisgood, 2012).

120

121 Management strategies for maximising genetic diversity and maintaining cohesive family
122 units are likely to be species specific, highlighting the need to understand dispersal behaviour
123 and patterns of philopatry on a species-by-species basis for effective conservation. These
124 factors are likely to be particularly important when selecting founding individuals, as the
125 success of translocation programs is often determined by the viability of the founding

126 population (e.g. sex and age ratios, numbers, genetic diversity) (Singer et al. 2000; Chauvenet
127 et al. 2013; Pacioni et al. 2019).

128

129 One species that has been the focus of multiple translocations over recent decades is the
130 greater stick-nest rat (*Leporillus conditor*), a relatively large (up to 450g), polygynous murid
131 rodent, which was once widespread across the semi-arid and arid zones of southern mainland
132 Australia (Copley 1999; Pearson et al. 1999; Webeck and Pearson 2005). The greater stick-
133 nest rat produces up to three litters a year, with a typical lifespan of five years in the wild and
134 a generation length of approximately two years (Procter 2007; Pacifici et al. 2013; Woinarski
135 and Burbidge 2016). With the arrival of introduced predators and grazing herbivores with
136 European settlers in the 1800s, greater stick-nest rats became extinct on the mainland by the
137 1930s, with the only surviving population on the Franklin Islands of South Australia
138 (Robinson 1975; Copley 1999). Due to this rapid contraction of population size and
139 geographical range, little was known about its habitat preferences and life history until
140 monitoring commenced on the Franklin Islands and, in recent decades, translocation
141 programs began on a number of islands and fenced mainland reserves (Robinson 1975;
142 Pedler and Copley 1993; Copley 1999; Moseby and Bice 2004; Short et al. 2017, 2019).
143 Greater stick-nest rats are nocturnal, feeding on vegetation, predominantly succulents (Ryan
144 et al. 2003), and constructing large nests of sticks and stones to shelter from predators and
145 temperature extremes during the day (Watts 1976; Copley 1999). Nests are often constructed
146 beneath perennial shrubs, under rocky overhangs, or over historical warrens dug by other
147 species (Copley 1999; Short et al. 2019). While the nests are communal and believed to be
148 shared within family groups (Copley 1988, 1999), little is known about how the nests are
149 passed on from generation to generation.

150

151 Although the behaviour of greater stick-nest rats in the wild is still understudied, in captivity
152 they have been observed to exhibit a matriarchal hierarchy, with the eldest female in the nest
153 assuming the dominant role (Procter 2007) and occasionally behaving aggressively towards
154 males in the vicinity of the female's natal nest (P. Copley, *pers. comm.* 2020). In addition,
155 field observations suggest that females in wild and reintroduced populations appear to be
156 sedentary, while males disperse readily (Robinson 1975; Pedler and Copley 1993; Copley
157 1999). Such behaviour suggests greater stick-nest rats may exhibit female philopatry and
158 male-biased dispersal, however no data have yet been published to demonstrate this. Such
159 social patterns are common in other matrilineal rodent species, such as the black-tailed prairie
160 dog (Hoogland 1995); females demonstrate strong philopatric behaviour whilst males are
161 more wide-ranging and less territorial (Aguilera-Miller et al., 2018; Christian, 1970).

162

163 We studied a translocated population of greater stick-nest rats at the Arid Recovery Reserve,
164 South Australia, in order to understand the social behaviours of the greater stick-nest rat and
165 inform future translocation strategies. Arid Recovery Reserve is located in an arid
166 environment with limited rainfall near the northern edge of the species' former range
167 (Moseby et al. 2011; Short et al. 2019). The translocation program began in 1998 with a trial
168 reintroduction, shortly followed by a full-scale reintroduction the following year (Moseby
169 and Bice 2004). The reintroduction was considered successful (Short et al. 2019), with
170 population growth, limited inbreeding, and up to 98% of genetic diversity retained from their
171 founding groups (Moseby et al. 2011; White et al. 2018); however, greater stick-nest rats
172 demonstrated increased mortality during the summer months and the population size was
173 adversely affected by drought and overbrowsing of vegetation by burrowing bettongs
174 (*Bettongia lesueur*) (Moseby et al. 2018).

175

176 By investigating the dispersal behaviours of the greater stick-nest rat, we aimed to establish
177 whether sex-biased dispersal and philopatry were present in the species and should therefore
178 be considered during the planning of subsequent translocation programs to increase their
179 chance of success. Previously, philopatry and dispersal in the wild have been difficult to
180 determine except through long-term observational studies. Here we use high-throughput
181 sequencing of DNA samples collected during the first four years following the reintroduction
182 of greater stick-nest rats at Arid Recovery Reserve to determine patterns of dispersal and
183 philopatry in this species.

184

185 **Methods**

186

187 **Sample Collection & DNA Sequencing**

188

189 The Arid Recovery Reserve is located 20 km north of Roxby Downs, South Australia, and
190 includes a 14 km² rabbit, cat and fox-proof enclosure of 50 mm fencing (the Main Enclosure)
191 encompassing a dune and swale landscape vegetated predominantly by chenopod and wattle
192 (*Acacia* spp.) (Moseby and Bice 2004). 30 mm foot netting runs along the bottom of the
193 fence, although greater stick-nest rats have been observed to climb this netting and disperse
194 through the 50 mm mesh. Following a successful trial release in 1998, 92 greater stick-nest
195 rats were released into the Main Enclosure in 1999 at random across a number of release
196 sites, as described by Moseby et al. 2011. From 1999 to 2002 (inclusive) tissue samples (tail
197 tips, ~5 mm length) were collected from a total of 56 individuals across 18 nest sites during
198 routine trapping and monitoring at Arid Recovery Reserve and stored at -20°C in 70%
199 ethanol. Trapping effort was equal across all nest sites, and included all known nests in the
200 reserve. Nests were located by radiotracking rats to nest sites. Individuals were a mixture of

201 age classes, some were part of the translocated cohort and some were born in the reserve.
202 Information on the sex, trapping coordinates, age, and nesting site of each individual were
203 recorded in the field. Traps were set in close proximity to the nest, and individuals caught
204 were presumed to inhabit that nest. Where multiple captures were recorded during the
205 lifetime of an individual, trapping location and data from the first adult capture were used
206 (adults were identified as animals >180g according to 7/07/2022 1:54:00 PMProcter, 2007).
207 DNA was then extracted from tissue by S. Barclay using the method described in Barclay et
208 al. (2006). These samples were submitted to commercial sequencing company Diversity
209 Arrays Pty Ltd (DArT) for single nucleotide polymorphism (SNP) genotyping. Diversity
210 Arrays employs a complexity reduction method (DArTseq) to generate SNP data for each
211 individual (Egea et al. 2017; Melville et al. 2017). DArT provided both raw FASTQ files for
212 each individual (subsequently used for sex assignment) and a coded matrix of SNP loci by
213 individual, which was then passed to a genlight object for kinship analysis.

214

215 **Sex Assignment**

216

217 Although field-determined sex data were available for most of the samples, a genetic sex
218 assignment approach was used also to ensure that sexing was accurate (Onley et al. 2021).
219 Briefly, greater stick-nest rat FASTQ sequencing data were first aligned to the house mouse
220 (*Mus musculus*) genome reference using the ‘mem’ algorithm in BWA v0.7.17 (Li and
221 Durbin 2009), after which per-scaffold read counts were extracted using SAMtools v1.10 (Li
222 et al. 2009). As described in Gower et al. (2019), we then used the Python script ‘sexassign’
223 (<https://github.com/grahamgower/sexassign>) to construct two binomial models (one for males
224 and one for females) for the X chromosome “read-dosage” versus that of the autosomes and
225 conduct a likelihood ratio test between them. Sex assignment using this method resulted in

226 ~94% concordance with field-determined sex, with the discrepancies determined to be due to
227 misidentification of individual sex in the field (Onley et al. 2021). This is consistent with
228 previously reported rates for human error when sexing rodents in the field, which are
229 typically around 10% (particularly during non-reproductive periods) (Williams et al. 2004;
230 Hoffmann et al. 2010; Jacques et al. 2015).

231

232 **Kinship Analysis**

233

234 Kinship analysis was performed on the DArTseq data to determine the degree of relatedness
235 of individuals within and between nest sites. Data filtration was performed on the SNP matrix
236 using the ‘dartR’ package in R v3.6.2 (Gruber et al. 2019). Monomorphic and secondary loci
237 were removed from the dataset, and SNPs with a locus call rate <0.80 and a repeatability
238 <0.9 were filtered out. Observed and expected heterozygosity were also calculated. We chose
239 not to filter the dataset based on minor allele frequencies, as this has been shown to mask
240 population structure in large datasets (Linck and Battey 2019; Wright et al. 2019). Following
241 this, an identity-by-descent (IBD) analysis using the KING method of moment was
242 conducted using the R package ‘SNPRelate’ (Zheng et al. 2012). This returned an estimated
243 kinship coefficient for pairings within the population, which was then used to create a
244 network graph to visualise relatedness. In addition, SNP data was also run through the
245 program COLONY v2.0.6.5 using a Full Likelihood analysis to produce full and half sibling
246 dyads. Due to memory constraints, 500 randomly selected SNP markers were used for the
247 COLONY run, with the following settings: polygyny for both males and females, inbreeding
248 present, medium run length, locus error rate of 0.02, and an allelic dropout rate of 0.

249

250 To determine whether male and female greater stick-nest rats displayed a higher degree of
251 relatedness at the cooperative group (nest site) level than within the population as a whole, a
252 Wilcoxon Rank Sum test was performed on kinship coefficients of pairings within and
253 between nest sites according to sex. A Wilcoxon Rank Sum test was chosen because the data
254 were not normally distributed. If sex-biased dispersal is occurring, individuals of the
255 dispersing sex are expected to demonstrate lower relatedness than the philopatric sex at the
256 cooperative group level (Liu et al. 2015).

257

258 **Spatial Autocorrelation**

259

260 To further examine the spatial genetic structure of the Arid Recovery Reserve population in
261 relation to nest sites, spatial autocorrelation analyses were conducted using GenAlEx v6.5
262 (Peakall and Smouse 2012). In order to meet GenAlEx memory requirements, we randomly
263 selected 5,000 filtered SNPs as a representative sample of the dataset. Only individuals that
264 appeared in kinship pairings determined by the IBD-KING analysis were used for spatial
265 autocorrelation analysis. Data were then transformed to the appropriate format using the
266 ‘poppr’ package in R (Kamvar et al. 2014). The SNP data were split into two separate
267 datasets for males and females and pairwise genetic distance was calculated separately for
268 each sex. Decimal latitude and longitude values of the nest locations for each individual were
269 used to calculate a matrix of geographic distance. Using these distance matrices, a spatial
270 structure analysis was implemented to test for spatial heterogeneity at even distance classes
271 of 0.5km intervals and to determine a correlation coefficient, r . This analysis was conducted
272 using a permutation procedure with 999 simulations to test for deviations from zero and 1000
273 bootstraps to estimate the confidence intervals around r . Where r exceeded the 95%
274 confidence intervals of the permutations and the bootstrap confidence intervals did not

275 exceed zero, spatial genetic structuring was declared (Peakall et al. 2003; Hazlitt et al. 2004).
276 Heterogeneity is determined by calculating an ‘Omega’ value and testing whether the
277 observed value is larger than expected under the null hypothesis of homogenous genetic
278 structure, wherein no significant spatial autocorrelation is observed ($P > 0.01$ where $P =$
279 $\Omega_{\text{rand}} \geq \Omega_{\text{data}}$) (Smouse et al. 2008; Banks and Peakall 2012).

280

281 **Male vs Female Nest Fidelity**

282

283 Finally, to corroborate any evidence of female philopatry, field trapping data were analysed
284 to identify rates of recapture over time by sex at the same nest site. This dataset included
285 recorded captures for individuals not included in the genetic analysis, so field recorded sex
286 was used where genetic sex determination data were not available.

287

288 **Results**

289

290 **Samples and SNP Data**

291

292 Fifty-six individuals (32 females and 24 males) were captured across 18 nests with 1-7
293 individuals sampled per nest (mean = 2.9) (Supplementary Information 1). The average
294 male:female ratio per nest was 1.2:1.6. Four individuals (two males and two females) did not
295 have nest site recorded (Supplementary Information 1). The initial dataset contained 21,792
296 SNPs. After filtering, 17,787 SNPs remained, with an expected heterozygosity of 0.323 and
297 observed heterozygosity of 0.301.

298

299 **Kinship Analysis**

300

301 Our IBD-KING analysis yielded 130 kinship pairings, with kinship coefficients ranging from
302 0.032 - 0.25 (Fig. 1), which corresponded with the pairings calculated by the COLONY run
303 (Supplementary Information 2). A kinship coefficient of 0.25 represents a parent-offspring or
304 full sibling relationship, while 0.15 is consistent with half siblings (Lopes et al. 2013).
305 Thirteen individuals showed no (or very low) genetic relatedness to any other sampled
306 individuals, while the remaining 43 individuals formed two clusters (Fig. 1). One cluster
307 contained 11 individuals mostly from three nests (1, 2, & 15) from the north-eastern section
308 of the Main Enclosure, while the second cluster contained 32 individuals from 12 of the 18
309 nests distributed across the entire sampling area (Fig. 1).

310

311 Of the pairings determined by IBD-KING analysis, 35 were female-female and 23 were
312 male-male. Female-female kinship coefficients were significantly lower between nests than
313 within nests (mean = 0.11 +/- 0.05, cf. mean = 0.18 +/- 0.04) whereas male-male kinship
314 coefficients were low and not significantly different between versus within nests (mean =
315 0.10 +/- 0.06, cf. mean = 0.11 +/- 0.02) (Fig. 2).

316

317 Cohabiting females demonstrated a significantly higher degree of relatedness than cohabiting
318 males (mean 0.18 versus 0.11, p-value 0.02) (Fig. 3).

319

320 **Spatial Autocorrelation**

321

322 Results of our spatial autocorrelation analyses for genetic data indicated that heterogeneous
323 spatial structuring was present for both males and females. Correlograms demonstrate that the
324 correlation coefficient between genetic and geographic distance, r , of females is strongest in

325 shared locations, well above the upper 95% confidence intervals of no observed spatial
326 autocorrelation (indicated by U and L in Figure 4), and decreases as physical distance
327 increases, while the r value for cohabiting males is much lower and remains fairly consistent
328 until distance class exceeds 1.5 km (Figure 4). This indicates that, while females did not
329 disperse far from their family groups, males readily dispersed up to 1.5 km from their natal
330 nest. However, confidence intervals overlap zero for both males and females in the first
331 distance class, so some level of uncertainty (likely due to small sample size) must be
332 acknowledged. There is also a slight rise in r at 4 km in both sexes, possibly due to high post-
333 release dispersal.

334

335 **Male vs. Female Nest Fidelity**

336

337 In the trapping dataset, 14 individuals were recaptured on multiple occasions over periods of
338 2 – 24 months (Table 1). Of these, 12 were females and two were males. Nine of these
339 females were recaptured at the same nest over periods of up to 16 months. The mean period
340 of recapture at the same nest site was nine months. The remaining three females were each
341 recaptured at one adjacent nest site to their natal nest. The distance of these adjacent nests
342 from the home nest did not exceed 330 m. Conversely, the two recaptured males were
343 trapped across multiple nest sites over a period of up to 12 months, at distances that ranged
344 from 3.38 km to 1.52 km. This appears consistent with the network graph (Figure 1), in
345 which some individuals (eg. ET183) were trapped at nests across the enclosure from their
346 closely related kin. Of the two individuals that were recaptured as subadults and then again as
347 adults – one male (ET198) and one female (ET147) – the male was recaptured at a different
348 nest site while the female was recaptured in the same nest.

349

350 **Discussion**

351

352 **Evidence for Female Philopatry and Male-Biased Dispersal**

353

354 Our results demonstrate a significantly higher degree of relatedness between female-female
355 pairings of greater stick-nest rat individuals sharing nest sites compared to those inhabiting
356 different nests, a trend not evident in male-male pairings within the same population. Further,
357 there was a significantly higher degree of relatedness between cohabiting female-female
358 pairings than male-male pairings. Females were repeatedly recaptured in the same or adjacent
359 nest sites, while recaptured males were recorded at multiple nest sites around the reserve.

360 One female was also captured in the same nest as a subadult and as an adult, consistent with
361 matrilineal nest inheritance – although the small sample size makes robust conclusions based
362 on this observation difficult. This is the first genetic evidence of female philopatry in greater
363 stick-nest rats, wherein males disperse from the natal nest and females remain in their
364 familial territory, a pattern that is often observed in other polygynous mammals (Greenwood
365 1980).

366

367 There are a number of potential advantages to male-biased dispersal strategies in polygynous
368 species, namely that males increase their chances of breeding by gaining access to multiple
369 females, while females maintain strong knowledge of their home range and available
370 resources, improving the chances of survival for both themselves and their young (Moses and
371 Millar 1994; Pärt 1995; Ruusila et al. 2001). Female site fidelity has been linked to increased
372 survival and reproduction success in several taxa (Cockburn et al. 1985; Bose et al. 2017;
373 Patrick and Weimerskirch 2017), particularly in species like the greater stick-nest rat that
374 invest considerable energy in nest or burrow construction, such as prairie dogs and yellow-

375 bellied marmots (Armitage 1991; Shier 2006). Over time, such systems can result in
376 geographically restricted matriline, with members of the resident sex in nesting sites or
377 territories becoming closely related (Kappeler et al. 2002). Our field results supported the
378 genetic data, with individual females exhibiting higher recapture rates in the same or closely
379 spaced nests over time compared to males.

380

381 While our results provide evidence for male-biased dispersal in the greater stick-nest rat
382 population at Arid Recovery Reserve, the applicability of our findings to other greater stick-
383 nest rat populations is subject to some caveats. Arid Recovery Reserve is a fenced reserve,
384 and greater stick-nest rats used in this study were confined within a 14km² area. Dispersal
385 distance may therefore have been limited by the presence of fences. Further research is
386 needed to determine whether reserve size impacts male dispersal distance in this species. In
387 addition, Arid Recovery Reserve is located in a desert environment, and it is unclear whether
388 climate and resource availability impact greater stick-nest rat dispersal distance. Similar
389 monitoring of populations in coastal or more mesic habitats would inform on this. In any
390 case, we believe that our results have a number of implications for conservation of the greater
391 stick-nest rat, particularly concerning the planning, harvesting, and subsequent management
392 of translocation programs.

393

394 **Conservation Implications & Recommendations for Future Translocations**

395

396 Post-release dispersal is an important, but often overlooked, component of translocation
397 success or failure (Gouar et al. 2012), so understanding dispersal patterns of greater stick-nest
398 rats is likely to be important for the ongoing success of future translocation programs.

399 Selection of wild-caught individuals for translocation from a source population is often

400 opportunistic or transect based and heavily impacted by factors such as trapping success and
401 accessible terrain (Coulson and Eldridge 2010). Further, guidelines around sampling regimes
402 for translocations are limited (Ewen et al. 2012). However, sex-biased dispersal can result in
403 fine-scale spatial genetic structuring, a factor that should be considered when harvesting
404 individuals to establish a new colony (Hazlitt et al. 2004; Banks and Peakall 2012; Pacioni et
405 al. 2020). For example, low levels of female dispersal in black-tailed deer (*Odocoileus*
406 *hemionus columbianus*) have led researchers to suggest that matrilineal groups should be
407 treated as the basic unit of genetic structuring in species demonstrating female philopatry, a
408 major consideration for conservation management (Bose et al. 2017).

409

410 Selection of multiple females from the same territory in a species demonstrating female
411 philopatry will likely result in a higher degree of relatedness than desired and could increase
412 the risk of inbreeding depression in the new population. For example, a genetic evaluation of
413 translocated freshwater fish (*Notropis heterodon* and *Notropis heterolepis*) in Illinois, U.S.A.,
414 determined that the lack of consideration for kinship structure during harvesting had resulted
415 in the selection of multiple full and half sibship pairings, thereby lowering the effective
416 population size of the reintroduced stock (Ozer and Ashley 2013). Ozer and Ashley (2013)
417 suggested that harvesting from multiple sites and across multiple trapping events may
418 decrease the overall relatedness of the new population and improve genetic representation.
419 However, it must also be acknowledged that several studies on mammals demonstrating kin
420 clustering and female philopatry have noted an increase in translocation success when entire
421 family groups were harvested. This has been attributed to the benefits associated with
422 resource sharing, as well as reduced aggression and stress and increased site fidelity during
423 reintroduction (Bradley et al., 2005; Goldenberg et al., 2019; Gusset et al., 2006; Shier and
424 Swaisgood, 2012; Watson et al., 1994) (but see also Franks et al., 2020). Consequently, when

425 translocating a species demonstrating female philopatry, managers should consider the
426 importance of increasing long-term genetic diversity by selecting unrelated founding
427 individuals against the potential survival benefits of maintaining close familial associations.

428

429 Pacioni et al. (2020) proposed a spatially explicit approach to selection of individuals for
430 translocation, wherein prior knowledge of a species' dispersal patterns is applied to determine
431 the appropriate separation distance between candidates to minimise relatedness. This
432 approach can be applied to all species with a predictable dispersal pattern. Trials using this
433 method on woylies (*Bettongia penicillata ogilbyi*) have proven far more effective than
434 conventional transect and grid trapping designs, with resulting samples exhibiting higher
435 genetic diversity and lower relatedness, while requiring minimal increases in time and
436 resource investment by managers (Pacioni et al. 2020). While some uncertainty exists around
437 the spatial autocorrelation analysis due to the small sample size of this study, our results have
438 shown that relatedness is significantly decreased beyond a 0.5 km radius of nest sites for
439 females and 1.5 km for males; an appropriate harvesting strategy would therefore involve
440 selecting small cohorts of males and females from multiple adjacent nest sites which are then
441 separated from the next group by a minimum distance of 1.5 km. This would allow for
442 founding females to retain family groups, while simultaneously maximising genetic diversity
443 and reducing the risk of inbreeding. Post-release monitoring of future translocations would
444 inform on the consistency of this spatial genetic structure when dispersal distances are not
445 limited by fencing.

446

447 Female philopatry is an important adaptive behaviour that increases breeding success,
448 ensuring long-term viability in a population (Stacey and Ligon 1991). In greater stick-nest
449 rats, permanent nest structures appear to be inherited maternally, and are maintained and used

450 by subsequent generations of related females, a strategy that has been shown to improve
451 offspring survival in other species (Armitage 1991; Moses and Millar 1994; Hatchwell and
452 Komdeur 2000; Lutermann et al. 2006). As the construction of such large and complex
453 shelter sites is energetically expensive, resource inheritance by female kin has an added
454 survival advantage, namely that subsequent generations of females in established nests are
455 not required to expend large amounts of energy on founding a new nest and can therefore
456 prioritise foraging for food and caring for young (Myles 1988; Hansell 1993; Almond et al.
457 2019). Since nest sites are central to the breeding behaviour and, consequently, the
458 population viability of the greater stick-nest rat (Aslin 1972; Copley 1999; Procter 2007), the
459 presence of adequate nesting sites should be a consideration for future conservation of the
460 species. An abundance of sticks and dry grass should be present for nest construction. More
461 importantly, rock overhangs and fissures, warrens and burrows, and low, thick perennial
462 shrubs such as *Maireana* spp. and *Rhagodia* spp. act as important substrates for nest building
463 and supply additional protection from predators and environmental extremes, as well as
464 providing a source of food (Copley 1988, 1999; Moseby and Bice 2004; Short et al. 2019).
465 Suitable habitat for future translocations of the greater stick-nest rat should contain a variety
466 of these structures within close proximity, providing ample shelter for both dispersing males
467 and females remaining in their natal territory. Shelter substrates should ideally not be more
468 than 300-500 m apart, as this was the maximum distance travelled by females in the trapping
469 dataset that visited nearby nests.

470

471 Finally, although our results suggest that maintaining related female groups with closely
472 spaced nests should be facilitated and encouraged during translocation, female greater stick-
473 nest rats have been observed to demonstrate aggressive territorial behaviour in captivity, thus
474 overcrowding and reduced capacity for dispersal may increase aggression within a population

475 (Jackson 2003; Procter 2007).. During a trial reintroduction of greater stick-nest rats at Arid
476 Recovery Reserve into an 8 ha release pen, the two largest of the three females quickly
477 established territories that did not overlap; the youngest female roamed between the two
478 territories, but whether this was due to her immaturity or the small size of the enclosure is
479 unclear (Moseby and Bice 2004). Small release pens for family groups may therefore also be
480 used to limit stress, maintain kin clusters and promote shelter establishment (Moseby et al.
481 2014, 2020), but managers should consider the long-term implications of this strategy; once
482 the translocated population has become settled and nests established – greater stick-nest rats
483 at Arid Recovery Reserve built nests within a few months of translocation (Moseby and Bice
484 2004) – larger areas should be provided to facilitate male dispersal, an important mechanism
485 for inbreeding avoidance (Cockburn et al. 1985; Wolff et al. 1988; Szulkin and Sheldon
486 2008).

487

488 **Conclusion**

489

490 Here we have presented the first empirical evidence of sex-biased dispersal behaviour in the
491 greater stick-nest rat. Data were collected within five years of the start of the reintroduction
492 program, suggesting that distinct local matrilineal lines in the greater stick-nest rat can develop over
493 only a few generations, and that male dispersal is likely the primary mechanism for
494 inbreeding avoidance in the species. Based on these results, we present two key
495 recommendations for future translocations of greater stick-nest rats using wild stock. Firstly,
496 an adaptive design for trapping founders, such as the method proposed by Pacioni et al.
497 (2020), would involve selecting small cohorts of males and females from multiple adjacent
498 nest sites that are then separated from the next group by a minimum distance of 1.5 km.
499 Secondly, as greater stick-nest rat matrilineal lines rely on the generational construction and

500 maintenance of nest sites that require a high degree of energy investment, future conservation
501 programs should consider releasing founder individuals in family groups into patches of
502 optimal nesting habitat ideally interspersed at distances not exceeding 300-500 m, thereby
503 encouraging shelter establishment, maintaining group structure, and limiting panic dispersal.

504

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757

758 **Figure Captions**

759

760 **Figure 1** (a) Relatedness network of male (squares) and female (circles) greater stick-nest
761 rats (*Leporillus conditor*) within the Main Exclosure at Arid Recovery Reserve, coloured by
762 nesting site. Thickness of links corresponds to degree of relatedness; (b) Location of the 18
763 sampled nests within the Main Exclosure.

764

765 **Figure 2** Violin plots for pairwise kinship coefficients between female (top panel) and male
766 (bottom panel) greater stick-nest rats (*Leporillus conditor*) trapped in the same or different
767 nests at Arid Recovery Reserve.

768

769 **Figure 3** Violin plots for pairwise kinship coefficients between cohabiting females and
770 cohabiting males of greater stick-nest rats (*Leporillus conditor*) at Arid Recovery Reserve (p-
771 value = 0.01958).

772

773 **Figure 4** Correlograms showing spatial genetic structure in male and female greater stick-
774 nest rats (*Leporillus conditor*). Genetic correlation coefficient (r) is displayed with 95%
775 confidence intervals (U = upper, L = lower) and error bars determined by bootstrapping.
776 Cohabiting females (i.e. distance class = 0) show a significantly higher value of r , with r
777 decreasing as physical distance increases, while cohabiting males show a lower value of r ,
778 which remains variable up to a distance of 1.5 km.

779 **Tables**

780

781 **Table 1** Nest site locations for individual greater stick-nest rats recaptured between August 1999 and October 2002 by capture month and sex. Asterisks

782 indicate individuals that were subadult at the time of trapping. Cells shaded in light grey represent a capture at a different site to the individual's preferred or

783 original nest site.

		Capture Month & Nest Site													
		ID	08/1999	09/1999	01/2000	02/2000	03/2000	04/2000	05/2000	06/2000	11/2000	12/2000	03/2001	10/2001	10/2002
Female Recaptures	ET29										17			17	
	ET42						2*	2*							
	ET44						1		1	1	1				
	ET55				6	7	7				7	7	7		
	ET63										6		6	5	5
	ET133												13	13	
	ET147												6*	6	
	ET149												1	2	
	ET3140		2	2			2	2	2	2	2	2			

	ET3599						12			12				
	ET5976											15	15	
	ET5997							9				9		
Male	ET198												5*	15 & 20
Recaptures	ET5992			7		9				7				

784

785 **Supplementary Information**

786 Table S1. Nest site capture data used in kinship and nest relatedness analysis (first adult

787 capture).

Nest Site	Number of individuals (M:F)
1	4 (3:1)
2	5 (2:3)
3	1 (0:1)
4	2 (1:1)
5	3 (1:2)
6	3 (1:2)
7	1 (0:1)
8	5 (3:2)
9	7 (4:3)
10	5 (1:4)
11	1 (0:1)
12	1 (0:1)
13	2 (1:1)
14	2 (1:1)
15	4 (2:2)
16	1 (0:1)
17	4 (1:3)
19	1 (1:0)

Unknown Nest 4 (2:2)

788

789

790 Table S2. Probability of full and half sibling dyads as determined by COLONY run.

	OffspringID1	OffspringID2	Probability
Full Siblings	ET102	ET103	0.707
	ET102	ET5967	0.706
	ET103	ET5967	0.706
	ET106	ET149	0.706
	ET119	ET259	0.706
	ET151	ET37	0.707
	ET153	ET158	0.707
	ET154	ET188	0.706
Half Siblings	ET106	ET154	0.294
	ET106	ET188	0.294
	ET147	ET163	0.294
	ET147	ET189	0.294
	ET148	ET177	0.294
	ET148	ET186	0.294
	ET149	ET154	0.294
	ET149	ET183	0.294
	ET149	ET188	0.294
	ET152	ET163	0.294
	ET152	ET195	0.294
	ET154	ET18	0.294

ET155	ET184	0.294
ET155	ET32	0.294
ET157	ET192	0.294
ET157	ET193	0.294
ET157	ET198	0.294
ET162	ET196	0.294
ET162	ET29	0.294
ET163	ET195	0.294
ET163	ET233	0.294
ET17	ET187	0.294
ET177	ET186	0.294
ET18	ET188	0.294
ET183	ET188	0.294
ET185	ET231	0.294
ET186	ET187	0.294
ET187	ET193	0.294
ET187	ET195	0.294
ET189	ET192	0.294
ET189	ET193	0.294
ET189	ET198	0.294
ET192	ET193	0.294
ET192	ET195	0.294
ET192	ET198	0.294
ET193	ET195	0.294
ET193	ET198	0.294

ET195	ET198	0.294
ET195	ET233	0.294
ET196	ET255	0.294
ET261	ET29	0.294
ET277	ET29	0.294
ET155	ET50.2	0.293
ET157	ET187	0.293
ET157	ET189	0.293
ET157	ET195	0.293
ET162	ET261	0.293
ET173	ET50	0.293
ET184	ET185	0.293
ET184	ET196	0.293
ET184	ET255	0.293
ET184	ET32	0.293
ET185	ET196	0.293
ET185	ET255	0.293
ET187	ET189	0.293
ET187	ET192	0.293
ET187	ET198	0.293
ET189	ET195	0.293
ET217	ET233	0.293
ET154	ET183	0.292
ET17	ET186	0.291
ET152	ET233	0.273

ET106	ET183	0.034
ET162	ET209	0.004
ET209	ET261	0.004
ET209	ET29	0.004
ET103	ET50	0.002

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