1 **CONSEQUENCES OF SPACE SHARING ON INDIVIDUAL**

2 **PHENOTYPES IN THE NEW ZEALAND HIHI.**

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20 **<u>ABSTRACT</u>**

21   In heterogeneous habitats, individuals sharing a larger part of their home-range are also

22   likely to live in a very similar environment. This 'common environment' effect can

23   generate phenotypic similarities between neighbours and lead to the structuring of

24   phenotypes through the habitat. In this study, we used an intensely monitored population

25   of hihi (or stitchbird, *Notiomystis cincta*) from New Zealand, to assess whether home-range

26   overlap and genetic relatedness between birds could generate phenotypic resemblance for

27   a wide panel of morphological and life-history traits. Using a multiple-matrix animal model

28   approach to partition the phenotypic variance present in the population, we included a

29   spatial matrix measuring home range overlap between birds and estimated the proportion

30   of variance attributable to space sharing. We detected a clear contribution of space sharing

31   to the overall phenotypic similarity for two traits: hatchling mass and laying date. We also

32   confirmed the very low estimates of genetic heritability already found for this species.

33   These results suggest that models including space sharing can offer further insight into the

34   determinants of individual differences in phenotype. In particular, the spatial matrix helps

35   to capture fine-scale variation of the environment that classic animal models would

36   potentially miss or miss-assign. In this species, results also suggest that small but significant

37   genetic heritability estimates are not upwardly biased by clustering of close relatives in

38   space.

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INTRODUCTION

The distribution of animals in their habitat is not random, with most individuals restricting their movements to their home-range, a relatively confined area where they conduct daily tasks to survive and reproduce (Burt 1943; Börger et al. 2008). Home-ranges of conspecifics often overlap, and it is not unusual that several individuals simultaneously use the same characteristics of their habitat, with or without direct interactions (Brown and Orians 1970; Börger et al. 2008). When habitat is heterogeneous, individuals sharing a larger part of their home-range are likely to share similar aspects of their environment (e.g. food sources, vegetation structure, predation risk or micro-climatic conditions). Often referred to as 'common environment' effects (Falconer and Mackay 1996), effects of shared environmental conditions may generate increased phenotypic similarities between neighbours (Kruuk and Hadfield 2007) and can lead to the structuring of phenotypes through the habitat. The magnitude of the common environment effect may vary among phenotypic traits. For example, traits subject to phenotypic plasticity (i.e. the ability of a genotype to produce different phenotypes when exposed to different environments) are by definition more likely to be locally affected by environmental heterogeneity (Via and Lande 1985; Agrawal 2001).

Evolutionary biologists have long been interested in understanding the origin of phenotypic variation in wild populations. The use of quantitative genetic models provides a powerful means to partition the phenotypic variance, and more specifically to estimate the proportion of phenotypic variance attributable to genetic differences between individuals (Falconer and Mackay 1996). These models are usually based on a simple assumption: relatives share an expected proportion of alleles and therefore should share phenotypic similarities (Falconer and Mackay 1996; Kruuk 2004). Accounting for the genetic non-independence between relatives in quantitative models was largely facilitated by the development of the 'animal model', a specific type of mixed effect model used to partition the origins of phenotypic variation

66 (Henderson 1973; Wilson et al. 2010). However, as discussed above, sources of phenotypic

67 similarities cannot be reduced to only genetic factors and other sources of individual

68 similarities are now incorporated in the models (e.g. year or region of birth, parental effects;

69 Kruuk & Hadfield, 2007; Wilson et al., 2010). Recently, it has been suggested that home-range

70 overlap should be considered as a potential source of similarity between individuals (Danchin

71 et al., 2011; Germain et al., 2016; Kruuk & Hadfield, 2007; Van Der Jeugd & McCleery, 2002).

72 In the animal model, additional random effects can be fitted for each source of non-

73 independence between individuals, and for each random effect it is possible to estimate the

74 corresponding amount of the total phenotypic variance it explains. In addition to the matrix of

75 additive genetic relatedness (usually denoted $\mathbf{A}$), used to measure the phenotypic similarity

76 among relatives attributable to additive genetic variance (V_A), it is therefore possible to design

77 a pairwise matrix of home-range overlap among individuals (here denoted $\mathbf{S}$), which accounts

78 for the phenotypic similarities attributable to space sharing in the environment (V_{space}; Regan

79 et al., 2017; Stopher et al., 2012, see Thomson et al., 2018 for a methodological tutorial).

80 Wild study systems in which it is possible to quantify the contribution of space sharing to

81 phenotypic variation between individuals are still rare. To date, the two studies incorporating

82 a spatial matrix in an animal model have been focussed on large mammals (red deer, *Cervus*

83 *elaphus,* Stopher et al., 2012 and Soay sheep, *Ovis aries*, Regan et al., 2017), species that can

84 be accurately tracked in their natural habitat. Unfortunately, it is not always easy (or even

85 possible) to obtain comprehensive data describing the full home range of individuals. A number

86 of other studies have however developed different proxies such as spatial buffers or spatial

87 autocorrelation to extend the study of evolutionary and ecological questions related to space

88 sharing (e.g. sensitivity to local environmental heterogeneity or habitat fragmentation) to many

89 other species already offering longitudinal data (Van Der Jeugd and McCleery 2002; Germain

90 et al. 2016).

91 In the present study, we used a well characterised species, the endangered New Zealand hihi

92 (or stitchbird, *Notiomystis cincta*), to dissect the effect of home-range overlap on phenotypic

93 variance. Hihi were reintroduced to Zealandia sanctuary (Wellington, New Zealand) in 2005

94 and have been extensively monitored since, offering a unique opportunity to collect spatial

95 observations for each individual. Zealandia sanctuary shelters a highly heterogeneous

96 landscape composed of intact native bush, planted exotic trees and regenerating forest patches

97 (Starbridge 2009). Previous quantitative genetic studies on another hihi population have

98 demonstrated low narrow-sense heritability for morphological and life history traits despite

99 large phenotypic variation between birds (de Villemereuil et al., 2018a; de Villemereuil et al.,

100 2019), reinforcing the need to explore other forces generating differences between individuals

101 such as the influence of the spatial structure of the population (Franks et al. 2019). First, we

102 studied dispersal patterns of hihi across Zealandia's landscape in order to understand how birds

103 establish their home-range. Second, we assessed whether home-range overlap generated

104 phenotypic similarities for a wide panel of morphological and life-history traits, while

105 accounting for other contributions to variance. Notably, to confirm low heritabilities in our

106 population, we reconstructed a genetic pedigree of the population so that we could include

107 genetic relatedness in our models and minimise any confounding effect between space-sharing

108 and genetic relatedness.

109

MATERIALS AND METHODS

Study species

Once spread across the North Island of New Zealand, the hihi was reduced to a single island population by the 1880s (Te Hauturu-o-Toi / Little Barrier Island, Hauraki Gulf, 36°11'56.88"S - 175° 4'56.45"E). Since 1982, hihi populations have been reintroduced to several locations across the country and now also persist in six other sanctuaries (Figure 1). Hihi are a sexually dimorphic passerine bird that usually nest in tree cavities but mainly use nestboxes in the reintroduced populations. Although the hihi diet is composed of a combination of fruit, nectar and small invertebrates (Castro et al. 1994), supplementary feeding (20% sugar water mix) is necessary for population survival in almost all reintroduced populations. In our study site (Zealandia sanctuary, see below), most of the adult hihi reproduce in their first year and live on average 2.8 years. Females lay clutches ranging between two to five eggs between September and March, during the Austral spring and summer. Multiple clutches can be laid within a season, with one or two usually successful. Within a season, males exhibit two different reproductive strategies. Territorial males defend their nests and mate-guard their female partner but also look for extra-pair partners in other territories (Ewen et al., 2004). Floater males (~30%), usually yearlings, do not possess a territory but harass settled females for copulations (Brekke et al., 2015). These strategies result in a high ratio of extra-pair paternity in the species (around 64% in Zealandia, this study, and 60% in Tiritiri Matangi Sanctuary, Brekke et al., 2013).

Zealandia sanctuary

Zealandia (formerly known as Karori Wildlife Sanctuary) is an urban eco-sanctuary, located in Wellington city (New Zealand, 41°17'26.29"S – 174°45'10.69"E) (Figure 2). The valley in which Zealandia is located has a mixed history of hunting, farming, mining and forestry. In the past century, the forest has been allowed to re-establish, resulting in a highly heterogeneous

135 habitat with both intact and regenerating forest patches. With the construction of a 2.2-meter-

136 high and 8.6 km long fence, the 225-hectare sanctuary has been mammalian pest-free since

137 2000. In 2005, a first group of 64 hihi translocated from Tiritiri Matangi Island and Pukaha

138 National Wildlife Centre was released in the valley (Figure 1). Subsequently, six other

139 translocations happened between 2005 and 2012 with a total of 57 birds released. Despite a

140 high mortality of reintroduced birds (65%), the hihi population in Zealandia has increased to

141 an estimated size of 112 individuals in 2017. Natural immigration in the park is impossible as

142 the closest hihi population resides on an offshore sanctuary (Kaptiti Island), 50 km away. Birds

143 have been observed emigrating outside of the park, but no nesting attempts have ever been

144 reported.

145 ***Phenotypic, life-history and spatial data collection***

146 For each nesting attempt (i) the identity of the social mother and social father, (ii) lay, hatch

147 and fledge dates, and (iii) the number of eggs, chicks and fledglings was recorded. Twenty days

148 after hatching, surviving hatchlings are measured (mass, tarsus length, head-bill length, wing

149 length) and banded with a unique combination of colour bands. Laying date is recorded as the

150 number of days starting at the first day of September (e.g. 12th of September corresponds to

151 day 12, 12th of January corresponds to day 103). Longevity was estimated from individual

152 survey data: since the population was established, rangers and volunteers have been carrying

153 out observations all year round. Most of the observations are made at feeding stations or close

154 to nest boxes, but also on the tracks and therefore can be associated with their GPS coordinates,

155 with position and timing uploaded into a database (containing 16,958 unique observations

156 between 2008 to 2016 included in this study; Table 1).

157 ***Dispersal estimates***

158 Natal and adult distances travelled during dispersal events were estimated for all males and

159 females. For fledglings, natal dispersal was recorded as the distance between the natal nest box

160 and the nest box used during the first breeding attempt. For nesting adults, two measures were

161 calculated: *(1)* the dispersal within the same reproductive season, based on the bird's movement

162 during a single reproductive season and *(2)* the dispersal between reproductive seasons, based

163 on the distance between the first nest box used during the year *y* and the last one used in year

164 *y-1*. Note that in the absence of dispersal, the distance was considered as zero. We used a

165 permutation test to assess whether birds were dispersing more or less than randomly expected.

166 To do so, we used for each bird that dispersed the nest box where the bird was last observed as

167 the starting nest box, then randomly drew a nest box of arrival from the list of all potential nest

168 boxes. The average distance travelled by birds during this artificial dispersal event was

169 calculated for the population. We repeated the procedure 50,000 times to create a distribution

170 of randomised dispersal distances, and then compared, for each sex, the observed mean

171 dispersal distance to the 97.5% and 2.5% percentiles of the randomised distribution. Finally,

172 we used a similar procedure to check whether or not relatives tended to cluster in space despite

173 natal dispersal. We identified all pairs (or trios) of siblings that survived to the next breeding

174 season and occupied a nest box, and calculated the distance between the two (or three) nest

175 boxes. To test whether siblings tend to establish nest boxes closer to each other than expected

176 by chance, we randomly chose two (or three) nest boxes among the occupied nest boxes and

177 estimated the average distance between them. Again, we repeated the procedure 50,000 times

178 to create a distribution of randomised clustering distances, and compared it to the observed

179 distance.

180 *Pedigree construction*

181 The social pedigree was constructed using colour band information of the social mother and

182 social father observed at each nest box. Since 2010, feather samples of hatchlings have been

183 collected, allowing us to build a genetic pedigree of the population. DNA was extracted from

184 feather samples using either the Promega Wizard® SV genomic DNA purification system

185 (PROMEGA) or the Qiagen DNeasy Blood and Tissue kits following the manufacturer's

186 instructions. To assess genetic paternities, we amplified 18 microsatellite markers developed

187 for the hihi (i.e. 15 specific markers, three designed for other passerines; Brekke et al., 2009).

188 We then used individual's genotypes in the software COLONY to reconstruct the pedigree

189 (Wang 2013). All parameters were set up as described in de Villemereuil et al. (2019). Briefly,

190 all social maternities were assumed to be correct. When female identity was missing, sibships

191 were grouped into the same family but mother identity was not specified. All males observed

192 in the population during the month of September prior to the breeding season and all males

193 observed in the population before June following the breeding season (except yearlings) were

194 considered as potential candidate fathers. The probability of parents being in the candidate list

195 was set as 0.9 for females and 0.8 for males following Brekke et al. (2015). Both sexes were

196 defined as polygamous. Allele frequencies and genotyping error rates were set conservatively

197 as 0.05 (although true genotyping error rates are up to 0.012 when assessed from repeat

198 genotyping of 10% of samples). In total, the pedigree contains 1,095 unique birds, across seven

199 generations, with an average inbreeding coefficient between birds of 0.008 ($\pm$0.028).

200 ***Home-range estimates and spatial matrix***

201 We extracted adult lifetime survey observations for all females and males present in the genetic

202 pedigree, excluding any individuals that had fewer than 10 observations and observed at less

203 than three different locations, following the method used in Stopher et al. (2012) and the

204 recommendations of Börger et al. (2006). Simulations suggest that, in our dataset, we capture

205 $90 \pm 0.9\%$ of the true home-range when reconstructing a home-range based on only 10 sightings

206 (See Appendix 1). On average, each bird was observed 153 times (between 10 and 1,487,

207 Figure S2). Because most of the observations were recorded at feeders or nest boxes, many

208 observations shared the exact same geographical coordinates, causing problems when

209 estimating individuals home-range using kernel methods (Tufto et al. 1996). To solve this

210 issue, we 'jittered' locations by adding a random number sampled between 1e-04 and 1e-05 to

211 X and Y GPS coordinates, a maximum change of approximately 13 m. Home-range sizes were

212 estimated for each female using a kernel density estimation from the package *adehabitatHR*

213 (Calenge 2006), using a 95% isopleth allowing us to discard observations considered to be

214 outliers. Note here that because the observations are made on discrete points within the range

215 (except tracks observations), our estimation of home-range is unlikely to be as accurate as home

216 ranges described in Stopher et al. (2012) or Regan et al. (2017). However, contrary to methods

217 using a spatial buffer to create individual's home-range or spatial autocorrelation, we allow

218 variation between individual home-range sizes, which reflects more closely the reality of the

219 spatial use of the habitat by the hihi.

220   We then calculated home-range overlap for all possible pairs of individuals using

221 Bhattacharyya's affinity (BA; Bhattacharyya, 1943) as computed in the *adehabitatHR* package

222 (see Figure 2 for an example). BA estimates provide three main advantages. First, as a three-

223 dimensional coefficient, BA not only accounts for space, but also for the probability of re-

224 sighting an individual at different locations within its home-range, therefore capturing the

225 utilised distribution of the home-range (Fieberg and Kochanny 2005). Second, BA ranges from

226 zero to one, making it comparable in scale to genetic relatedness. Finally, this coefficient is

227 non-directional and symmetric, as it uses the joint distribution of the home-ranges of the two

228 focal individuals. Altogether, we created a spatial matrix (**S** matrix) containing pairwise

229 similarity metrics for 143 females and 191 males (334 birds and a sex ratio of 1.3:1; see Figure

230 S3 for the distribution of BA values). Finally, note that for morphological traits (measured on

231 hatchlings), we used maternal home-ranges to estimate the spatial overlaps included in the **S**

232 matrix. We chose not to include a spatial matrix for paternal home-ranges as males contribute

233 little compared to females in chick provisioning (Ewen & Armstrong, 2000). We are also aware

234 that, because birds are confined to a sanctuary, home ranges may be smaller, and overlap could

235   be higher than expected in a free-ranging population. However, nest boxes are mainly

236   concentrated on the North-Western slopes of Zealandia valley (see Figure 2.a) and nesting

237   outside of nest boxes in the South-Eastern side of the park is very rare. For this reason, we

238   don't think that competition for space between birds is a major concern.

239   ***Partitioning of phenotypic variance***

240   All analyses were performed with R statistical software (version 3.3.2, R Development Core

241   Team 2016). We fitted animal models to estimate the contribution of space sharing to

242   phenotypic similarity, along with other random and fixed effects, for: *(i)* morphological traits

243   (hatchling mass (g), hatchling tarsus length, head-bill length and wing length (mm)), and *(ii)*

244   female life history traits (laying date, number of eggs laid, number of fledglings, fledgling

245   success, probability of recruitment, longevity). To partition the phenotypic variance, we used

246   the phenotypic and pedigree information collected between seasons 2010/2011 and 2016/2017,

247   and implemented in generalised linear mixed effect models (GLMM) using the package

248   MCMCglmm (Hadfield 2010). Depending on the trait modelled, we included fixed effects

249   identified by de Villemereuil (2019) as influencing the trait (e.g. such as sex, mass, clutch

250   number, lay date or female age; see Table 2 for details). Laying dates, number of eggs laid,

251   number of fledglings and hatching success were only considered for females. Note that for

252   longevity, we only used birds hatched between 2010 to 2014 to avoid bias for recent chicks for

253   whom longevity is not yet available (See Table 2).

254   For each trait, we compared two sets of models (with or without spatial effect) varying in the

255   structure of their random effects. For the first set, we included *(i)* individual identity to estimate

256   variance due to additive genetic effect (V_A), *(ii)* identity of the mother (V_{mother}) and of the social

257   father (V_{father}) to incorporate variance linked to non-genetic parental effects and *(iii)* year (V_{year})

258   and month of hatching when relevant (V_{month}) to partition the variation attributable to seasonal

259   characteristics of the environment. Note that for female-based traits such as laying date, we

260 used the identity of the female (V_{female}) and of her social partner (V_{male}) to account for repeated

261 measures (see Table S1) and potential residual autocorrelation. In the second set of models we

262 accounted for space sharing by including the spatial matrix (**S** matrix) of the focal individual

263 as an additional random effect. To do so, we included the inverse of this matrix using the

264 '*ginverse*' parameter of the MCMCglmm package (following the recommendations of

265 Thomson et al., 2018). Note that to ensure the **S** matrix inverse was positive definite, we

266 transformed it using the *make.positive.definite* function from the lqmm package (Geraci, 2014,

267 see Figure S3 for comparison of both matrices). The error distribution was chosen to fit each

268 trait (see Table 2). The number of iterations and the thinning interval were chosen to ensure

269 that the MCMC effective sample size for all parameters was higher than 1,000. Burn-in was

270 set to a minimum of 3,000 iterations and increased if convergence was not reached.

271 Convergence of all parameters was assessed graphically and using the Heidelberger and Walch

272 test (1981) as implemented in the 'coda' package (Plummer et al. 2006).

273 We analysed outputs of the animal models according to their error distribution. For Gaussian

274 traits, proportions of variance, including narrow-sense heritability (h^2), are directly computed

275 from the outputs of the model as the ratio of the variance of interest on the sum of variance

276 estimated for fixed and random effects (de Villemereuil 2018a). Note that the lay date, number

277 of eggs and the number of fledglings were considered here as Gaussian traits as their

278 distribution is close to Gaussian after we accounted for the clutch number in the models (see

279 de Villemereuil et al., 2018). For non-Gaussian traits, variance decomposition was performed

280 using the *QGicc* function from the *QGglmm* package (de Villemereuil et al., 2016) which

281 computes intra-class correlation coefficients (ICCs) for each random component. In GLMM,

282 ICCs are not additive (i.e. their sum is not equal to one) as the link function is not linear, which

283 means that h^2 is no longer an ICC (i.e. additive genetic variance must be additive by definition).

284 To enable comparison of the genetic variance with all other random components of the model,

285   we thus chose to report the total genetic variance (i.e. including the non-additive part of the

286   genetic variance generated by the link function) and therefore use the broad-sense heritability

287   (H^2, i.e. the actual ICC associated with genetic variance) for these non-Gaussian traits. See de

288   Villemereuil, 2018 and de Villemereuil et al., 2016 for more information on the subject.

289   Finally, note that variance parameters are reported as medians and their median absolute

290   deviations (an equivalent for the medians as the standard deviation of a mean; mad R function,

291   R core Team 2020).

292

293   **RESULTS**

294   *Dispersal*

295   On average, fledgling travel 779m (s.d. = 450m) between their natal nest box and the nest box

296   they use for their first breeding attempt. Note that female fledglings travelled on average

297   slightly further (824m) than males (745m). According to our permutation test, there is no over-

298   or under-dispersion for natal dispersal distance for the males (p = 0.32, Figure S4a), while

299   significant natal over-dispersion was observed for females (p = 0.01, Figure S4a). In other

300   words, male fledglings disperse randomly, while female fledglings disperse significantly

301   further from their natal nest box than would be expected by chance.

302   The average observed adult dispersal distance between reproductive seasons is 107m (s.d. =

303   259m) with females dispersing on average 68m and males 145m. This time, significant under-

304   dispersion is observed (p < 2e-5, Figure S4b). Similarly, dispersal events between reproductive

305   attempts in a single season are scarce, as the average distance travelled by birds is 57m (s.d. =

306   199m). Females have an average dispersal distance of 59m and males of 54m, with again

307   significant under-dispersion (p < 2e-5, Figure S4c). Finally, we only observed 44 clutches with

308   more than one offspring surviving the first winter and nesting the next spring (n= 59

309   fledglings). The average distance between siblings was 722 ± 429m. According to the

310 permutation test, there is no over- or under-clustering between siblings after natal dispersal (p

311 = 0.86, Figure S4d), suggesting no tendency of siblings to establish home ranges close together

312 following dispersal from the natal nest.

313 *Variance of morphological traits*

314 When adding the spatial matrix, the proportion of phenotypic variance explained by space

315 sharing was relatively small for all morphological traits except hatchling mass and head-bill

316 length, but the lower interval did not reach zero only for hatchling mass (hatchling mass

317 (posterior median= 0.11, ± median absolute deviation = 0.09), tarsus length (0.01 ± 0.01), head-

318 bill length (0.04 ± 0.06), and wing length (0.02 ± 0.02), Figure 3, Supplementary Table S1 a-

319 d). Except for tarsus length, the proportion of phenotypic variance explained by genetic

320 relatedness between relatives was relatively small: the posterior median or V_a was: hatchling

321 mass (without **S** matrix: 0.03; with the **S** matrix: 0.02), tarsus length (0.14; 0.14), head-bill

322 length (0.03; 0.03) and wing length (0.02; 0.02). Low posterior modes could either reflect very

323 low additive genetic variance or a lack of power from our dataset to precisely infer variance

324 parameters. However, our previous study on another population of hihi, incorporating power

325 analyses for a similar pedigree, found similar estimates for additive genetic variance (de

326 Villemereuil et al. 2019), making the second hypothesis unlikely. For all sets of models (with

327 or without the **S** matrix), sex was a significant effect for all morphological traits, reflecting the

328 dimorphism between hihi males and females (i.e. males being larger than females, all pMCMC

329 < 0.03). In contrast, clutch size only significantly influenced tarsus length (pMCMC = 0.04,

330 for both sets of models). The proportion of variance explained by other factors is described in

331 Figure 3 and Tables S1a-d.

332 *Breeding and life-history traits*

333 In contrast to morphological traits that all presented similar patterns, results were less

334 concordant across breeding and life history traits. For lay date, space sharing between

335   individuals explained a small but significant part of the total phenotypic variance (posterior

336   median = 0.06, ± median absolute deviation = 0.05, see Figure 3 and Table S1e for more

337   information). The part of phenotypic variance explained by genetic variance was consistent

338   between both sets of models (without $\mathbf{S}$ matrix: 0.08 ± 0.07, with $\mathbf{S}$ matrix: 0.09 ± 0.08). Laying

339   date is influenced by the clutch order (pMCMC values < 2.01 e-05).

340   Space sharing had little effect on the number of eggs (posterior median of the variance

341   explained = 0.01 ± 0.01, see Figure 3 and Table S1f for more information) and genetic variance

342   explained approximately 6% of the total phenotypic variance in both models (with and without

343    $\mathbf{S}$ matrix: posterior median= 0.06 ± 0.06 and 0.06 ± 0.06, respectively). The number of eggs

344   produced per clutch was significantly influenced by laying date, early clutches being more

345   successful than late ones (pMCMC value < 2.0 e-05).

346   The effect of space sharing on the number of fledglings produced by each bird was close to

347   zero (posterior median = 0.01 ± 0.2, Figure 3, Table S1g). The part of phenotypic variance

348   explained by genetic relatedness between the model without spatial terms (posterior median =

349   0.05 ± 0.05) and the model with the $\mathbf{S}$ matrix (posterior median = 0.06 ± 0.06) is again

350   consistent. Neither the laying date, the age of the female nor the clutch size significantly

351   influenced the number fledged at the end of the nesting period, and this was true with or without

352   the $\mathbf{S}$ matrix (pMCMC all > 0.23).

353   Finally, for the non-Gaussian traits (longevity, recruitment, fledging success), estimates for

354   both genetic and spatial components of the phenotypic variance are all below 0.02 (see Figure

355   3 and Tables S1h-j). Concerning fixed effects, sex did not influence longevity (pMCMC value

356   = 0.81), and hatchling mass did not influence the probability of recruitment (pMCMC value =

357   0.11). Fledgling success was positively correlated with laying date (pMCMC value < 0.005)

358   but was negatively correlated with the square of laying date (pMCMC value = 0.001), reflecting

359   a nonlinear relationship between the two.

360

DISCUSSION

Here, we used an extensive observational dataset to understand the effect of space sharing on phenotypic diversity between hihi in the Zealandia population. Our results show a clear contribution of space sharing to overall phenotypic similarity for hatchling mass and laying date but was not significant for the other traits we studied. These results suggest that models including space sharing can offer further insight into the determinants of individual differences in phenotype.

a. Individual dispersal

As a first step, we assessed whether or not, i) home-range overlaps were stable over individuals' lifespans and ii) dispersal patterns prevent the clustering of relatives in space. Our results show that hihi dispersal differs with age: fledglings distribute widely across the landscape (average dispersal distance of 779m), but once established in a territory, adults have strong site-fidelity within and between breeding seasons, a trend ubiquitous among birds (Greenwood 1980). This result supports previous work on the Tiritiri Matangi Island population and Maungatautari sanctuary hihi populations (Ewen et al., 2004; Richardson et al., 2010). Consequently, home-range overlap between individuals should be relatively stable across time and we can expect roughly permanent effects of shared environment on hihi phenotypes. Moreover, we couldn't find any evidence of siblings clustering in space when selecting a nest box for reproduction (average distance between nest-siblings of 722m). These results support the idea that natal dispersal should ensure that home-range overlap is independent from genetic relatedness and reduces the chances of confounding genetic and spatial effects in the animal model (see section *d* for a specific discussion on this topic).

b. Global influence of the spatial matrix

384   For hatchling mass and laying date, we found that home-range overlap between hihi explain a

385   low but significant part of the variation between birds. We did not detect any influence of the

386   **S** matrix for any other traits we studied. More precisely, we found that spatial overlap explained

387   10.6% (± median absolute deviation= 8.8%) of the variation in hatchling mass and 5.9% (±

388   5.2%) of the variation of laying date between hihi. It is interesting to note that our results are

389   consistent with the previous results published in the literature for species with very different

390   social, ecological and life-history characteristics. Despite these important differences between

391   the hihi and the Soay sheep or the red deer, both Regan et al. (2017) and Stopher et al. (2012)

392   found similar influence of the spatial matrix on new-borns mass (respectively 6.0% ± 4.8% for

393   the Soay sheep lambs and 5.9% ± 4.8% for red deer fawns). Regan et al. (2017) also found a

394   significant effect of the **S** matrix on Soay sheep birth date (5.6 ± 4.0%). The influence of the

395   micro-habitat on hatchling mass and laying date is not surprising, as shown by the numerous

396   papers studying the impact of the environment on those two phenotypes published in the last

397   decades (e.g. Crick & Sparks, 1999; García-Guerrero et al., 2013; Nussey, Wilson, &

398   Brommer, 2007). However, even when accounting for large scale environmental variation in

399   the animal model (i.e. by adding temperature or year as a fixed or random effect), the addition

400   of the **S** matrix significantly helps to better assign a part of the overall phenotypic variation for

401   both mass at birth and laying date for all three species aforementioned.

402   The absence of influence of the **S** matrix on other morphological traits (tarsus length, wing

403   length and head-bill width), on the number of eggs laid and on the number of hatchlings is a

404   result partly shared by Regan et al. (2017). Indeed, they found weak influence of the spatial

405   matrix on jaw length or any other adult traits. This could be explained by the relative robustness

406   of morphological traits to environmental variation or (for adult traits at least), by the fact that

407   the spatial matrix is not constructed at an appropriate time scale (see last paragraph of the

408   discussion below). For the non-Gaussian traits studied in the hihi population (longevity,

409 recruitment and fledgling success), the low contribution to variance from all random effects of

410 the animal model (including space sharing) could also be linked to a methodological issue:

411 using GLMM, parameters for non-Gaussian traits were inferred on the latent scale and needed

412 to be back-transformed to allow correct interpretation and comparisons between traits. For

413 several reasons discussed in de Villemereuil (2018b), GLMM models are usually considered

414 as 'noisy' statistical models and this assumed uncertainty generally results in small ratios of

415 the random effect variances to the total variance (e.g. broad-sense heritability for recruitment

416 was estimated as 0.03 [2.3^{e-10} – 0.14] on the latent scale and 0.01 [8.6^{e-11} – 0.05] on the data

417 scale).

418 *c. Dissecting the spatial matrix*

419 Even if it is clear that the **S** matrix explains some aspects of the phenotypic variance, this

420 variance decomposition framework does not identify which biological processes contribute to

421 the phenotypic similarities between conspecifics that share a part of their home-range. In our

422 situation the strongest driver of phenotypic diversity captured by the **S** matrix is likely to rely

423 on fine scale resource heterogeneity, known to classically impact both lay date and hatching

424 mass (Blondel et al. 1993; Carrete et al. 2016). Despite variations of temperatures between

425 years (already known to influence hihi laying date in another population, de Villemereuil et al.,

426 2018a; and explaining up to 23% of the variation for laying date in our models), variation in

427 home-range quality can also emerge from the vegetation structure or the landscape topography

428 surrounding individuals' nest boxes. In Zealandia, these variations are likely to be partly

429 buffered by the presence of feeders, used by birds year-round as a source of supplementary

430 energy when fruits or flowers are rare in the habitat. However, sugar water is mainly

431 carbohydrates and lacks protein, fibre and lipids, essential for growth and particularly

432 important during chick rearing (Marciniak et al., 2007; Walker et al., 2013). To satisfy the

433 nutritional requirements of their chicks (as well as their own requirements), hihi are known to

434 change their diet during the year, switching from a diet based on flower nectar in winter (65%)

435 to a diet essentially composed of insects (87%) during spring and summer (data from Kapiti

436 Island sanctuary, Castro et al., 1994). The heterogeneous structure of the forest around each

437 territory, and consequently the heterogeneous access to high-nutrient resources, could therefore

438 be captured in the **S** matrix, explaining its effect on hatchling mass but also on laying date if

439 females try to synchronize their reproduction with the quality of resources present in their

440 home-range (Brekke et al. 2013).

441 For the hihi, but more likely for species adopting high social organisation, other characteristics

442 might also be captured by the matrix, in particular, transmitted social information between

443 unrelated individuals, also referred as cultural inheritance (Danchin et al. 2011; Sheppard et al.

444 2018). Individuals sharing an important part of their home-range are more likely to interact

445 with each other than with non-neighbouring individuals. Copying other individuals' behaviour

446 is frequently observed in wild animal populations (Dugatkin 1996; Laland 2004), including the

447 hihi (Franks and Thorogood 2018; Franks et al. 2019), and can result in the rapid spread of

448 specific behavioural phenotypes, ultimately increasing behavioural heterogeneity between

449 groups. For example, variation in behaviour can be observed locally for traits such as foraging

450 (Coolen et al., 2003), parental care (Champagne, 2008), mate and habitat choice (Dugatkin

451 1996; Doligez et al. 2002) or predator evasion (Halloy et al. 2007). While achievable from an

452 analytical perspective, disentangling social effects from spatial effects is however extremely

453 challenging in term of data collection as it would require a full understanding of what aspect

454 of the environment is varying spatially (e.g. food resources, predation, population density,

455 topography) and a precise social network of the studied population (including the outputs of

456 social interactions in terms of costs and benefits). Such a fine scale study is obviously

457 extremely hard to obtain in wild populations, and conclusions about the **S** matrix should

458 therefore be made with caution, especially when considering highly social species.

d. *Genetic and spatial relatedness: missed or miss-assigned phenotypical variation?*

In addition to including the spatial matrix, our models also accounted for genetic relatedness. Estimates of both narrow- and broad-sense heritabilities were low and varied between 0.01 for the probability of fledgling recruitment to 0.14 for tarsus length. Moreover, most of the estimates have the lower bound of the credible interval very close to zero. We have already observed a similar pattern of low additive genetic variance in the Tiritiri Matangi population, which was shown to be robust to the pedigree size available for hihi populations (de Villemereuil et al., 2018a; de Villemereuil et al., 2019). This absence of heritability for these traits reflects a lack of adaptive potential, especially as they are known to be under strong selection (see de Villemereuil et al., 2019 for more discussion on this subject).

Although small in this study, the proportion of phenotypic variation explained by genetic variance has been the main focus of most studies that included space sharing in quantitative genetic models. Indeed, Van der Jeugd & McCleery (2002), Stopher et al., (2012) and Regan et al., (2017) were all concerned about a potential bias of heritability estimates due to close relatives being clustered in space (de Villemereuil, Gimenez, & Doligez, 2013; Kruuk & Hadfield, 2007). When relatives are clustered, they share both environments and genes, resulting in biased estimation of heritability estimates as they can be inflated by effects attributable to shared environment. While the three studies found mixed evidence of significant bias in heritability estimates, it is unlikely that heritability estimates are miss-assigned in our models as a consequence of the spatial organisation of hihi. Although the hihi heritabilities detected were small, there was very little correlation between the S matrix and the G matrix (Pearson's correlation coefficient between off-diagonal elements = 0.03). Further, as discussed previously, the dispersal pattern of juveniles and adults, combined with the relatively weak survival to adulthood (based on our observational data, ~37% of fledglings recruit into the population) prevents relatives being clustered in space. However, it remains relevant to

484   question how the redistribution of the variance occurs between models that include or do not

485   include the **S** matrix.

486   Interestingly, the variance attributable to home-range overlap predominantly comes from a

487   redistribution of the estimated maternal effects. Comparing models for hatchling mass, 8 out

488   of the 10.6% of the phenotypic variation explained by home-range overlap was captured by the

489   maternal component of the model (V_{female}) when the **S** matrix was not considered. Similarly, 5

490   out of the 5.9% of phenotypic variation attributable to home-range overlap was captured by the

491   social maternal component of the model for laying date. This result demonstrates that it is

492   possible to refine our understanding of social effects on differences between individual

493   phenotypes, suggesting here that a part of the variance usually attributed to a difference

494   between social mothers is actually attributable to the way they use their close environment.

495   More importantly, this observation also suggests that the variance explained by space sharing

496   may already be captured in classical quantitative genetics models (e.g. using maternal effects

497   in this example), as only a very limited additional part of the residual variance is captured when

498   including the **S** matrix in our models (approximately 3% for hatchling mass). Finally, note that

499   for most of the phenotypes studied here, a large part of the variance therefore remains

500   unexplained in this study (up to 75% for the number of eggs), and its origin remains an open

501   question.

502   *e.*   ***Where to go next?***

503   In the light of our results, we would like to raise some recommendations and share exciting

504   directions for future research. Firstly, we encourage researchers to include spatial variation of

505   the environment in their quantitative genetic models to fully understand the micro-

506   environmental drivers of phenotypic variation, but also to better assess the degree of bias in

507   quantitative genetic parameters due to this component. We understand that obtaining home-

508   ranges requires an incredible effort of localisation of individuals, from the early stage of the

509   pedigree reconstruction. To circumvent this step, it is possible to implement spatial

510   autocorrelation (SAC) in quantitative genetic models, a method largely used in forestry science

511   (Banerjee et al., 2010; Silva, Dutkowski, & Gilmour, 2001) but also with wild animals (Van

512   Der Jeugd and McCleery 2002; Stopher et al. 2012). It is also possible to use a circular spatial

513   buffer around individuals' breeding or capture locations and infer individual home-range from

514   there (Germain et al. 2016). Although less effort is needed to implement SAC or to create a

515   circular spatial buffer, one should note that these methods are unlikely to be as accurate as an

516   approach using the **S** matrix, mainly because they assume very little variation in individuals'

517   distribution in space use which is rarely relevant to wild systems (Regan et al. 2017).

518   Another limitation, this time shared by the model used in our study, is the absence of temporal

519   variation in both environmental conditions and in individual's home-range over time. Such a

520   situation is unlikely to be realistic, especially when considering the survey period necessary to

521   build pedigree-based analyses. Moreover, models of home-range overlap often presuppose that

522   all individuals are alive at the same time (e.g. they are compiled in the same **S** matrix), even if

523   their lives never overlapped. If the environment is stable, this situation is not a major issue.

524   However, in a changeable environment, this approach could create similarities between

525   individuals that do not exist. We see two solutions to solve this problem. First, it would be

526   possible to design a spatial matrix with multiple entries for each individual, one per event in

527   the analyses (e.g. reproductive season) but this approach would be extremely data hungry.

528   Another approach would consist of eliminating the need for a long-term pedigree (and therefore

529   from temporal variation of space over the length of the pedigree) by using genomic approaches.

530   This would provide an "instantaneous snapshot" of genetic similarities in the population

531   (Bérénos et al., 2014; Santure, Cauwer, & Robinson, 2013; Yang et al., 2011), that could be

532   combined with a "snapshot" of environmental similarities between individuals to partition trait

533   variation.

534 Finally, traits likely to be impacted by both genetic and spatial elements such as ranging

535 behaviour, dispersal or fitness can present inherently non-Gaussian distributions. Our attempt

536 to provide estimates of the proportion of variance explain by the genetic structure or the spatial

537 organisation of the population for non-Gaussian traits (i.e. longevity, fledgling success and

538 recruitment) was not conclusive. Datasets built on a longer period of time should however have

539 enough statistical power to provide such estimates. Further, the recent development of

540 statistical methodologies using non-normal distributions for quantitative genetic inference

541 (Ayres et al., 2013; de Villemereuil, 2018b; Morrissey et al., 2014) may enable this to become

542 more common practice.

543

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735
736

FIGURE CAPTIONS

738 **Figure 1: Hihi populations across New Zealand** with a focus on *Te Hauturu-o-Toi*, the

739 remnant population (larger yellow point). Also represented are the studied population from

740 *Zealandia Sanctuary* (small orange dot) as well as five other reintroduced populations (small

741 yellow dots), including Tiritiri Matangi Island, Pukaha National Wildlife Sanctuary, sanctuary

742 mountain Maungatautari and Kapiti Island. Image modified from Wikimedia Commons.

743

744 **Figure 2. Locations of Zealandia nest boxes and feeders,** and example of home-range overlap

745 computed with adeHabitat. The first panel (a) represents all feeders and nest boxes available for birds

746 over the period of the study. Note that very few locations are permanent and that many have been

747 relocated according to landscape change or management considerations. The second panel (b), plots

748 the utilized distribution (UD) of a single individual, using the kernelUD function (*adeHabitat* R

749 package). Note that some observations (yellow points) are not included in the UD by the function as

750 they are considered as outliers, according to the chosen threshold implemented in the function (here

751 a 95% isopleth). The last panel (c), represents the UDs for three individuals and their respective home-

752 range overlap, calculated using Bhattacharyya's Affinity, as indicated in the table. Note here that

753 home ranges are not always continuous and can be patchy.

754

755 **Figure 3: Proportions of variance** explained by animal models for four hatchling

756 morphological traits (mass and tarsus, head-bill and wing length) and six life-history traits

757 (laying date, number of eggs, number of fledglings, longevity, probability of recruitment and

758 fledgling success). For all traits, a model without any spatial component and a model including

759 home-range overlap (i.e. the **S** matrix) is shown. Proportions are the median of the posterior

760 distribution for each trait.

761 **Figure 4: Proportions of variance explained by the Spatial matrix** for morphological traits

762 (mass and tarsus, head-bill and wing length) and three life-history traits (laying date, number

763 of eggs, number of fledglings). Traits exhibiting a proportion less than 1 % are not represented

764 here. Proportions are the median of the posterior distribution for each trait (± median absolute

765 deviation).

766

TABLES

768

769 **Table 1. Number of hihi observations per location type in Zealandia sanctuary**. During

770 the period 2008 to 2016 almost 17,000 unique observations were recorded around feeders, nest

771 boxes or on the sanctuary tracks. In total, 28 different feeders were placed in the sanctuary (13

772 main feeders and 15 temporary ones, usually present for a short period of time) and 179 unique

773 nest boxes distributed across 58 different locations were available. Because of degradation due

774 to weather or poor visitation rate, nest boxes are frequently removed, replaced or relocated.

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Location	Number	Frequency
Feeder	11,999	0.70
Nest boxes	4,518	0.27
Tracks	437	0.03
Unassigned	3	0.00
Total	16,958	-

781 **Table 2. Fixed and random effects included in the animal models.** V_A refers to additive genetic variance, V_{space} refers to variance associated to home
782 range-overlap, V_{mother} refers to mother identity, V_{father} refers to the social father, V_{year} and V_{month} refers to year and month of phenotype collection. For
783 repeated female-based measures, V_{female} referes to the measured female and V_{male} to the social mate. Also included are the sample size (number of
784 individuals or number of records for repeated mesures) used for each model. Note that for comparison, each phenotype has been analysed with two sets of
785 models, including or not including V_{space}.

Response Variable	Fixed effects	Random effects	Sample size	Error distribution
Hatchling Mass	Sex + Clutch size	$V_A + V_{space} + V_{mother} + V_{father} + V_{year} + V_{month}$	554	Gaussian
Tarsus length	Sex + Clutch size	$V_A + V_{space} + V_{mother} + V_{father} + V_{year} + V_{month}$	505	Gaussian
Head-bill length	Sex + Clutch size	$V_A + V_{space} + V_{mother} + V_{father} + V_{year} + V_{month}$	475	Gaussian
Wing length	Sex + Clutch size	$V_A + V_{space} + V_{mother} + V_{father} + V_{year} + V_{month}$	479	Gaussian
Lay Date	Clutch order	$V_A + V_{space} + V_{female} + V_{male} + V_{year}$	375	Gaussian
Number of Eggs	Age + Laying date	$V_A + V_{space} + V_{female} + V_{male} + V_{year} + V_{month}$	375	Gaussian
Number of Fledglings	Age + Number of eggs	$V_A + V_{space} + V_{female} + V_{male} + V_{year}$	315	Gaussian
Longevity	Sex	$V_A + V_{space} + V_{mother} + V_{father} + V_{year} + V_{month}$	113	Poisson
Probability of recruitment	Hatchling mass	$V_A + V_{space} + V_{mother} + V_{father} + V_{year} + V_{month}$	478	Binomial
Fledging success	Laying date + Laying date^2	$V_A + V_{space} + V_{mother} + V_{father} + V_{year}$	375	Poisson

786

SUPPLEMENTARY FIGURE CAPTIONS

788 **Supplementary Figure S1: Number of sightings required to estimate individual's home-**
789 **range.** To identify the acceptable number of sightings required to have a good estimation of
790 any individual's home-range, we randomly chose 10 birds in our dataset that had between 110
791 and 180 sightings (roughly mean ± sd). We tested for each bird whether a sub-sampling rate of
792 5, 10, 15, 20, 25, 50 or 100 sightings was adequate to represent its home-range. For each bird,
793 and for each sampling rate, we sub-sampled the list of observations 500 times, to create 500
794 new home-ranges per individual. Home-range sizes were then estimated as described in the
795 manuscript using the *adehabitatHR* (95% isopleth). Finally, home-range overlap between all
796 pairs of newly created home-range for a given sub-sampling rate were estimated using again
797 the *adehabitatHR* package. Note that just like in our main analyses, any sub-sample with less
798 than 3 different sighting spots was discarded. We calculated the median of the distribution of
799 all home-range overlaps for each individual and for each sub-sampling rate. The below graph
800 represents the average median (± median absolute deviation) over the 10 individuals used for
801 this analysis. On average, with 10 sightings (vertical red line), the median overlap between two
802 home-ranges is 90 ± 0.9 %.

803

804 **Supplementary Figure S2: Histogram of observations.** Each bird in the study may have been
805 observed at feeders, nest-boxes and/or elsewhere in the park. We discarded from our analyses
806 any individuals that had fewer than 10 observations and those that were observed at less than
807 three different locations. On average, each bird was observed 153 times and observation counts
808 ranged between 10 and 1,487 times per bird.

809

810 **Supplementary Figure S3: Distribution of BA values and comparison of original and**
811 **'make.positive.definite' S matrices.** Matrix of home range overlap and distribution of
812 Bhattacharyya's coefficient before (panels a and c) and after transformation using the
813 *make.positive.definite* function from the *lqmm* package (panels b and d; Geraci, 2014).
814 Distributions are mainly similar but differ in their extreme values, as the function mainly
815 transforms 0 and 1.

816

817   **Supplementary Figure S4: Distribution of randomised dispersal distance** from the

818   permutation tests. Solid lines represent the observed distance of male (blue) and female

819   (yellow) dispersal for juvenile (Fig.S4.a), within season adult dispersal(Fig.S4.b) and between

820   season adult dispersal (Fig.S4.c). In the last panel (Fig.S4.d), average observed distance

821   between relatives after settlement is represented in blue while average computed distance and

822   90% bounds are represented in grey.