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Abstract

In heterogeneous habitats, individuals sharing a larger part of their home-range are also likely to live in a very similar environment. This 'common environment' effect can generate phenotypic similarities between neighbours and lead to the structuring of phenotypes through the habitat. In this study, we used an intensely monitored population of hihi (or stitchbird, *Notiomystis cincta*) from New Zealand, to assess whether home-range overlap and genetic relatedness between birds could generate phenotypic resemblance for a wide panel of morphological and life-history traits. Using a multiple-matrix animal model approach to partition the phenotypic variance present in the population, we included a spatial matrix measuring home range overlap between birds and estimated the proportion of variance attributable to space sharing. We detected a clear contribution of space sharing to the overall phenotypic similarity for two traits: hatchling mass and laying date. We also confirmed the very low estimates of genetic heritability already found for this species. These results suggest that models including space sharing can offer further insight into the determinants of individual differences in phenotype. In particular, the spatial matrix helps to capture fine-scale variation of the environment that classic animal models would potentially miss or miss-assign. In this species, results also suggest that small but significant genetic heritability estimates are not upwardly biased by clustering of close relatives in space.

Keywords Stitchbird · Animal model · Spatial matrix · Heritability · Common environment · Phenotypic variation

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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 (Henderson 1973; Wilson et al. 2010). However, as discussed above, sources of phenotypic similarities cannot be reduced to only genetic factors and other sources of individual similarities are now incorporated in the models (e.g. year or region of birth, parental effects; Kruuk and Hadfield, 2007; Wilson et al. 2010). Recently, it has been suggested that home-range overlap should be considered as a potential source of similarity between individuals (Danchin et al. 2011; Germain et al. 2016; Kruuk and Hadfield, 2007; Van Der Jeugd and McCleery, 2002). In the animal model, additional random effects can be fitted for each source of non-independence between individuals, and for each random effect it is possible to estimate the corresponding amount of the total phenotypic variance it explains. In addition to the matrix of additive genetic relatedness (usually denoted **A**), used to measure the phenotypic similarity among relatives attributable to additive genetic variance (V_A), it is therefore possible to design a pairwise matrix of home-range overlap among individuals (here denoted **S**), which accounts for the phenotypic similarities attributable to space sharing in the environment (V_{space}; Regan et al. 2017; Stopher et al. 2012, see Thomson et al. 2018 for a methodological tutorial).

Wild study systems in which it is possible to quantify the contribution of space sharing to phenotypic variation between individuals are still rare. To date, the two studies incorporating a spatial matrix in an animal model have been focussed on large mammals (red deer, *Cervus elaphus* Stopher et al. 2012, and Soay sheep, *Ovis aries*, Regan et al. 2017), species that can be accurately tracked in their natural habitat. Unfortunately, it is not always easy (or even possible) to obtain comprehensive data describing the full home range of

individuals. A number of other studies have however developed different proxies such as spatial buffers or spatial autocorrelation to extend the study of evolutionary and ecological questions related to space sharing (e.g. sensitivity to local environmental heterogeneity or habitat fragmentation) to many other species already offering longitudinal data (Van Der Jeugd and McCleery 2002; Germain et al. 2016).

In the present study, we used a well characterised species, the endangered New Zealand hihi (or stitchbird, *Notiomystis cincta*), to dissect the effect of home-range overlap on phenotypic variance. Hihi were reintroduced to Zealandia sanctuary (Wellington, New Zealand) in 2005 and have been extensively monitored since, offering a unique opportunity to collect spatial observations for each individual. Zealandia sanctuary shelters a highly heterogeneous landscape composed of intact native bush, planted exotic trees and regenerating forest patches (Starbridge 2009). Previous quantitative genetic studies on another hihi population have demonstrated low narrow-sense heritability for morphological and life history traits despite large phenotypic variation between birds (de Villemereuil 2018a; de Villemereuil et al. 2019), reinforcing the need to explore other forces generating differences between individuals such as the influence of the spatial structure of the population (Franks et al. 2019). First, we studied dispersal patterns of hihi across Zealandia's landscape in order to understand how birds establish their home-range. Second, we assessed whether home-range overlap generated phenotypic similarities for a wide panel of morphological and life-history traits, while accounting for other contributions to variance. Notably, to confirm low heritabilities in our population, we reconstructed a genetic pedigree of the population so that we could include genetic relatedness in our models and minimise any confounding effect between space-sharing and genetic relatedness.

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 (Fig. 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).

Fig. 1 Hihi populations across New Zealand with a focus on *Te Hauturu-o-Toi*, the remnant population (larger yellow point). Also represented are the studied population from *Zealandia Sanctuary* (small orange dot) as well as five other reintroduced populations (small yellow dots), including Tiritiri Matangi Island, Pukaha National Wildlife Sanctuary, Sanctuary Mountain Maungatautari and Kapiti Island. Image modified from Wikimedia Commons

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) (Fig. 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 habitat with both intact and regenerating forest patches. With the construction of a 2.2-m-high and 8.6 km long fence, the 225-hectare sanctuary has been mammalian pest-free since 2000. In 2005, a first group of 64 hihi translocated from Tiritiri Matangi Island and Pukaha National Wildlife Centre was released in the valley (Fig. 1). Subsequently, six other translocations happened between 2005 and 2012 with a total of 57 birds released. Despite a high mortality of reintroduced birds (65%), the hihi population in Zealandia had increased to an estimated size of 112 individuals in 2017. Natural immigration in the park is impossible as the closest hihi population resides on an offshore sanctuary (Kaptiti Island), 50 km away. Birds have been observed emigrating outside of the park, but no nesting attempts have ever been reported.

Phenotypic, life-history and spatial data collection

For each nesting attempt (i) the identity of the social mother and social father, (ii) lay, hatch and fledge dates, and (iii) the number of eggs, chicks and fledglings was recorded.

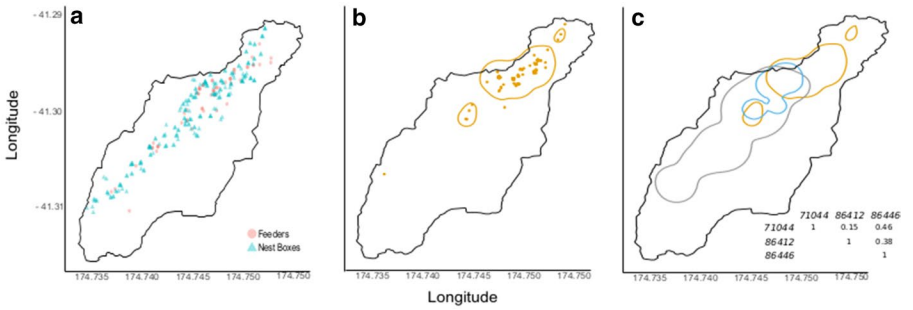

Fig. 2 Locations of Zealandia nest boxes and feeders, and example of home-range overlap computed with adeHabitat. The first panel **a** represents all feeders and nest boxes available for birds over the period of the study. Note that very few locations are permanent and that many have been relocated according to landscape change or management considerations. The second panel **b**, plots the utilized distribution (UD) of a single individual, using the kernelUD function (*adeHabitat* R package). Note that some observations (yellow points) are not included in the UD by the function as they are considered as outliers, according to the chosen threshold implemented in the function (here a 95% isopleth). The last panel **c**, represents the UDs for three individuals and their respective home-range overlap, calculated using Bhattacharyya's Affinity, as indicated in the table. Note here that home ranges are not always continuous and can be patchy

Twenty days after hatching, surviving hatchlings are measured (mass, tarsus length, head-bill length, wing length) and banded with a unique combination of colour bands. Laying date is recorded as the number of days starting at the first day of September (e.g. 12th of September corresponds to day 12, 12th of January corresponds to day 103). Longevity was estimated from individual survey data: since the population was established, rangers and volunteers have been carrying out observations all year round. Most of the observations are made at feeding stations or close to nest boxes, but also on the tracks and therefore can be associated with their GPS coordinates, with position and timing uploaded into a database (containing 16,958 unique observations between 2008 to 2016 included in this study; Table 1).

Table 1 Number of hihi observations per location type in Zealandia sanctuary

Location	Number	Frequency
Feeder	11,999	0.70
Nest boxes	4518	0.27
Tracks	437	0.03
Unassigned	3	0.00
Total	16,958	–

During the period 2008 to 2016 almost 17,000 unique observations were recorded around feeders, nest boxes or on the sanctuary tracks. In total, 28 different feeders were placed in the sanctuary (13 main feeders and 15 temporary ones, usually present for a short period of time) and 179 unique nest boxes distributed across 58 different locations were available. Because of degradation due to weather or poor visitation rate, nest boxes are frequently removed, replaced or relocated

Dispersal estimates

Natal and adult distances travelled during dispersal events were estimated for all males and females. For fledglings, natal dispersal was recorded as the distance between the natal nest box and the nest box used during the first breeding attempt. For nesting adults, two measures were calculated: *(1)* the dispersal within the same reproductive season, based on the bird's movement during a single reproductive season and *(2)* the dispersal between reproductive seasons, based on the distance between the first nest box used during the year *y* and the last one used in year *y-1*. Note that in the absence of dispersal, the distance was considered as zero. We used a permutation test to assess whether birds were dispersing more or less than randomly expected. To do so, we used for each bird that dispersed the nest box where the bird was last observed as the starting nest box, then randomly drew a nest box of arrival from the list of all potential nest boxes. The average distance travelled by birds during this artificial dispersal event was calculated for the population. We repeated the procedure 50,000 times to create a distribution of randomised dispersal distances, and then compared, for each sex, the observed mean dispersal distance to the 97.5% and 2.5% percentiles of the randomised distribution. Finally, we used a similar procedure to check whether or not relatives tended to cluster in space despite natal dispersal. We identified all pairs (or trios) of siblings that survived to the next breeding season and occupied a nest box, and calculated the distance between the two (or three) nest boxes. To test whether siblings tend to establish nest boxes closer to each other than expected by chance, we randomly chose two (or three) nest boxes among the occupied nest boxes and estimated the average distance between them. Again, we repeated the procedure 50,000 times to create a distribution of randomised clustering distances, and compared it to the observed distance.

Pedigree construction

The social pedigree was constructed using colour band information of the social mother and social father observed at each nest box. Since 2010, feather samples of hatchlings have been collected, allowing us to build a genetic pedigree of the population. DNA was extracted from feather samples using either the Promega Wizard® SV genomic DNA purification system (PROMEGA) or the Qiagen DNeasy Blood and Tissue kits following the manufacturer's instructions. To assess genetic paternities, we amplified 18 microsatellite markers developed for the hihi (i.e. 15 specific markers, three designed for other passerines; Brekke et al. 2009). We then used individual's genotypes in the software COLONY to reconstruct the pedigree (Wang 2013). All parameters were set up as described in de Villemereuil et al. (2019). Briefly, all social maternities were assumed to be correct. When female identity was missing, sibships were grouped into the same family but mother identity was not specified. All males observed in the population during the month of September prior to the breeding season and all males observed in the population before June following the breeding season (except yearlings) were considered as potential candidate fathers. The probability of parents being in the candidate list was set as 0.9 for females and 0.8 for males following Brekke et al. (2015). Both sexes were defined as polygamous. Allelic dropout and genotyping error rates were set conservatively as 0.05 (although true genotyping error rates are up to 0.012 when assessed from repeat genotyping of 10% of samples). In total, the pedigree contains 1,095 unique birds, across seven generations, with an average inbreeding coefficient between birds of 0.008 ($\pm$0.028).

Home-range estimates and spatial matrix

We extracted adult lifetime survey observations for all females and males present in the genetic pedigree, excluding any individuals that had fewer than 10 observations and observed at less than three different locations, following the method used in Stopher et al. (2012) and the recommendations of Börger et al. (2006). Simulations suggest that, in our dataset, we capture $90 \pm 0.9\%$ of the true home-range when reconstructing a home-range based on only 10 sightings (See Appendix 1). On average, each bird was observed 153 times (between 10 and 1487, Figure S2). Because most of the observations were recorded at feeders or nest boxes, many observations shared the exact same geographical coordinates, causing problems when estimating individuals home-range using kernel methods (Tufto et al. 1996). To solve this issue, we 'jittered' locations by adding a random number sampled between 1e−04 and 1e−05 to X and Y GPS coordinates, a maximum change of approximately 13 m. Home-range sizes were estimated for each female using a kernel density estimation from the R package *adehabitatHR* (Calenge 2006), using a 95% isopleth allowing us to discard observations considered to be outliers. Note here that because the observations are made on discrete points within the range (except tracks observations), our estimation of home-range is unlikely to be as accurate as home ranges described in Stopher et al. (2012) or Regan et al. (2017). However, contrary to methods using a spatial buffer to create individual's home-range or spatial autocorrelation, we allow variation between individual home-range sizes, which reflects more closely the reality of the spatial use of the habitat by the hihi.

We then calculated home-range overlap for all possible pairs of individuals using Bhattacharyya's affinity (BA; Bhattacharyya, 1943) as computed in the *adehabitatHR* package (see Fig. 2 for an example). BA estimates provide three main advantages. First, as a three-dimensional coefficient, BA not only accounts for space, but also for the probability of re-sighting an individual at different locations within its home-range, therefore capturing the utilised distribution of the home-range (Fieberg and Kochanny 2005). Second, BA ranges from zero to one, making it comparable in scale to genetic relatedness. Finally, this coefficient is non-directional and symmetric, as it uses the joint distribution of the home-ranges of the two focal individuals. Altogether, we created a spatial matrix (**S** matrix) containing pairwise similarity metrics for 143 females and 191 males (334 birds and a sex ratio of 1.3:1; see Figure S3 for the distribution of BA values). Finally, note that for morphological traits (measured on hatchlings), we used maternal home-ranges to estimate the spatial overlaps included in the **S** matrix. We chose not to include a spatial matrix for paternal home-ranges as males contribute little compared to females in chick provisioning (Ewen and Armstrong, 2000). We are also aware that, because birds are confined to a sanctuary, home ranges may be smaller, and overlap could be higher than expected in a free-ranging population. However, nest boxes are mainly concentrated on the North-Western slopes of Zealandia valley (see Fig. 2.a) and nesting outside of nest boxes in the South-Eastern side of the park is very rare. For this reason, we don't think that competition for space between birds is a major concern.

Partitioning of phenotypic variance

All analyses were performed with R statistical software (version 3.3.2, R Development Core Team 2016). We fitted animal models to estimate the contribution of space sharing

to phenotypic similarity, along with other random and fixed effects, for: (i) morphological traits (hatchling mass (g), hatchling tarsus length, head-bill length and wing length (mm)), and (ii) female life history traits (laying date, number of eggs laid, number of fledglings, fledgling success, probability of recruitment, longevity). To partition the phenotypic variance, we used the phenotypic and pedigree information collected between seasons 2010/2011 and 2016/2017, and implemented in generalised linear mixed effect models (GLMM) using the package MCMCglmm (Hadfield 2010). Depending on the trait modelled, we included fixed effects identified by de Villemereuil et al. (2019) as influencing the trait (e.g. such as sex, mass, clutch number, lay date or female age; see Table 2 for details). Laying dates, number of eggs laid, number of fledglings and hatching success were only considered for females. Note that for longevity, we only used birds hatched between 2010 and 2014 to avoid bias for recent chicks for whom longevity is not yet available (See Table 2).

For each trait, we compared two sets of models (with or without spatial effect) varying in the structure of their random effects. For the first set, we included (i) individual identity to estimate variance due to additive genetic effect (V_A), (ii) identity of the mother (V_{mother}) and of the social father (V_{father}) to incorporate variance linked to non-genetic parental effects and (iii) year (V_{year}) and month of hatching when relevant (V_{month}) to partition the variation attributable to seasonal characteristics of the environment. Note that for female-based traits such as laying date, we used the identity of the female (V_{female}) and of her social partner (V_{male}) to account for repeated measures (see Table S1) and potential residual autocorrelation. In the second set of models we accounted for space sharing by including the spatial matrix (**S** matrix) of the focal individual as an additional random effect. To do so, we included the inverse of this matrix using the'*ginverse*' parameter of the MCMCglmm package (following the recommendations of Thomson et al. 2018). Note that to ensure the **S** matrix inverse was positive definite, we transformed it using the *make.positive.definite* function from the lqmm package (Geraci 2014, see Figure S3 for comparison of both matrices). The error distribution was chosen to fit each trait (see Table 2). The number of iterations and the thinning interval were chosen to ensure that the MCMC effective sample size for all parameters was higher than 1,000. Burn-in was set to a minimum of 3000 iterations and increased if convergence was not reached. Convergence of all parameters was assessed graphically and using the Heidelberger and Walch test (1981) as implemented in the 'coda' package (Plummer et al. 2006).

We analysed outputs of the animal models according to their error distribution. For Gaussian traits, proportions of variance, including narrow-sense heritability (h^2), are directly computed from the outputs of the model as the ratio of the variance of interest on the sum of variance estimated for fixed and random effects (de Villemereuil 2018a). Note that the lay date, number of eggs and the number of fledglings were considered here as Gaussian traits as their distribution is close to Gaussian after we accounted for the clutch number in the models (see de Villemereuil et al. 2018). For non-Gaussian traits, variance decomposition was performed using the *QGicc* function from the *QGglmm* package (de Villemereuil et al. 2016) which computes intra-class correlation coefficients (ICCs) for each random component. In GLMM, ICCs are not additive (i.e. their sum is not equal to one) as the link function is not linear, which means that h^2 is no longer an ICC (i.e. additive genetic variance must be additive by definition). To enable comparison of the genetic variance with all other random components of the model, we thus chose to report the total genetic variance (i.e. including the non-additive part of the genetic variance generated by the link function) and therefore use the broad-sense heritability (H^2, i.e. the actual ICC associated with genetic variance) for these non-Gaussian traits. See de Villemereuil 2018a,

Table 2 Fixed and random effects included in the animal models

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

V_A refers to additive genetic variance, V_{space} refers to variance associated to home 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 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 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 models, including or not including V_{space}

b and de Villemereuil et al. 2016 for more information on the subject. Finally, note that variance parameters are reported as medians and their median absolute deviations (an equivalent for the medians as the standard deviation of a mean; mad R function, R core Team 2020).

Results

Dispersal

On average, fledgling travel 779 m (SD = 450 m) between their natal nest box and the nest box they use for their first breeding attempt. Note that female fledglings travelled on average slightly further (824 m) than males (745 m). According to our permutation test, there is no over- or under-dispersion for natal dispersal distance for the males ($p = 0.32$, Figure S4a), while significant natal over-dispersion was observed for females ($p = 0.01$, Figure S4a). In other words, male fledglings disperse randomly, while female fledglings disperse significantly further from their natal nest box than would be expected by chance.

The average observed adult dispersal distance between reproductive seasons is 107 m (SD = 259 m) with females dispersing on average 68 m and males 145 m. This time, significant under-dispersion is observed ($p < 2e{-}5$, Figure S4b). Similarly, dispersal events between reproductive attempts in a single season are scarce, as the average distance travelled by birds is 57 m (SD = 199 m). Females have an average dispersal distance of 59 m and males of 54 m, with again significant under-dispersion ($p < 2e{-}5$, Figure S4c). Finally, we only observed 44 clutches with more than one offspring surviving the first winter and nesting the next spring (n = 59 fledglings). The average distance between siblings was 722 ± 429 m. According to the permutation test, there is no over- or under-clustering between siblings after natal dispersal ($p = 0.86$, Figure S4d), suggesting no tendency of siblings to establish home ranges close together following dispersal from the natal nest.

Variance of morphological traits

When adding the spatial matrix, the proportion of phenotypic variance explained by space sharing was relatively small for all morphological traits except hatchling mass and head-bill length, but the lower interval did not reach zero only for hatchling mass (hatchling mass (posterior median = 0.11, ± median absolute deviation = 0.09), tarsus length (0.01 ± 0.01), head-bill length (0.04 ± 0.06), and wing length (0.02 ± 0.02), Fig. 3, Supplementary Table S1 a-d). Except for tarsus length, the proportion of phenotypic variance explained by genetic relatedness between relatives was relatively small: the posterior median of V_A was: hatchling mass (without **S** matrix: 0.03; with the **S** matrix: 0.02), tarsus length (0.14; 0.14), head-bill length (0.03; 0.03) and wing length (0.02; 0.02). Low posterior modes could either reflect very low additive genetic variance or a lack of power from our dataset to precisely infer variance parameters. However, our previous study on another population of hihi, incorporating power analyses for a similar pedigree, found similar estimates for additive genetic variance (de Villemereuil et al. 2019), making the second hypothesis unlikely. For all sets of models (with or without the **S** matrix), sex was a significant effect for all morphological traits, reflecting the dimorphism between hihi males and females (i.e. males being larger than females, all pMCMC < 0.03). In contrast, clutch size only significantly

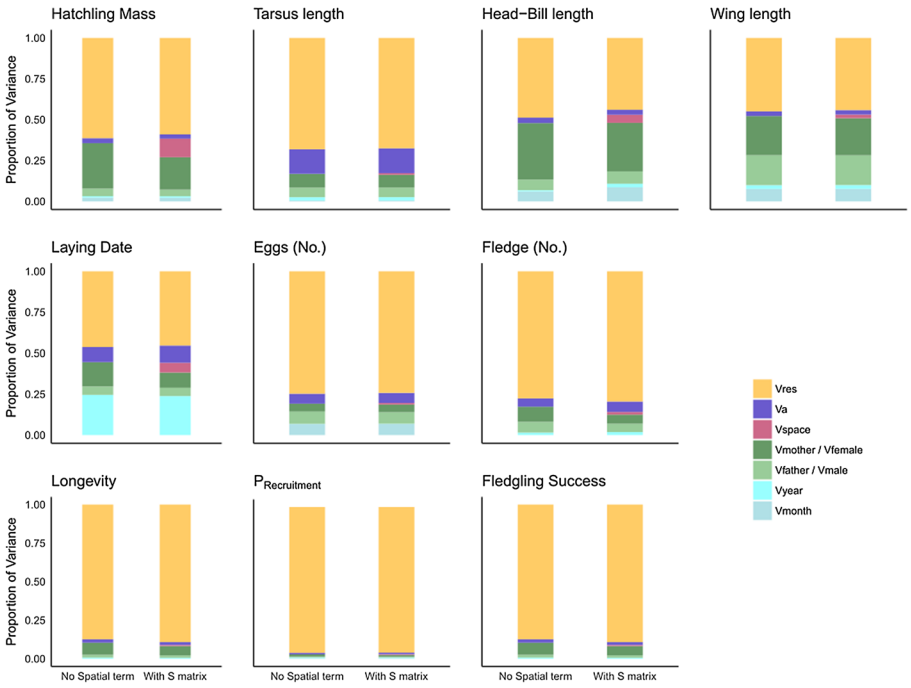

Fig. 3 Proportions of variance explained by animal models for four hatchling morphological traits (mass and tarsus, head-bill and wing length) and six life-history traits (laying date, number of eggs, number of fledglings, longevity, probability of recruitment and fledgling success). For all traits, a model without any spatial component and a model including home-range overlap (i.e. the **S** matrix) is shown. Proportions are the median of the posterior distribution for each trait

influenced tarsus length (pMCMC = 0.04, for both sets of models). The proportion of variance explained by other factors is described in Fig. 3 and Tables S1a-d.

Breeding and life-history traits

In contrast to morphological traits that all presented similar patterns, results were less concordant across breeding and life history traits. For lay date, space sharing between individuals explained a small but significant part of the total phenotypic variance (posterior median = 0.06, ± median absolute deviation = 0.05, see Fig. 3 and Table S1e for more information). The part of phenotypic variance explained by genetic variance was consistent between both sets of models (without **S** matrix: 0.08 ± 0.07, with **S** matrix: 0.09 ± 0.08). Laying date is influenced by the clutch order (pMCMC values < 2.01 e-05).

Space sharing had little effect on the number of eggs (posterior median of the variance explained = 0.01 ± 0.01, see Fig. 3 and Table S1f for more information) and genetic variance explained approximately 6% of the total phenotypic variance in both models (with and without **S** matrix: posterior median = 0.06 ± 0.06 and 0.06 ± 0.06, respectively). The number of eggs produced per clutch was significantly influenced by laying date, early clutches being more successful than late ones (pMCMC value < 2.0 e-05).

The effect of space sharing on the number of fledglings produced by each bird was close to zero (posterior median = 0.01 ± 0.2, Fig. 3, Table S1g). The part of phenotypic variance explained by genetic relatedness between the model without spatial terms (posterior median = 0.05 ± 0.05) and the model with the **S** matrix (posterior median = 0.06 ± 0.06) is again consistent. Neither the laying date, the age of the female nor the clutch size significantly influenced the number fledged at the end of the nesting period, and this was true with or without the **S** matrix (pMCMC all > 0.23).

Finally, for the non-Gaussian traits (longevity, recruitment, fledging success), estimates for both genetic and spatial components of the phenotypic variance are all below 0.02 (see Fig. 3 and Tables S1h-j). Concerning fixed effects, sex did not influence longevity (pMCMC value = 0.81), and hatchling mass did not influence the probability of recruitment (pMCMC value = 0.11). Fledgling success was positively correlated with laying date (pMCMC value < 0.005) but was negatively correlated with the square of laying date (pMCMC value = 0.001), reflecting a nonlinear relationship between the two (Fig. 4).

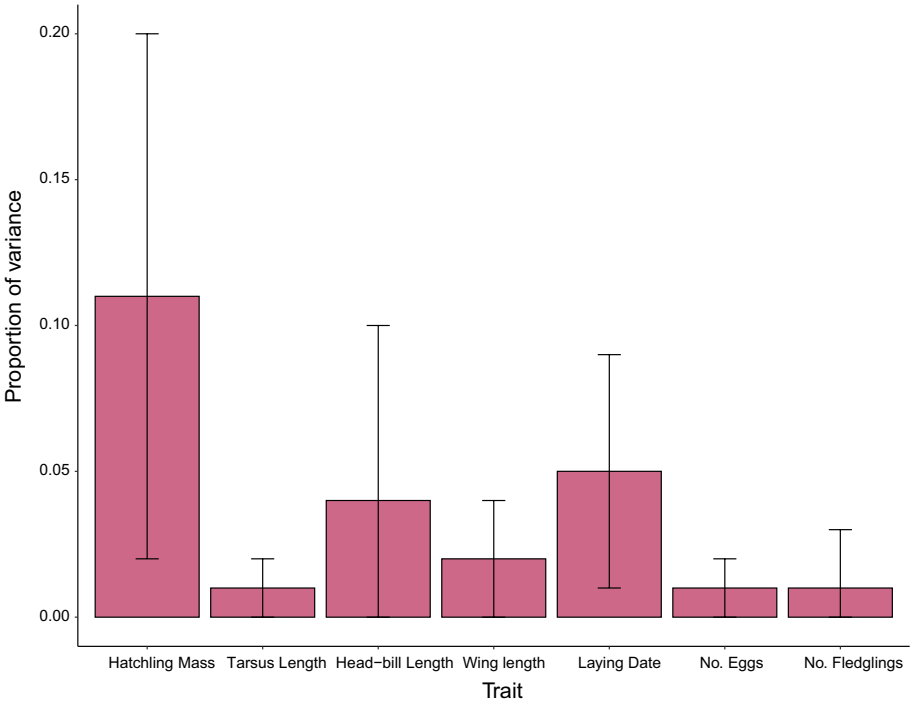

Fig. 4 Proportions of variance explained by the Spatial matrix for morphological traits (mass and tarsus, head-bill and wing length) and three life-history traits (laying date, number of eggs, number of fledglings). Traits exhibiting a proportion less than 1% are not represented here. Proportions are the median of the posterior distribution for each trait (± median absolute deviation)

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 779 m), 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 722 m). 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

For hatchling mass and laying date, we found that home-range overlap between hihi explain a low but significant part of the variation between birds. We did not detect any influence of the **S** matrix for any other traits we studied. More precisely, we found that spatial overlap explained 10.6% ($\pm$ median absolute deviation = 8.8%) of the variation in hatchling mass and 5.9% ($\pm$ 5.2%) of the variation of laying date between hihi. It is interesting to note that our results are consistent with the previous results published in the literature for species with very different social, ecological and life-history characteristics. Despite important differences between the hihi and the Soay sheep or the red deer, both Regan et al. (2017) and Stopher et al. (2012) found similar influence of the spatial matrix on new-borns mass (respectively 6.0% $\pm$ 4.8% for the Soay sheep lambs and 5.9% $\pm$ 4.8% for red deer fawns). Regan et al. (2017) also found a significant effect of the **S** matrix on Soay sheep birth date (5.6 $\pm$ 4.0%). The influence of the micro-habitat on hatchling mass and laying date is not surprising, as shown by the numerous papers studying the impact of the environment on those two phenotypes published in the last decades (e.g. Crick and Sparks, 1999; García-Guerrero et al. 2013; Nussey et al. 2007). However, even when accounting for large scale environmental variation in the animal model (i.e. by adding temperature or year as a fixed or random effect), the addition of the **S** matrix significantly helps to better assign a part of the overall phenotypic variation for both mass at birth and laying date for all three species aforementioned.

The absence of influence of the **S** matrix on other morphological traits (tarsus length, wing length and head-bill width), on the number of eggs laid and on the number of hatchlings is a result partly shared by Regan et al. (2017). Indeed, they found weak influ-

ence of the spatial matrix on jaw length or any other adult traits. This could be explained by the relative robustness of morphological traits to environmental variation or (for adult traits at least), by the fact that the spatial matrix is not constructed at an appropriate time scale (see last paragraph of the discussion below). For the non-Gaussian traits studied in the hihi population (longevity, recruitment and fledgling success), the low contribution to variance from all random effects of the animal model (including space sharing) could also be linked to a methodological issue: using GLMM, parameters for non-Gaussian traits were inferred on the latent scale and needed to be back-transformed to allow correct interpretation and comparisons between traits. For several reasons discussed in de Villemereuil (2018b), GLMM models are usually considered as 'noisy' statistical models and this assumed uncertainty generally results in small ratios of the random effect variances to the total variance (e.g. broad-sense heritability for recruitment 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 scale).

c. Dissecting the spatial matrix

Even if it is clear that the **S** matrix explains some aspects of the phenotypic variance, this variance decomposition framework does not identify which biological processes contribute to the phenotypic similarities between conspecifics that share a part of their home-range. In our situation the strongest driver of phenotypic diversity captured by the **S** matrix is likely to rely on fine scale resource heterogeneity, known to classically impact both lay date and hatching mass (Blondel et al. 1993; Carrete et al. 2016). Despite variations of temperatures between years (already known to influence hihi laying date in another population, de Villemereuil 2018a; and explaining up to 23% of the variation for laying date in our models), variation in home-range quality can also emerge from the vegetation structure or the landscape topography surrounding individuals' nest boxes. In Zealandia, these variations are likely to be partly buffered by the presence of feeders, used by birds year-round as a source of supplementary energy when fruits or flowers are rare in the habitat. However, sugar water is mainly carbohydrates and lacks protein, fibre and lipids, essential for growth and particularly important during chick rearing (Marciniak et al. 2007; Walker et al. 2013). To satisfy the nutritional requirements of their chicks (as well as their own requirements), hihi are known to change their diet during the year, switching from a diet based on flower nectar in winter (65%) to a diet essentially composed of insects (87%) during spring and summer (data from Kapiti Island sanctuary, Castro et al. 1994). The heterogeneous structure of the forest around each territory, and consequently the heterogeneous access to high-nutrient resources, could therefore be captured in the **S** matrix, explaining its effect on hatchling mass but also on laying date if females try to synchronize their reproduction with the quality of resources present in their home-range (Brekke et al. 2013).

For the hihi, but more likely for species adopting high social organisation, other characteristics might also be captured by the matrix, in particular, transmitted social information between unrelated individuals, also referred as cultural inheritance (Danchin et al. 2011; Sheppard et al. 2018). Individuals sharing an important part of their home-range are more likely to interact with each other than with non-neighbouring individuals. Copying other individuals' behaviour is frequently observed in wild animal populations (Dugatkin 1996; Laland 2004), including the hihi (Franks and Thorogood 2018; Franks et al. 2019), and can result in the rapid spread of specific behavioural phenotypes, ultimately increasing behavioural heterogeneity between groups. For example, variation in behaviour can be observed locally for traits such as foraging (Coolen et al. 2003), parental care (Champagne, 2008), mate and habitat choice (Dugatkin 1996; Doligez

et al. 2002) or predator evasion (Halloy et al. 2007). While achievable from an analytical perspective, disentangling social effects from spatial effects is however extremely challenging in term of data collection as it would require a full understanding of what aspect of the environment is varying spatially (e.g. food resources, predation, population density, topography) and a precise social network of the studied population (including the outputs of social interactions in terms of costs and benefits). Such a fine scale study is obviously extremely hard to obtain in wild populations, and conclusions about the **S** matrix should 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 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 and 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 et al. 2013; Kruuk and 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 question how the redistribution of the variance occurs between models that include or do not include the **S** matrix.

Interestingly, the variance attributable to home-range overlap predominantly comes from a redistribution of the estimated maternal effects. Comparing models for hatchling mass, 8 out of the 10.6% of the phenotypic variation explained by home-range overlap was captured by the maternal component of the model (V_{female}) when the **S** matrix was not considered. Similarly, 5 out of the 5.9% of phenotypic variation attributable to home-range overlap was captured by the social maternal component of the model for laying date. This result demonstrates that it is possible to refine our understanding of social effects on differences between individual phenotypes, suggesting here that a part of the variance usually attributed to a difference between social mothers is actually attributable to the way they use their close environment. More importantly, this observation also suggests that the variance explained by space sharing may already be captured in classical quantitative genetics models (e.g. using maternal effects in this example), as

only a very limited additional part of the residual variance is captured when including the **S** matrix in our models (approximately 3% for hatchling mass). Finally, note that for most of the phenotypes studied here, a large part of the variance therefore remains unexplained in this study (up to 75% for the number of eggs), and its origin remains an open question.

e. Where to go next?

In light of our results, we would like to raise some recommendations and share exciting directions for future research. Firstly, we encourage researchers to include spatial variation of the environment in their quantitative genetic models to fully understand the micro-environmental drivers of phenotypic variation, but also to better assess the degree of bias in quantitative genetic parameters due to this component. We understand that obtaining home-ranges requires an incredible effort of localisation of individuals, from the early stage of the pedigree reconstruction. To circumvent this step, it is possible to implement spatial autocorrelation (SAC) in quantitative genetic models, a method largely used in forestry science (Banerjee et al. 2010; Silva et al. 2001) but also with wild animals (Van Der Jeugd and McCleery 2002; Stopher et al. 2012). It is also possible to use a circular spatial buffer around individuals' breeding or capture locations and infer individual home-range from there (Germain et al. 2016). Although less effort is needed to implement SAC or to create a circular spatial buffer, one should note that these methods are unlikely to be as accurate as an approach using the **S** matrix, mainly because they assume very little variation in individuals' distribution in space use which is rarely relevant to wild systems (Regan et al. 2017).

Another limitation, this time shared by the model used in our study, is the absence of temporal variation in both environmental conditions and in individual's home-range over time. Such a situation is unlikely to be realistic, especially when considering the survey period necessary to build pedigree-based analyses. Moreover, models of home-range overlap often presuppose that all individuals are alive at the same time (e.g. they are compiled in the same **S** matrix), even if their lives never overlapped. If the environment is stable, this situation is not a major issue. However, in a changeable environment, this approach could create similarities between individuals that do not exist. We see two solutions to solve this problem. First, it would be possible to design a spatial matrix with multiple entries for each individual, one per event in the analyses (e.g. reproductive season) but this approach would be extremely data hungry. Another approach would consist of eliminating the need for a long-term pedigree (and therefore from temporal variation of space over the length of the pedigree) by using genomic approaches. This would provide an "instantaneous snapshot" of genetic similarities in the population (Bérénos et al. 2014; Santure et al. 2013; Yang et al. 2011), that could be combined with a "snapshot" of environmental similarities between individuals to partition trait variation.

Finally, traits likely to be impacted by both genetic and spatial elements such as ranging behaviour, dispersal or fitness can present inherently non-Gaussian distributions. Our attempt to provide estimates of the proportion of variance explain by the genetic structure or the spatial organisation of the population for non-Gaussian traits (i.e. longevity, fledgling success and recruitment) was not conclusive. Datasets built on a longer period of time should however have enough statistical power to provide such estimates. Further, the recent development of statistical methodologies using non-normal distributions for quantitative genetic inference (Ayres et al. 2013; de Villemereuil, 2018b; Morrissey et al. 2014) may enable this to become more common practice.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

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