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Demographic influences of translocated individuals on a resident population of house sparrows

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Abstract: Translocation of individuals from source populations to augment small populations facing risk of extinction is an important conservation tool. Here we examine sex-specific differences between resident and translocated house sparrows *Passer domesticus* in reproductive success and survival, and the contribution of translocated individuals to the growth of a local population. We found evidence for assortative mating based on origin revealed by fewer parentages between translocated males and resident females than expected, and the total number of fledglings produced by such pairs was lower. Interestingly, the reproductive success of translocated males was positively related to the size of the throat badge (a sexual ornament), such that translocated males with a large badge size were as successful as resident males. However, offspring with parents of different origin had higher survival than offspring with parents of same origin, which suggests hybrid vigour. The contribution of resident and translocated individuals to the stochastic component of the long-run growth rate of the population was similar; neither the mean individual contributions in fitness nor the demographic variance differed between the two groups. Thus, this experiment shows that translocated individuals may have a similar demographic influence on the growth of local populations as resident individuals. Still, the intermixing of translocated and resident individuals was low, and fitness differed according to origin in relation to individual differences in a sexually selected trait. In addition, hybrid vigour with respect to offspring recruitment seemed to partially relax the negative fitness consequences of the assortative mating based on origin.

Keywords *Assortative mating, badge size, demographic stochasticity, hybrid vigour, individual fitness,* Passer domesticus*, phenotypic differences, reproductive success, translocation*

Introduction

Translocation is a widely used conservation tool to increase viability of threatened populations (Griffith et al. 1989, Fischer and Lindenmayer 2000, Armstrong and Seddon 2008). Translocated individuals may increase population genetic variation, alleviating negative impacts from inbreeding depression and genetic drift in small populations (Westemeier et al. 1998, Madsen et al. 1999). However, this relies on that the contribution of translocated individuals to population demographic parameters such as growth, matches that of the resident individuals, but few studies have experimentally monitored the demographic contribution of translocated individuals to a local population. There is therefore a need for studies comparing the reproductive success and survival of resident and translocated individuals, using either data before the translocation or the resident individuals after translocation as reference baseline (Pinter-Wollman et al. 2009, Roe et al. 2010). Such studies may provide insights to the specific demographic and ecological drivers affecting the success of a translocation (Armstrong and Seddon 2008).

Fitness advantages for translocated individuals over residents have been reported in a few translocation experiments, i.e. through increased mating success for translocated males (Jones et al. 1995) and indirectly through hybrid vigour in offspring from parents of mixed origin in inbred populations (Ebert et al. 2002). However, translocated individuals may be subject to adverse effects, both directly through transportation and stress, and indirectly through lack of acclimatisation and familiarity with the environment or other individuals (Letty et al. 2007). This can for instance result in increased dispersal rates of translocated individuals (Skjelseth et al. 2007, Roe et al. 2010). Thus, the impact of translocated individuals on local population dynamics depends on how well individuals cope with their new surroundings, and how successful these individuals are, both with respect to fecundity

and survival. Thus, an important part of individual contribution to the next generation is through reproduction, which depends on a plethora of circumstances, including mating success (Emlen and Oring 1977). Therefore, if mating success among translocated individuals differs from that of resident individuals (Sigg et al. 2005, Lewis et al. 2012), it might limit their contribution to the next year's breeding population, and in the long-run the population growth (Tuberville et al. 2011). Increased variation in mating success between resident and translocated individuals could potentially decrease genetic diversity, especially in small populations (Miller et al. 2009). In translocations, such differences may result from assortative mating, e.g. where individuals pair assort with respect to origin (Bradley et al. 2014). Assortative mating could cause increased variation in mating success, where the total population may suffer a decrease in effective population size (Wright 1931, Anthony and Blumstein 2000, Bradley et al. 2014) and may have consequences for demographic variance and viability of small populations (Lande 1988, Lee et al. 2011).

Population augmentations as a conservation tool aim to improve growth and viability of local populations, and reduce the risk of extinction. In the absence of density dependence this means to improve the long-run growth rate of the population (Lande et al. 2003), which is reduced by demographic and environmental stochasticity. Thus, examining the demographic consequences of translocations requires estimates of the expected contributions of an individual to the next generation as well as its variance. Although translocation of individuals may strongly affect the vital rates of a population, few empirical studies of vertebrates have examined how translocated individuals affect the demographic variation in population growth of a local population (Fischer and Lindenmayer 2000, Goossens et al. 2002, Sigg et al. 2005, Seddon et al. 2007). Here we will partition the contribution of individuals with different sources of origin to the population growth into deterministic and stochastic components, following the approach of Engen et al. (1998), Sæther et al. (1998) and Engen and Sæther

(2014). The annual mean individual fitness can be partitioned into components caused by mean differences in fecundity and survival, as well as components due to random variation among individuals generating demographic variance (Engen et al. 1998, Engen and Sæther 2014). This allows us to compare the contribution of individuals of different origin to key population properties affecting population dynamics and viability.

In this experiment we translocated house sparrows *Passer domesticus* from a distant population, into a metapopualtion to investigate how translocated individuals influenced the demography of the population they were introduced to. The resident individuals served as a reference to the performance of translocated individuals (see Pinter-Wollman et al. 2009, Roe et al. 2010). We used an experimental design that kept sex -ratios equal in all subpopulations. In addition, the selected populations (receipt and donor) had only minor differences in population density and size, and had experienced similar environmental conditions. With its sedentary nature, preference for urban and agricultural areas, and easily accessible nests, the house sparrow is a suitable model species for investigating fitness consequences of translocation. . Our first objective was to compare sex-specific fitness differences between resident and translocated individuals to predict the annual contribution from the two groups of origin. We recorded the following fitness components; number of mates, eggs, fledglings and recruits in addition to whether the individual survived to the next breeding season or later. Second, because several morphological traits have shown to influence lifetime reproductive success (see e.g. Jensen et al. 2004), we examined if there were any sex-specific relationships between phenotypic characteristics and fitness that differed between resident and translocated individuals. Third, we examined whether translocated and resident individuals mated assortatively. Fourth, we investigated whether offspring recruitment probability depended on the origin of parents, to test for hybrid vigour. Finally, we estimated the contributions of resident and translocated individuals to the demographic variance.

Methods

Experimental design and field procedures

In February-March 2002, before the translocation, two house sparrow populations were visited, one at the island Vega (65.65° N, 11.90° E) and the other at Vikna archipelago (64.91° N, 10.90° E) located approximately 95 km south along the Norwegian coast (Supplementary material Appendix 1 Fig. A1). House sparrows were captured with mist nets, and banded with a numbered aluminium ring and plastic colour rings of unique individual combinations. At capture we measured body mass (± 0.05 g), wing length (± 0.5 mm; maximum length (Svensson 1992)), tarsus length (± 0.05 mm), bill depth (± 0.05 mm), bill length (± 0.05 mm), and badge size (males only). The badge size was defined as the total area covered with black pigmented feathers including feathers with black bases and grey tips on the throat and the chest when the bird was held with its head in a perpendicular angle to its body (see Jensen et al. 2006). The area of the badge were calculated according to Møller (1987):

$$\textit{total badge size}\ (mm^2) = 166.7 + (0.45 \times h \times w),$$

where h denotes the height (± 0.5 mm) of the badge and w the width (± 0.5 mm). Except for the measure of badge size, we adjusted each trait for differences between fieldworkers due to variation in measurement techniques. Paired *t*-test comparisons for each phenotypic trait were made with samples of birds measured by each fieldworker together with T. H. R. Except for eight birds, all morphological measurements were taken at the beginning of the translocation experiment (i.e. in February-March 2002). Thus, we avoided any inter-individual variation owing to different abrasion of feathers or bills, or differences in body mass due to seasonal variation (see e.g. Anderson 2006). Mean adjustments of wing length were 0.84 mm, bill height 0.25 mm and bill length 0.38 mm, however the measurements of tarsus length did not differ significantly between any of the fieldworkers, and were thus not adjusted. A small

sample of blood (ca. 25 µl) for parental analyses was drawn for each individual from its brachial vein.

In March 2002, we translocated 126 (63 male and 63 female) house sparrows from the population at Vega to the population at Vikna. The two locations have similar topography: hills, lakes and fjords, sparsely populated with small beef- or dairy-farms, where the house sparrows breed in small subpopulations (defined by individuals residing on a farm separated by at least 1 km from a neighbouring farm). The two populations had minor differences in size and structure, Vega being the largest in total (population size = 246, number of subpopulations = 24, mean size of subpopulations = 10.3, range size of subpopulations = 2-34) compared to the total population at Vikna (population size = 192, number of subpopulations = 17, mean size of subpopulations = 11.3, range size of subpopulations = 1-29). Removal of individuals on Vega due to a selection experiment (Kvalnes 2016), created an opportunity to perform this translocation experiment. Within each sex all individuals with a tarsus length longer than the mean minus 0.3 standard deviations were translocated from Vega to Vikna. Since tarsus length does not increase with age after their first winter, the selection should create an unbiased translocation propagule with respect to age. Moreover, since the subpopulations were rather stable in size during several years before the experiment (local farmers, pers. comm.) the age-distribution of both resident and translocated individuals of the population should be similar. Possible age-dependent fitness effects (such as actuarial senescence (Holand et al. 2016) could therefore be assumed to be similar between the two groups. The translocated individuals only differed from residents having larger bill depth in both sexes (males: $t = 6.00$, $df = 120$, $p < 0.001$, females: $t = 4.36$, $df = 122$, $p < 0.001$) and badge size in males ($t = 3.76$, $df = 119$, $p < 0.001$). Hence, for other measured traits there were no significant differences between resident and translocated individuals (All $p \geq 0.109$, Supplementary material Appendix 2 Table A1).

165 Immediately before the translocation, the Vikna population was reduced to 120
166 individuals, adjusting the size of the resident population to match the number of translocated
167 individuals. Experience from former translocations reveals heavy loss during the
168 establishment phase (Krogstad et al. 1996, Letty et al. 2007). Hence, the subpopulation sizes
169 were increased to some extent (on average by 3.18 individuals) to account for some of this
170 loss, and therefore the density were increased slightly for both groups at the initiation of the
171 experiment. Resident individuals were randomly removed for each sex (within each
172 subpopulation, when all local birds were caught) and transported to a distant location
173 (Steinkjer; 64.01° N, 11.29° E) approximately 110 km to the southeast. None of the
174 individuals that were removed returned to Vikna, but two individuals translocated from Vega
175 to Vikna returned to their origin at Vega. All individuals included in the experiment (resident
176 and translocated) went through the same experimental treatment, though differed only in the
177 transportation (95 km) and time between capture and release (approximately one additional
178 week for translocated individuals). House sparrows seem to cope with captivity well based on
179 previous experiments (Krogstad et al. 1996), hence they were conveniently kept in aviaries
180 and provided with food and water *ad libitum* for logistical reasons. The experimentally
181 merged population at Vikna (population size = 246, number of subpopulations = 17, mean
182 size of subpopulations = 14.5, range size of subpopulations = 5-33) was thus larger in size
183 than the original Vikna population and the sex-ratios were adjusted to 0.5 ± 0.1 in all
184 subpopulations.
185 We started the monitoring of the subpopulations in the Vikna archipelago on April 15th
186 2002 (approximately one month after the translocation), which corresponds to the normal
187 onset of breeding in the area. Only individuals present at Vikna after this date were
188 considered established and included in the analyses. From the 246 individuals which were
189 released, 120 (59 males and 61 females) originated from Vikna ("resident"), whereas 126 (63

190 males and 63 females) had been translocated from Vega ("translocated"). Additionally, 27
191 adult individuals (17 males and 10 females) were captured by use of mist nets and banded at
192 Vikna within the breeding season of 2002. These 27 individuals were thus not a part of the
193 translocation experiment, but 9 of these individuals produced offspring that were included in
194 the offspring survival analysis (see below). Of the 246 individuals released in March 2002,
195 161 (65%) were present at Vikna in the 2002 breeding season, i.e. they were captured or
196 observed at Vikna after 15th April 2002, or were genetic parent of nestlings or juveniles
197 hatched at Vikna in 2002. The majority of these individuals was recorded during the field
198 season (n = 146): 82 (42 males and 40 females) were resident, and 64 (30 males and 34
199 females) were translocated. Moreover, 15 individuals were identified as present only through
200 genetic parentage analyses (i.e. they had offspring assigned to them), but these individuals
201 were excluded from the analyses of fitness differences between resident and translocated
202 individuals, to ensure an unbiased sampling method.
203 Within the 2002 breeding season all available nests were visited and monitored closely
204 during the breeding season. At the age of 7-13 days we banded fledglings in all nests
205 individually with a numbered aluminium ring and a unique combination of colour rings. Even
206 though all farms were very thoroughly searched for nests, a few inaccessible and/or
207 undiscovered nests were present. Therefore, any unmarked fledged juvenile was captured
208 with mist nets, either during the breeding season, or when the Vikna population were
209 revisited in end of September and beginning of October 2002. During the breeding season
210 2002 we recorded 232 fledglings and fledged juveniles in the Vikna archipelago. Of these,
211 210 were banded as fledglings and 22 were captured as newly fledged juveniles within the
212 breeding season. All fledglings and juveniles were included in the genetic parentage analyses.
213 ***Genetic parentage analyses***

214 The procedure for determining the genetic parentage of fledglings and fledged juveniles is
215 described in the supplementary material (Supplementary material Appendix 5). We used 11
216 polymorphic microsatellite markers in the parentage analyses, and had a total non-exclusion
217 probability of $p = 6.68x10^{-6}$ and $p = 4.00x10^{-8}$ for first and second parents respectively. All
218 individuals released in the Vikna archipelago were included as candidate parents, except for
219 one male and one female. In addition, the 17 adult males and 10 adult females that were
220 captured in the population within the 2002 breeding season were included as candidate
221 parents, giving a total of 138 males and 133 females as candidate parents in the parentage
222 analyses. For parentage determination, we used the software CERVUS 3.0 (Kalinowski et al.
223 2007). Based on observations of unbanded individuals in the Vikna archipelago, the average
224 proportion of potential mothers and fathers sampled was estimated to be 0.850, i.e. we
225 assumed that 15 % of the adult population was not sampled and genotyped. To account for
226 any inbreeding and resulting close relatedness among candidate parents in the Vikna
227 archipelago, we assumed that 1 % of the candidate mothers and fathers were related by a
228 factor of 0.25 to other potential parents of the same sex. Thus, we assumed a similar level of
229 relatedness among candidate parents as the average level of inbreeding found in a house
230 sparrow archipelago of similar size approximately 200 km north along the coast (Jensen et al.
231 2007; excluding data from one highly inbred population). The genetic fathers were assigned
232 after genetic mothers were identified. For both maternity and paternity analyses the average
233 proportion of loci typed was 0.892. In order to minimize potential erroneous assignments of
234 parentage, the proportion mistyped loci was estimated to 0.01. The level of confidence in our
235 parentage analyses was set to 95 %. Hence, less than 5 % of the genetically assigned mothers
236 or fathers should be incorrectly assigned (Kalinowski et al. 2007).
237 Successful assignment of both parents was achieved for 168 (72.4 %) offspring,
238 whereas 46 (19.8 %) offspring were only assigned a mother, one (0.4 %) was only assigned a

father, and 17 (7.3 %) offspring had unknown genetic parents. One male was recorded as having sired fledglings at two different, but closely situated farms. Except for this male each adult individual had reproduced on one single farm (i.e. subpopulation). Offspring with unknown genetic parents were assigned to the population clusters to control for bias in assignment in relation to origin of parents (Supplementary material Appendix 6 Table A4). Examining how the 232 offspring were distributed among clutches, 210 fledglings was assigned to 66 clutches (154 assigned to 49 clutches with known parents, 39 of these with pairs consisting of experimental adults (n = 120 offspring)), and the 22 offspring captured as fledged juveniles (14 was assigned to 11 clutches with known parents, 7 of these pairs consisting of experimental (resident or translocated) adults (n = 8 offspring)).

Statistical analyses

Resident and translocated individuals were compared with respect to several fitness components. For each reproductive component, we used the total annual production: number of mates (for males; measured by the number of females with shared parentage), number of eggs produced (for females), and number of fledglings and recruits produced. It should be noted that these components stem from parentage analyses of fledglings, and thus depend on the success of the incubation and early nestling stage of the breeding. The annual individual fitness was calculated as the sum of an adult individual's own survival (0 or 1) and its fecundity; the number of recruits (surviving offspring) to the breeding population the year after (Sæther and Engen 2015). The differences between translocated and resident individuals ("origin") for the different fitness components (except survival) were analysed using generalized linear models (GLM; Crawley 2007). Based on an evaluation of model fit, we used Poisson family with log link when analysing number of mates (males), quasi-Poisson family with log link when analysing number of eggs produced (females), and negative-binomial family with log link when analysing number of fledglings and recruits produced,

264 whereas annual individual fitness was analysed using Poisson family and log link. The error
265 distributions were selected to fit the variable's error structure in order to avoid over-
266 dispersion. The house sparrow is a sexually selected species, with sexual dimorphism in size,
267 morphology and behaviour (Anderson 2006). The fitness effects of the translocation may thus
268 differ between sexes. We therefore included the main effect of sex and the interaction
269 between origin and sex in our GLM analyses, and analysed survival and demographic
270 variance separately for the sexes. Furthermore, because individual fitness in both male and
271 female house sparrows is related to adult morphology (e.g. Jensen et al. 2004, 2008) we
272 included morphological traits (body mass, tarsus length, wing length, bill length, and bill
273 depth for both sexes, and badge size in addition for males) as covariates that potentially could
274 explain variation in fitness among individuals (for summary statistics of the morphological
275 traits, see Supplementary material Appendix 3 Table A2). The significance of the interactions
276 was tested with likelihood-ratio tests. Badge size area was square root transformed and body
277 mass was log transformed prior to the statistical analyses in order to operate on the same
278 scale for morphological measurements.
279 To investigate whether individuals mated assortatively based on their origin, we
280 compared the expected parentage combinations under random mating with the distribution of
281 parentage combinations from our parentage analysis. We also compared the expected
282 distribution fledgling and recruit production among pair combinations (in relation to origin)
283 to the outcome in our study population. To compare whether the distribution differed we
284 performed Pearson's χ^2-contingency tests (Crawley 2007). In these analyses we also included
285 some newly fledged juveniles banded within the breeding season at Vikna (n = 8), and their
286 respective parents, since they were identified as adults (from the 246) that were released in
287 March 2002.

288 To examine whether adult survival probability differed between residents and
289 translocated individuals we used information on whether an individual was observed or
290 captured in the Vikna archipelago after April 15th 2003 (the start of the breeding season one
291 year after the translocation experiment). Because annual re-capture rates for the individuals
292 banded in 2002 were somewhat lower than one, additional capture and observation data in the
293 years 2004-2007 were also used when performing a capture-mark-recapture analysis. Adult
294 survival was analysed with a multi-event Bayesian model following Kéry and Schaub (2012),
295 run with 3 chains each with 10 000 iterations and a thinning rate of 4; the first 6 000
296 iterations were discarded ("burn in"). We assessed the chain mixing and convergence to a
297 stationary distribution by visual inspection of traceplots and the Brooks–Gelman–Rubin
298 criterion (R-hat, Brooks and Gelman 1998). Origin and sex were added as additive covariates
299 in our analysis. Significance was determined from whether the Bayesian 95% credibility
300 interval of the posterior distribution of the difference between groups (Delta) included zero.
301 A similar model was applied to analyse whether survival differed between offspring with
302 parents with similar origin (either two resident parents or two translocated parents), and
303 offspring with a mixed parent pair (a resident and a translocated parent). Thus, in analyses of
304 offspring survival pair combination was added as a covariate. To increase statistical power,
305 additional offspring (n = 34) from pairs involving 9 adults banded in the Vikna archipelago
306 within the breeding season shortly after release (and thus regarded as residents), were
307 included. This analysis examined the existence of any hybrid vigour, evident if offspring
308 from mixed parent pairs had higher recruitment probability than offspring from single origin
309 pairs (Ebert et al. 2002). In this analysis we included 154 offspring from 80 parents
310 distributed among 49 pair combinations, from which only 4 pairs had more than one recruit.
311 Accounting for similar background of siblings was not possible in our capture-mark-
312 recapture model.

Finally, we calculated the demographic variance separately for resident and translocated, males and females. Demographic variance is the expected variance in the individual fitness within years (Lande et al. 2003). Following e.g. Engen et al. (1998), Sæther et al. (1998) and Engen and Sæther (2014) the relationship between adult survival and the number of recruits produced (fecundity) enabled us to partition the deterministic and stochastic components of the contribution to future growth. We could then estimate the contribution from each group of origin (resident and translocated) to the total population demographic variance, by using the equation for females (used for both sexes separately) from Engen et al. (2007):

$$\sigma^2_{df} = b_f q(1-q) + \sigma^2_f q^2 + s_f(1-s_f) + 2qc_f,$$

where σ^2_{df} denotes the demographic variance, and b_f, σ^2_f, s_f, and c_f denotes the parameters for individual level data for the respective number of recruits, variance in recruit production, survival and the covariance between recruit production and survival. Assuming an equal sex-ratio among offspring q is set to 0.5. In order to estimate the sampling error of our estimates, mean estimates and standard error of the demographic variance were estimated from separate samples consisting of 10 000 bootstrap replicates drawn randomly from our data dependent on sex and origin. All statistical analyses were performed in R version 3.3.0 (R Core Team 2016). For the capture-mark-recapture analyses we used the 'r-jags'-package ver. 4-6 (Plummer 2016).

Results

From the breeding season in 2002, parentage analyses showed that 40.5 % (17) of resident males remained unmated, 42.9 % (18) had one mate, and 16.7 % (7) had two mates. Among the translocated males 69.0 % (20) remained unmated, 27.6 % (8) had one mate, and only 3.4 % (1) had two mates.

337 Resident males acquired more mates than translocated males (Table 1), revealed by a
338 higher number of parentages than translocated males. However, there were no statistically
339 significant differences between resident and translocated individuals in the other fitness
340 components, or in the measure of annual individual fitness (Table 1). The effect of origin on
341 number of fledglings, number of recruits and the annual individual fitness did not differ
342 between males and females, as indicated by the non-significant sex × origin interactions
343 (number of fledglings: $\chi^2_1 = 1.52$, n = 144, p = 0.217; number of recruits: $\chi^2_1 = 0.85$, n = 144,
344 p = 0.358, annual individual fitness: $\chi^2_1 = 0.57$, n = 144, p = 0.451).
345 There seemed to be a positive interaction between male badge size and origin on the
346 number of mates (badge size × origin interaction: $\beta = 1.03 \pm 0.55$, $\chi^2_1 = 3.90$, n = 71, p =
347 0.048), however this was not significant after controlling for multiple tests. The positive
348 relationship between badge size and the number of fledglings was stronger in translocated
349 males than in resident males (badge size × origin interaction: $\beta = 2.04 \pm 0.70$, $\chi^2_1 = 8.25$, n =
350 71, p = 0.004, Fig. 1). The difference in effect of resident and translocated males on the
351 negative relationship between bill length and both the number of fledglings and recruits did
352 not remain significant after controlling for multiple tests. There were no differences in the
353 relationship to fitness components between resident and translocated individuals due to the
354 other morphological traits measured (males: All $\chi^2_1 \leq 2.38$, n =72, $p \geq 0.123$; females: All χ^2_1
355 ≤ 3.51, n = 74, $p \geq 0.061$, Supplementary material Appendix 3 Table A2).
356 The overall observed mating pattern (see the expected and observed distributions in
357 Supplementary material Appendix 4 Table A3), i.e. whether the genetic fathers and mothers
358 in a pair had the same or different origin, deviated from what was expected from random
359 mating. The overall pattern suggested that mating was assortative based on origin ($\chi^2_1 =$
360 11.64, n = 46 pairs, $p < 0.001$; Fig. 2), where in particular translocated males were very
361 unlikely to mate with resident females. The mating pattern was subsequently apparent with a

362 significant deviation in the production of fledglings compared to what is expected from a
363 random fledgling production among parent pair types ($\chi^2_1 = 43.36$, n = 128 fledglings, $p <$
364 0.001; Fig. 2). The distribution in production of recruits among the pair types however, did
365 not deviate from the expected distribution ($\chi^2_1 = 2.24$, n = 19 recruits, p = 0.135).

366 The adult survival probability from the breeding season to the next year was similar for
367 resident and translocated individuals in both sexes (Table 2). The analysis of offspring
368 survival revealed however that the survival probability was significantly higher for offspring
369 produced by parents of different origin than for offspring produced by parents of similar
370 origin ($Deltas_{(different)-S(similar)} = 0.25 \pm 0.08$, CI = (0.10, 0.41), n = 154, Table 2). The Brooks-
371 Gelman-Rubin statistic for convergence was less than or equal to 1.008 and 1.004
372 respectively, for all parameters in the two simulations.

373 Finally, we examined the variance in individual fitness to estimate the contribution
374 from each origin to the demographic variance in the population. Estimates of the sex-specific
375 demographic variance ranged from $\sigma^2_d = 0.33 \pm 0.06$ SE in translocated males to $\sigma^2_d = 0.60 \pm$
376 0.16 SE in translocated females (Table 3). The sex-specific demographic variance did not
377 differ consistently between resident and translocated individuals in either sex, indicating that
378 individuals from both origins contribute to the demographic variance of the population.

379 Discussion

380 We found a stronger positive relationship between badge size and the production of
381 fledglings among translocated males than among resident males (Fig. 1). This can have
382 contributed to an assortative mating based on origin, causing unexpectedly few number of
383 parentages and number of fledglings from pairs of parents with mixed origin, especially pairs
384 consisting of translocated males and resident females (Fig. 2). The low total number of
385 fledglings from pairs of mixed origin seem to have been relaxed to some extent by an

386 increased recruitment probability in offspring from pairs of parents with mixed origin (Table
387 2, Fig. 2), suggesting hybrid vigour.

388 The comparison of fitness components between resident and translocated individuals
389 revealed that resident males acquired more mates than translocated males (Table 1), however,
390 this did not result in higher reproductive success. Due to morphological differences between
391 resident and translocated individuals (Table A1), and a positive relationship between badge
392 size and lifetime reproductive success (Jensen et al. 2004), one should also expect a
393 difference in reproductive success between resident and translocated males. Neither of the
394 other fitness components, nor a measure of annual individual fitness in either sex differed
395 between resident and translocated individuals. Even though few translocation studies
396 compare fitness components with a reference baseline, some bird translocations among rather
397 similar populations and habitats indicate small differences in fitness between resident and
398 translocated individuals after establishment (Krogstad et al. 1996, Kaler et al. 2010), often
399 apparent only in components of fitness measured early in the breeding cycle (Kaler et al.
400 2010). In contrast, fitness of translocated individuals may also exceed that of the resident
401 individuals e.g. if the translocated individuals have increased mating success compared to the
402 resident(Jones et al. 1995).

403 In house sparrows, the size of the black throat badge is important for the dominance
404 structure in sparrow flocks (Møller 1987, Solberg and Ringsby 1997) and badge size is often
405 positively related to reproductive success (Jensen et al. 2004, Nakagawa et al. 2007, Jensen et
406 al. 2008). Interestingly, we found a stronger positive relationship between badge size and
407 number of fledglings in translocated males compared to resident males (Fig. 1). This implies
408 that only the larger badged translocated males (with badge size in the upper 27 %) produced
409 equally many or more fledglings as resident males, while translocated males with smaller
410 badge size (the remaining 73 %) on average produced fewer fledglings compared to resident

411 males with equal badge size. The weaker effect of badge size on the number of fledglings for
412 resident males may be an effect of living in small populations where individuals know each
413 other's fighting ability from previous encounters (the individual recognition hypothesis;
414 Solberg and Ringsby 1997). Hence, the translocated males may experience increased costs in
415 terms of aggressive interference encounters because resident males test the reliability of their
416 badge signal.. Accordingly, the only morphological trait that affected fitness of translocated
417 and resident individual differently was related to sexual selection and male-male competition
418 for mates.

419 Although the two groups of origin perform equally well with respect to fitness
420 components and annual individual fitness (Table 1), further examination of parentage showed
421 an assortative mating based on origin (Fig. 2). Only 6.7% of resident mothers produced
422 offspring with a translocated father, emphasizing the reduced mating success for translocated
423 males with respect to resident females. Reproductive skew caused by assortative mating has
424 previously been found in translocation studies, e.g. related to male body mass (Sigg et al.
425 2005) and male song affected by source of origin (Bradley et al. 2014). The low success for
426 translocated males to mate with resident females (and partly also translocated females with
427 resident males) limited the intermixing of the translocated individuals into the local
428 population (Fig 2).

429 In our analyses of adult survival, we found no differences between resident and
430 translocated individuals in either sex. Unlike the similar adult survival rates, our results on
431 the fledgling survival probability until recruitment showed an effect of hybrid vigour, as the
432 recruitment probability was significantly higher for offspring with parents of mixed origin
433 than for offspring with parents of the similar origin. In the present experiment hybrid vigour
434 seem to have been important for alleviating the observed skew in the distribution of parentage
435 and fledglings for pairs of mixed origin (Fig. 2), and might have enhanced gene flow between

436 the resident and the translocated individuals of the population (Ebert et al. 2002). Similarly,
437 Marr et al. (2002) found increased performance e.g. offspring survival, in offspring from
438 immigrant-resident pairs in song sparrows *Melospiza melodia* on Mandarte Island, Canada.
439 Our results did not indicate any differences between resident and translocated
440 individuals in the sex-specific estimates of demographic variance, and the estimates were
441 within the range of what has been reported for temperate passerines (Sæther et al. 2004). The
442 contribution to the demographic variance from the two groups of origin (Table 3) might be
443 according to what was expected due to the lack of significant differences between residents
444 and translocated individuals in most fitness components (Table 1, 2). A potential bias
445 estimating demographic variance in this population was related to an underestimation of vital
446 rates. The CMR-analysis predicted a slightly higher adult survival rate compared to our
447 individual data (Table 3), which could potentially overestimate the demographic variance to
448 some extent. However, this bias should be independent of source of origin, thus not influence
449 the difference in the contribution to the demographic variance. Additionally, the integration
450 of survival rates from the CMR-analysis had only marginal effects on the estimates of
451 contribution to demographic variance. Although we lack demographic data to estimate
452 demographic variance in the period before the translocation, our estimates are within the
453 variation in a neighbouring population of house sparrows (Sæther et al. 1999, Ringsby et al.
454 2006), indicating that our estimates seem reliable.
455 The present study has experimentally demonstrated that translocated individuals of both
456 sexes contribute to the future population dynamics, since there were no differences in either the
457 individual contributions nor the demographic variance between resident and translocated
458 individuals. Moreover, the experiment revealed that the success of translocated individuals may
459 depend on their sex-specific phenotypic characteristics, and furthermore, that the contributions to
460 the local population might also be affected by the recruitment probability of offspring. Our

findings have substantial implications for conservation programs and the understanding of individual ecology of translocated individuals in recipient populations.

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Author contribution statement BES, HJ, and THR conceived and designed the experiments. BGS, HJ and THR performed the experiments. HJ, SS and ÅAB carried out the genetic parentage analyses. HP, IH, PSR, SS, and TK analysed the data. HP, PSR, and SS wrote the manuscript with input from the other authors. **Conflict of interest** All the authors declare that they have no conflict of interest.

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590 Supplementary material (Appendix oik-XXXXX at

591 <www.oikosjournal.org/readers/appendix>). Appendix 1–6.

Tables

Table 1. Means and parameter estimates for tests of difference in fitness components between resident and translocated house sparrows in the Vikna archipelago in Norway the breeding season 2002. Analyses of the number of mates were carried out with Poisson error distribution, the number of eggs with quasi-Poisson error distribution, the number of fledglings and recruits with negative binomial error distribution, and analyses of annual individual fitness (Ann. fitness) was carried out with a Poisson error distribution. e^{β}-values represents the difference between resident and translocated individuals retransformed from the link-scale, with corresponding standard errors retransformed with the delta method. The degrees of freedom = 1 for all tests, and significant p-values are depicted in bold.

	Resident	**Translocated**			
	mean ±SD	**mean ±SD**	e^{β} **±SE**	**z**	**p**
Males (n = 71)					
Mates	0.76 ±0.73	0.35 ±0.55	2.20 ±0.80	2.19	**0.029**
Fledglings	1.88 ±2.29	1.07 ±2.22	1.76 ±0.74	1.34	0.181
Recruits	0.29 ±0.81	0.21 ±0.49	1.38 ±0.92	0.49	0.627
Ann. fitness	0.79 ±1.05	0.59 ±0.68	1.34 ±0.40	0.98	0.327
Females (n = 73)					
Eggs	2.35 ±3.43	2.58 ±3.78	0.91 ±0.31	-0.27	0.790
Fledglings	1.65 ±2.54	2.09 ±3.05	0.79 ±0.39	-0.48	0.632
Recruits	0.23 ±0.58	0.36 ±0.82	0.62 ±0.36	-0.83	0.407
Ann. fitness	0.75 ±0.74	0.76 ±1.03	0.99 ±0.27	-0.04	0.970

Table 2. Estimates of mean survival probability for established adults and for offspring from different composition of parent pairs based on source of origin. Estimates of mean survival rate (Mean) and 95 % credibility intervals (CI) are obtained from capture-mark-recapture models. Mean resighting probability (and corresponding credibility intervals) for adults and offspring, 0.65 (CI: 0.52, 0.77) and 0.65 (CI: 0.51, 0.77) respectively.

Origin	Mean	CI
Adult (n = 146)		
Resident males	0.56	(0.44, 0.70)
Resident females	0.59	(0.46, 0.73)
Translocated males	0.55	(0.40, 0.70)
Translocated females	0.48	(0.33, 0.64)
Offspring (n = 154)		
Parents of similar origin	0.29	(0.20, 0.38)
Parents of different origin	0.54	(0.40, 0.68)

Table 3. Demographic variance (σ_d^2) and its components for resident and translocated, male and female, house sparrows. Individual rate of production of recruits to the next year breeding population (b), survival rate (s) and covariance between recruitment rate and survival rate (cov(b, s)). Standard errors represents the sampling error of the estimates.

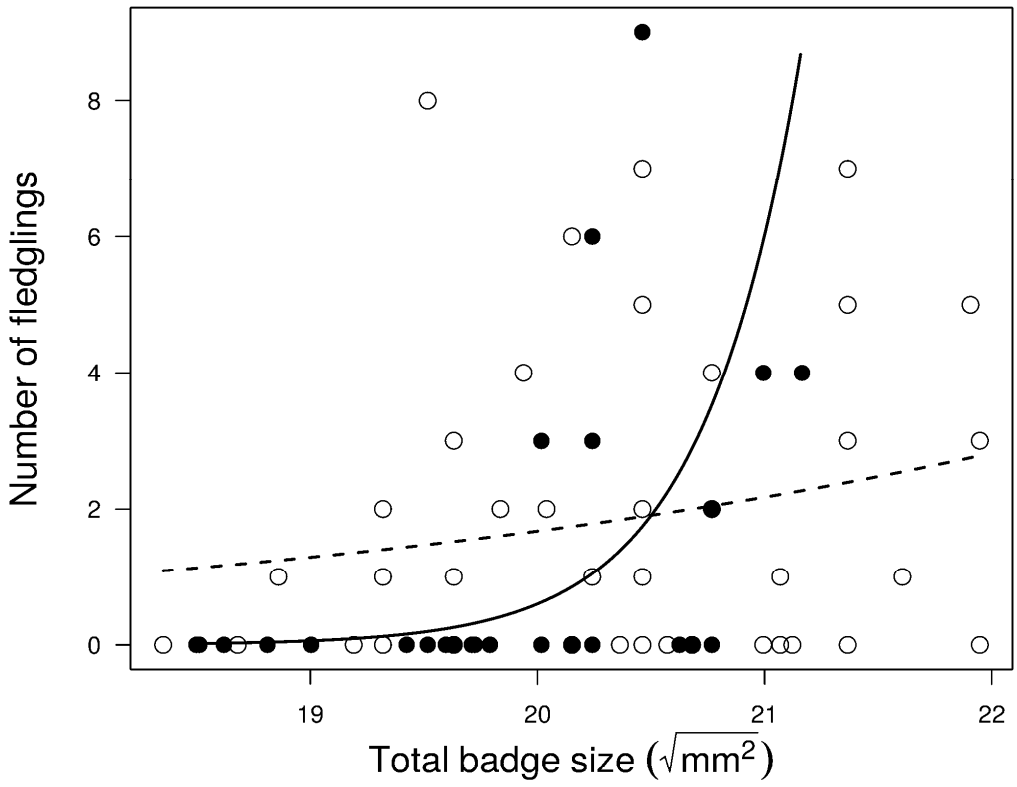
Origin	**b**	**s**	**cov(b, s)**	**σ_d^2**	**±SE**
Male					
Resident	0.29	0.50	0.10	0.58	±0.20
Translocated	0.21	0.38	-0.02	0.33	±0.06
Female					
Resident	0.23	0.53	-0.01	0.38	±0.06
Translocated	0.36	0.39	0.09	0.60	±0.16

643 ## Figure legends

644 **Fig. 1** The relationship between a sexually selected trait, the badge size, and the number of
645 fledglings produced by translocated (n = 29; filled circles and solid line) and resident (n = 42;
646 open circles and dashed line) male house sparrows.

647 **Fig. 2** Number of parentage pairs, fledgling- and recruit production based on genetic
648 parentage in resident and translocated house sparrows. Dark bars represents the number of
649 pairs (Mates, n = 46), grey bars represents the number of fledglings (Fledglings, n = 128) and
650 the white bars represents the number of recruits (Recruits, n = 19). Res = resident, and Tra =
651 translocated.

652 **Figure 1**



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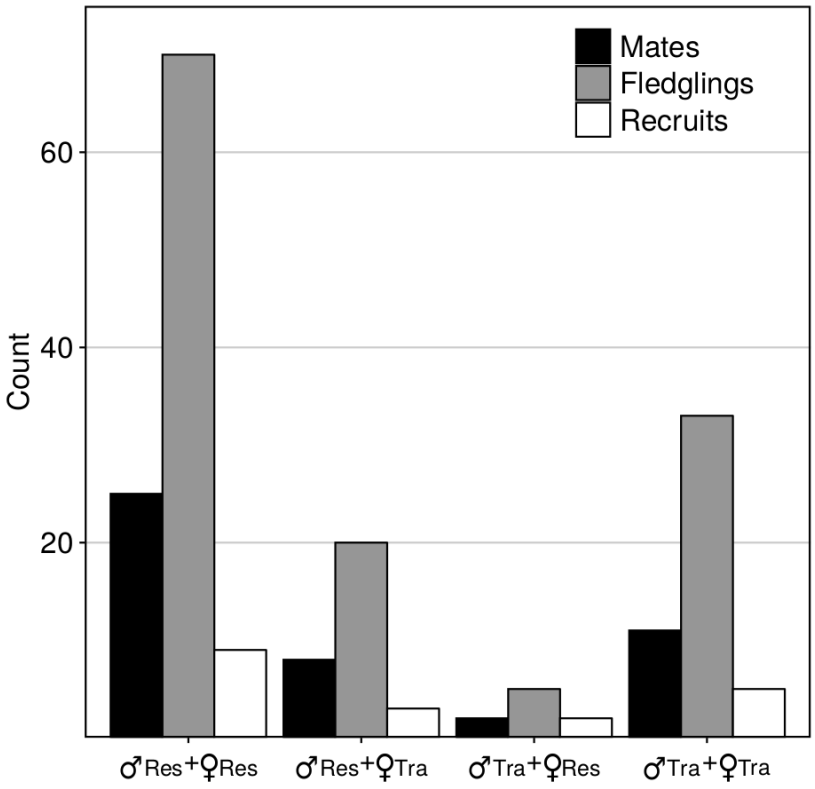
655 **Figure 2**



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