

Maryam Kazemi

Demographic changes in female-skewed populations of house sparrow (*Passer domesticus*)

An experimental study

Master's thesis in Ecology, Behaviour, Evolution and Biosystematics

Supervisor: Henrik Jensen

Co-supervisor: Thor Harald Ringsby, Bernt-Erik Sæther, Hamish Andrew Burnett, Ane M. Myhre

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Abstract

In nature, an unequal sex-ratio in wild populations is a common occurrence. Many factors could result in skewed sex-ratios, for instance, selective hunting, sex-specific mortality, sex-biased dispersal, etc. A biased sex-ratio could affect offspring production and survival of individuals and consequently growth rate. In this study, I investigated how the female-skewed population of house sparrows (*Passer domesticus*) affected population dynamics.

The house sparrow populations were monitored from 2013 to 2015 in eight study sites, including six islands and two populations in the mainland, along the coast of mid and northern Norway. Fieldwork was carried out during winter every year. Each year, all adult sparrows were captured with mist nets, marked with a numbered metal ring and a unique combination of three colored plastic rings, and sampled for blood. During the winter of 2014 half of the males, randomly chosen, were removed from each population. This allowed me to examine the effects of female-biased population on the survival of adults, number of recruits produced, population growth rate, and whether parents are able to adjust the sex-ratio of recruits toward the rarer sex.

The result showed that one year after the manipulation of the sex-ratio, all populations recovered approximately to the same population sizes as before the manipulation with a roughly equal sex-ratio. In 2015 the average number of recruits produced by female parents did not differ significantly from 2014. However, in 2015 male parents produced on average more recruits and the number of males parents who had zero recruits decreased dramatically in compared to 2014. The higher average recruit production among males maybe because fewer males must serve the female segment with copulations of reproduction females. Also, as some of males did not have the opportunity to produce offspring when the sex-ratio was 1:1 but after removing half of the males most of them have a chance to have recruits. Since the number of recruits only increased for male parents, not females, the total number of recruits only increased slightly; this indicated that the population might recover mostly as a result of immigration. Also, I found out that the survival of parents was not affected by our experiment, but female parents generally had lower survival than males in both years. Accordingly, the study revealed that the adult sex-ratio in the house sparrow populations did not affect the sex-ratio of recruits produced. For future studies, more attention could be focused on the proportion of mated males as well to understand how the experiment affected polygyny, and how polygyny could affect the survival of recruits and adults.

Keywords:

Sex-ratio manipulation, altered sex-ratio, unequal sex-ratio, biased sex-ratio, skewed sex-ratio

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Maryam Kazemi

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Introduction

The sex-ratio in a population, measured as the proportion of males relative females can have profound consequences on population dynamics. Based on Fisher's (1930) theory, natural selection acts on the sex-ratio and tends to stabilize it at equilibrium. Assuming equal costs of producing each sex, he stated that selection favors those parents that invest equally in both sexes of offspring, and any bias in sex-ratio, would favor individuals of rarer sex which leads to equality in the sex-ratio. A general acceptance of his theory dampened interest in the adult sex-ratio and result in a general acceptance of balanced sex-ratio in most populations (Breitwisch, 1989). However, Mayr (1939) stated that in many bird populations, males outnumbered females by around 10-20%. McIlhenny (1940) and Payevsky (1993) also affirmed an excess of males across a range of species. Naturally or artificially skewed sex-ratio might have a great impact on the growth rate and survival of endangered populations, so it needs more attention in conservation biology (Wedekind, 2002).

There are many factors that may cause biases in sex-ratio in wild populations, both natural and anthropogenic, including sex-specific mortality (Donald, 2007), selective hunting only on one sex (Ginsberg & Milner-Gulland, 1994), environmental conditions (Korpelainen, 1990), habitat degradation and fragmentation (Butler & Merton, 1992), sex-biased dispersal (Dale, 2001), as well as demographic stochasticity in small populations (Dale, 2001; Engen et al., 2003).

However, the underpinning factors that causes skewed sex-ratio in wild populations may not be obvious and may act indirectly. For instance, in the study of Black Robin at Chatham Island in New Zealand, habitat degradation caused higher exposure of nests to predators and result in higher mortality of females, and thus led to a male-biased in the population (Butler & Merton, 1992). Habitat fragmentation has also proved to affect the sex-ratio in other bird species (Helle et al., 1999; Sun et al., 2003; Zanette, 2001), mammals (Banks et al., 2005; Estrada et al., 2002), and amphibia (Pröhl, 2002) as well. Environmental conditions like temperature during a specific period of embryonic development could determine sex in reptiles (Bull, 1980). In mammals higher mortality of males occurs through trophy hunting (Langvatn & Loison, 1999). Temporarily skewed sex-ratios have been recorded in declining populations of capercaillie Tetrao urogallus (Helle et al., 1999; Wilkinson et al., 2002) because in small populations demographic stochasticity can lead to higher production of one sex by chance (Lande, 1993). An other important factor that may results in skewed sex-ratios is dispersal (Clarke et al., 1997). In mammals, natal dispersal is usually male-biased (Dale, 2001) and in birds, females are the most dispersive one, which results in male-biased sex-ratios in small, isolated, or fragmented populations (Clarke et al., 1997; Greenwood, 1980; Greenwood & Harvey, 1982).

A skewed sex-ratio could influence behaviors like polygyny, extra-pair copulation, and cooperative breeding (Murray Jr, 1991). Curry and Grant (1989) in the study of Galapagos Mockingbird presented that when the sex-ratio is male-biased, a higher proportion of males become nest helpers, and when is female-biased all females are able to breed since the shortage of males compensated by polygyny. Smith et al. (1982) demonstrated that sex-ratio could affect mating status and when the number of females outnumbered males, monogamous Song Sparrows turned to polygyny. Mating status could affect the productivity and breeding success of individuals (Bertram, 2014; Castro et al., 2004), and eventually, it has an impact on the population dynamics (Boukal & Berec, 2002; Brook et al., 2000; Deeming & Wadland, 2002).

Moreover, polygynous males could not contribute to the feeding and raising of chicks as monogamous males, thereby it would affect the survival of offspring and result in few numbers of recruits and a decline in population size. Garamszegi et al. (2004) found that polygamous mated females had lower breeding success, which could be as a result of less parental help from males during chicks feeding. Török et al. (1998) discovered widowed females who raised chicks alone, lost more body mass due to increased feeding rate. Lundberg and Alatalo (2010) also found that in the pied flycatcher species, the secondary females received no assistance or reduced assistance during raising nestling and experienced a reduced number of recruits. Gustafsson (1989) Showed secondary females of flycatchers have a lower number of recruits. Indeed, both primary and secondary females receive less male assistance from their mates than monogamous females (Lundberg & Alatalo, 2010). However, Moreno et al. (2002) found in spotless starlings, female breeding success is weakly affected by mating status but strongly relied on inherent quality differences between females.

Furthermore, sex-ratio is a central parameter in the formulas defining effective population size (N_e). an unequal sex-ratio influences effective N_e (Nomura, 2002; Wright, 1990), and deviation of the sex-ratio away from equality will reduce N_e . A skewed sex-ratio could lead to increased inbreeding and consequently genetic loss (Wedekind, 2002).

A skewed adult sex-ratio in the population might affect the sex-ratio of offspring. Historically, it was assumed that in species with genetic sex determination like mammals and birds, parents could not manipulate the sex-ratio of offspring. However by extensive research in a variety of organisms revealed that parents in many species manipulate the sex-ratio of their offspring in different ways to increase their fitness (Davies et al., 2012). Thus, based on the adaptive sex-ratio theory, if the fitness of male and female offspring differ with environmental conditions, parents should manipulate the primary sex-ratio correspondingly to maximize their fitness (Frank, 1990; Trivers & Willard, 1973; Williams, 1979). Some studies support theoretical expectations of adaptive sex-ratio (Badyaev et al., 2002; Dijkstra et al., 1990; Ellegren et al., 1996; Komdeur et al., 1997; Westerdahl et al., 2000) whereas others fail to support theoretical predictions of adaptive sex-ratio (Leech et al., 2001; Radford & Blakey, 2000; Westneat et al., 2002) and there are many compelling examples of sex allocation in bird species (Heinsohn et al., 1997; Komdeur et al., 1997)

Understanding the consequence of a skewed sex-ratio and how it affects populations is important for the management of small and declining populations. However, from the perspective of conservation biology, population with a male-biased sex-ratio is more vulnerable and to go to extinction, because the population growth rate to a large extent depends on the number of females rather than males (Wedekind, 2002). Based on logistic growth model a sudden decline of the number in one sex, reduced the population size to below carrying capacity (K), should trigger a positive population growth rate until it reaches K due to less competitions for resources. Accordingly, there is more attention in the scientific literature towards male-biased populations, but still, it is important to study the effect of a female-biased population and how it will affect the population growth rates and survival.

In this survey, I investigate the demographic consequence of female-skewed sex-ratios in local populations and their effects on recruit production, survival of parents, and sex-ratio of offspring. The study was done in house sparrow populations as a model system where local populations were manipulated toward more females by removing half of the males from eight local populations in northern Norway, just before the onset of breeding and then I investigated the demographic changes in the populations one year after as a consequence of the experiment. First, I investigate how changes in the sex-ratio affected population size. Then, I investigate how recruit production was affected by the

experiment. Because of the experimental reduction of adult population size I expected less competition for resources among parents and thus an increase in the population growth rate compared to before the experiment. I will also discuss, as a counteracting effect, I expected a decrease in the number of recruits because in avians both parents contribute to raising offspring and changing the sex-ratio from 1:1 to 1:2, might potentially result in more polygynous males and less male assistance during feeding and raising nestlings and subsequently less survival of offspring.

Then, I investigated the effect of the female-skewed sex-ratio on the survival of adults. Female-biased Sex-ratio could affect the mating status and potentially result in more polygynous males. I will discuss how the potential increase in expected polygyny not only might affect the survival of recruits, but also the survival of parents, as they may have increased their individual parental costs due to the experiment. On the other hand, lower competition for food and other resources between the remaining males and females was expected to counteract and increase their survival. Lastly, I investigated the effect of the female-skewed population on the sex-ratio of recruits, testing whether parents adjusted the sex-ratio of offspring towards male bias as a consequence of the experiment.

Methods

Study design

House sparrow is a socially monogamous species, with some level of extra-pair copulation (Jensen et al., 2008) where both parents contribute to raising nestlings (Ringsby et al., 2009). The breeding season in our study area is ca. 4 months and starts from May till August, and each pair produces between 1 to 3 clutches during this time (Ringsby et al., 2002).

The study was carried out from 2013 to 2015, along the coast of mid and northern Norway, in the eight populations including Røvass, Handnesøy, Løkta, Austbø, Herøy, Rånes, Stokkøya, Linesøya. The Røvass population is located in a remote valley south of the glacier Svartisen in Nordland county, six populations Handnesøy, Løkta, Austbø, Herøy, Stokkøya, Linesøya are located on islands along the coast of Nordland in the north to Trøndelag county in the south, and the last population, Rånes is located on a peninsula at the coast of Trøndelag (Figure 1).

All the study localities were sparsely populated by humans, and sparrows in these populations live in close association with humans, where they live in loose colonies on dairy farms and nest inside barns. Fieldwork was conducted during the winter from February to March each year. All adult house sparrows were captured with mist nets, and ringed and sampled for blood. Each sparrow was marked with a numbered metal ring and a unique combination of three colored plastic rings which allowed for later individual recognition of the birds in the field to record survival. Blood samples were taken from the brachial vein underneath the wing and provided the necessary DNA for determining the parentage of new recruits. For a description of the molecular analysis and genetic parentage analyses see (Husby et al., 2006; Stubberud et al., 2017).

Since no individuals had been captured in the study populations before 2013, the age of the sparrows that were captured in 2013 was unknown. Similarly, individuals that were captured as unringed adults in 2014 and 2015 were assumed to be hatched in the previous year and considered as one year old recruits. Birds were assumed as survivors until the last year they were either observed or captured. I

consider two age categories, one year old, and older than one year old which includes two or three years old in my data set. In February-March 2014 half of the males randomly were removed from each population.

Our dataset included the population size, and individual recruit productions for all sparrows for 3 years from 2013 to 2015 and two breeding seasons (2013 before the experiment, and 2014 after the experiment).

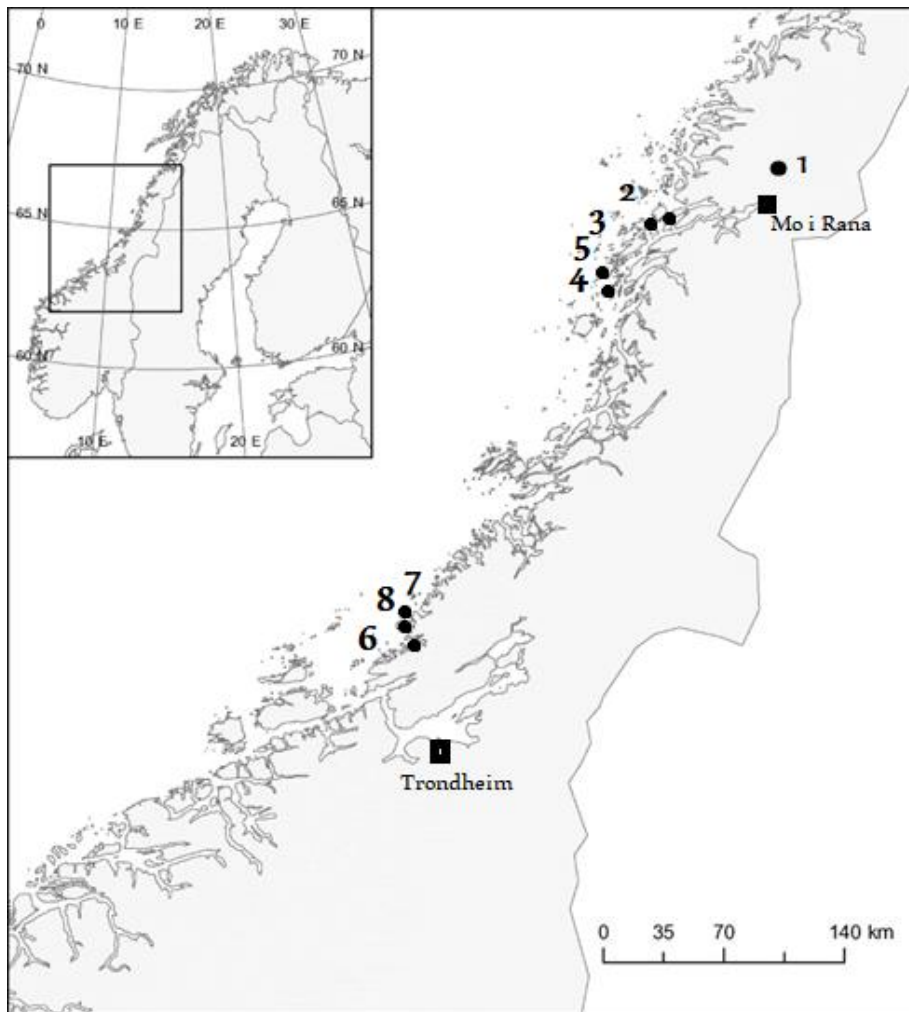


Figure 1. The map of study sites, including Røvass (1), Handnesøy (2), Løkta (3), Austbø (4), Herøy (5), Rånes (6), Stokkøya (7), Linesøya (8).

Statistical analysis

Data analyses were carried out in R version 4.1.2. A paired t-test was used to compare the size (i.e., number of adult house sparrows) of each population before the manipulation of the sex-ratio in 2014 and in 2015. Also, a paired t-test was used to examine whether the population-specific growth rates from 2013 to 2014 (prior to experiment control) and from 2014 (after the experiment) to 2015 were

different. The population-specific growth rate (r) was calculated as: $r = (N - N_0) / N_0$, where N is the final population size and N_0 is the initial population size.

To examine whether the individual reproduction (i.e. production of recruits) changed after the sex-ratio manipulation, a negative binomial generalized linear mixed-effect model using the function `glmer.nb` (Bates et al., 2015). I used the number of recruits produced by an individual as the response variable and year, population size, age, and interaction between age and population size as fixed factors. Because the habitat quality among islands is likely to differ as well as individual house sparrows might intrinsically produce more recruits than others, I included these variables as random factors in the analyses. First, I fitted the full model, and then I successively removed non-significant variables from the model and fitted it again. Then I compared the models based on AIC and I chose the model with the lowest AIC (look at Appendix 8). The dataset includes only 5 sites (Handnesøy, Løkta, Rånes, Linesøya, Røvass). The year 2013 is a control year and 2014 is an after manipulation. For age, there are only two categories, 1 means one year old, and 2 means older which includes 2 or 3 years old. I did the analyses separately for female and male parents to see how the number of recruits changed in comparison to the year before the manipulation (i.e. 2013). For males I had 210 observations and 176 individuals and for females, I had 256 observations and 204 individuals.

To examine whether the survival was affected by sex-ratio manipulation, I applied Generalized Linear Mixed Models using Template Model Builder using the `glmmTMB` function (Brooks et al., 2017) with a binomial family. I tested whether the survival of males and females differed among years, and to see if there was a difference between males and females. Thus, I included survival as a response variable and year, population size, sex, and all two-way- interactions between them as fixed factors. I ran the full model and then removed the non-significant ones, and then based on the lowest AIC chose the best model (Appendix 9), which include sex, population size, and year as fixed factors. I had 684 observations and 555 individuals in eight study sites.

To examine whether the sex-ratio offspring deviated from $P = 0,50$ a generalized linear mixed model (`glmer`) (Bates et al., 2015) was fitted with a binomial family. I used the `cbind` command and considered the number of male and female recruits within clutches as response variables and year as a predictor variable. Since I only interested whether the sex-ratio differed between years, I only included year as a fixed factor, and to control the effect of different environments and individuals, I considered study site as random factors. Before running the models, I removed the number of recruits for both male and female parents that are zero. The analysis performed separately for male and female parents. For male parents the model did not converge, I tried to use `glmmTMB` instead of `glmer`, but still I got the converge error. However, in most cases, the results will usually not be strongly affected, thus we present the model.

Results

Change in population size

The mean population size in 2015 was lower than 2014. In four of the study sites (Austbø, Handnesøy, Linseøya, and Rånes), the population decreased, in two sites (Herøy and Stokkøya) the population did not change much and in the two remaining sites (Løkta and Røvass) the population increased in 2014 (Figure 2). However, the result of paired t-test revealed no significant difference in the population sizes between the two years (P -value = 0.25, df =7). Accordingly, the overall pattern showed that the study population in 2015 bounced back to the same level as it was before manipulation in 2014. Table 1 shows the population size in each site during the experiment.

Table 1: Annual adult population sizes from 2013 to 2015 in 8 study populations of house sparrows in mid- and northern Norway. 50% of the males were removed from each study site in 2014. Accordingly, the population sizes before and after removal in 2014 are presented.

Number	Sites	2013	2014		2015
			Before removal	After removal	
1	Røvass	20	17	13	22
2	Handnesøy	57	77	58	67
3	Løkta	48	44	34	55
4	Austbø	56	65	51	50
5	Herøy	18	10	8	10
6	Rånes	52	73	54	42
7	Stokkøya	62	42	32	43
8	Linesøya	80	69	52	62

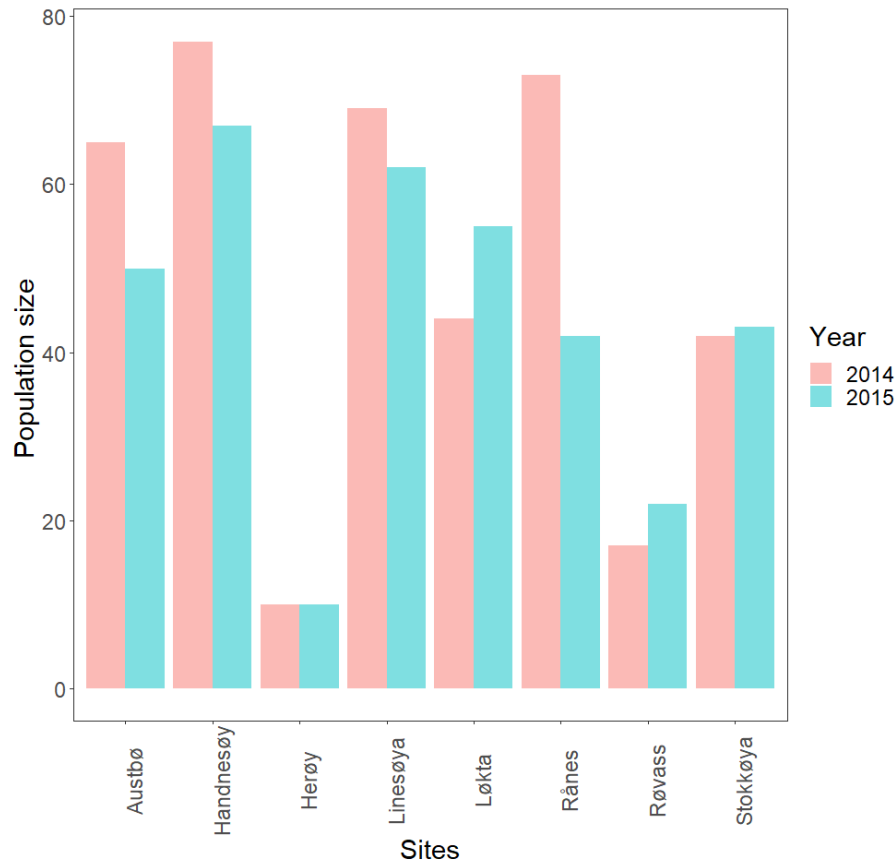


Figure 2: A bar plot of population sizes before manipulation in 2014 and a year after manipulation in 2015 for 8 study sites.

The growth rates for 2013-2014 and 2014-2015 were calculated, respectively. The growth rate before and after manipulation were tested with paired t-test. As Table 2 shows, there were high variations in growth rates among populations, some increased while others decreased, and there was no general change in growth rates before and after manipulation. The result of paired t-test showed the growth rate did not change significantly (p -value = 0.33, $df = 7$).

Table 2: The growth rate in 2013 and 2014.

Sites	r2013	r2014
Røvass	-0.15	0.41
Handnesøy	0.35	0.13
Løkta	-0.08	0.38
Austbø	0.16	-0.02
Herøy	-0.44	0.20
Rånes	0.40	-0.29
Stokkøya	-0.32	0.24
Linesøya	-0.14	0.16

Change in reproduction

To examine if the population returned to the same population sizes as before the manipulation as a result of higher reproduction, a negative binomial generalized mixed model was applied with the number of recruits as a response variable and age and year as predictors. Analysis was done separately for male and female parents.

The result for male parents showed that the number of recruits produced in 2014 significantly increased compared to 2013 ($b = 0.53$, $SE = 0.16$, $P = 0,001$). Also, the analyses indicated tendency, where older males produced a higher number of recruits, though the relationship was not significant ($b = 0.28$, $SE = 0.18$, $P = 0.11$). Correspondingly for female parents, the number of recruits was neither affected by year ($b = 0.09$, $SE = 0.17$, $P = 0.57$) nor age ($b = 0.07$, $SE = 0.19$, $P = 0.68$). The output of models for male and female parents respectively are summarized in Appendix 1 and Appendix 2.

To make the numbers easy to understand and interpret, I calculated the average marginal effect (AME) for both male and female parents summarized in Table 3, and I also calculated adjusted predictions of predictors (Appendix 3).

In 2014, male parents on average produced 0.48 percent more recruits, but for female parents, it increased by only 0.06 percent. Furthermore, older males (2 or 3 years) produced on average 0.24 percent more recruits, but for older females, it increased by only 0.05 percent.

Table 3: The output of AME (The average marginal effect) for male and female parents estimated over all study sites. Age 2 includes 2- and 3-years old house sparrows.

	factor	AME	SE	z	p	lower	upper
Male parents	Year 2014	0.4813	0.1664	2.8919	0.0038	0.1551	0.8075
	Age 2	0.2491	0.1706	1.4602	0.1442	-0.0852	0.5834
Female parents	Year 2014	0.0639	0.1159	0.5515	0.5813	-0.1632	0.2910
	Age 2	0.0507	0.1274	0.3978	0.6908	-0.1991	0.3004

The effect of age and year on the number of recruits is presented in Figure 3. It shows year and age both affected the number of recruits for male parents but for females, it has a very negligible effect.

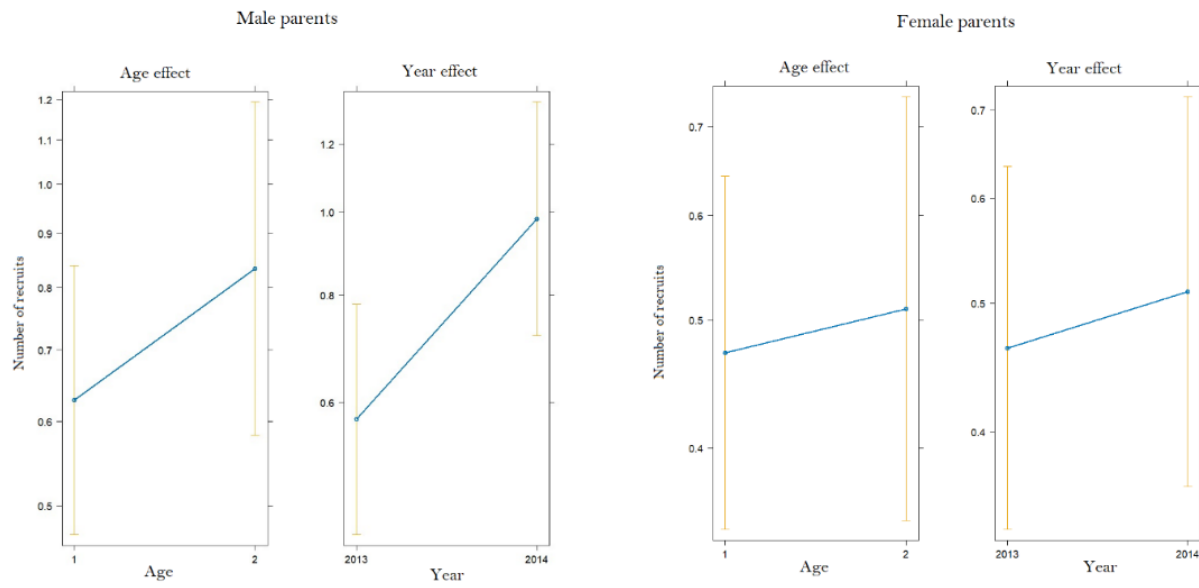


Figure 3: The effects of year and age on the mean number of recruits produced. Male and female parents in left and right panels respectively. Error bars represent standard errors. Age category 1 includes one year old, and age category 2 includes two or three years old.

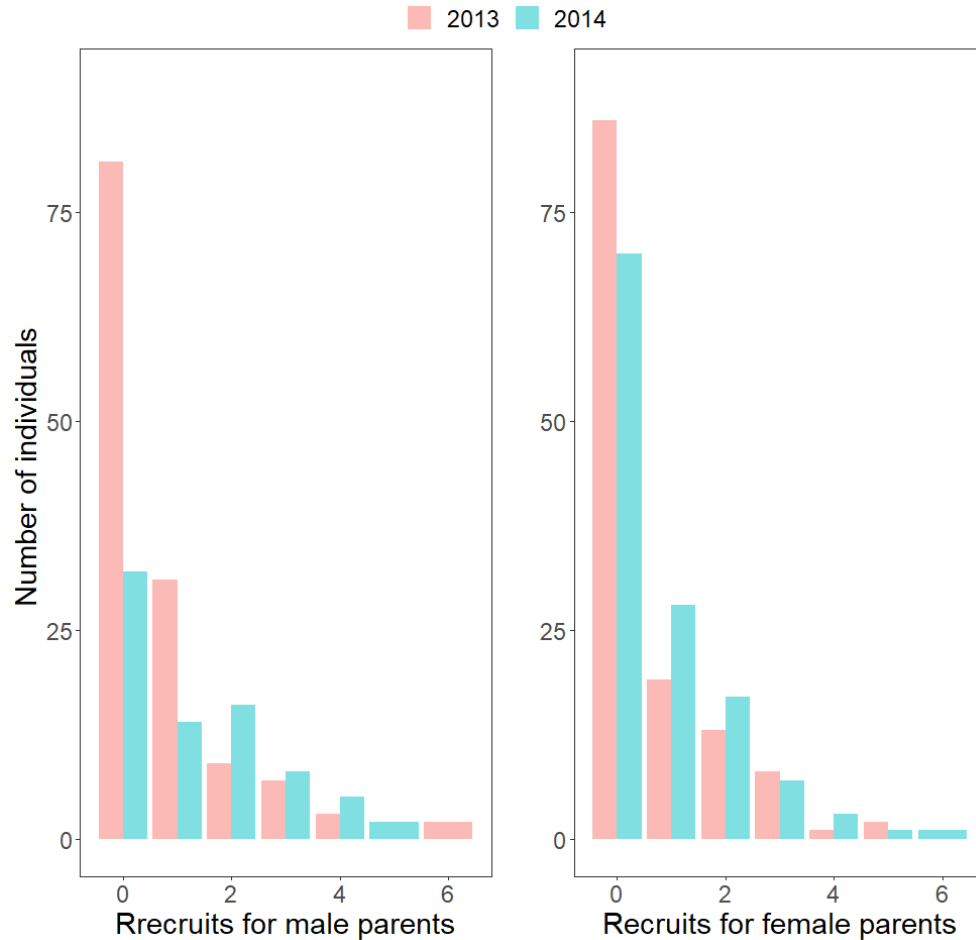


Figure 4: Distribution of number of recruits for male parents (left) and female parents (right) in 2013 (red) and 2014 (blue). The x-axis shows the distribution of number of recruits among sparrows produced during the breeding season.

The distribution of recruits produced in 2013 and 2014 showed a distinct pattern (Figure 4). In 2013 which is the control year, the number of male and female parents that produced zero recruits was about the almost produce the same number. However, in 2014 after the experiment, the number of zero recruits for male parents decreased dramatically.

Change in survival

Next, I examined whether the adult populations had higher survival rates after removing half of the males as predicted as a consequence of reduced population size (i.e. reduced intra-specific competition). The result showed that there were no change in the propability of survival between the years ($b = 0.04$, $SE = 0.17$, $P = 0.80$), however, the probability of survival among females was significantly lower than for males ($b = -0.33$, $SE = 0.16$, $P = 0.04$) in both years. Moreover, there was also a positive and significant relationship between survival and population size ($b = 0.011$, $SE = 0.005$, $P = 0.03$). The output of the models is summarized in Appendix 4.

To make the effect more clear and more understandable, I calculated AME (The average marginal effect) for the survival model, the output is summarized in Table 4, and also, I calculated adjusted predictions of predictors which are shown in Appendix 5.

As Table 4 shows, one unit increase in population size increases survival by on average 0.002, and females have -0.08 lower survival than males. Year had no significant effect on survival.

Table 4: The output of AME (The average marginal effect) for the survival model

factors	AME	SE	z	p	lower	upper
Population size	0.0029	0.0013	2.1249	0.0336	0.0002	0.0055
Year 2014	0.0108	0.0432	0.2505	0.8022	-0.0739	0.0956
Sex (females)	-0.0823	0.0405	-2.0342	0.0419	-0.1616	-0.0030

Figure 5 shows the effect of sex and year on survival clearly. Females have lower survival than males both before and after manipulation. Also, we can see in larger populations, survival is higher, and year had no effect on survival.

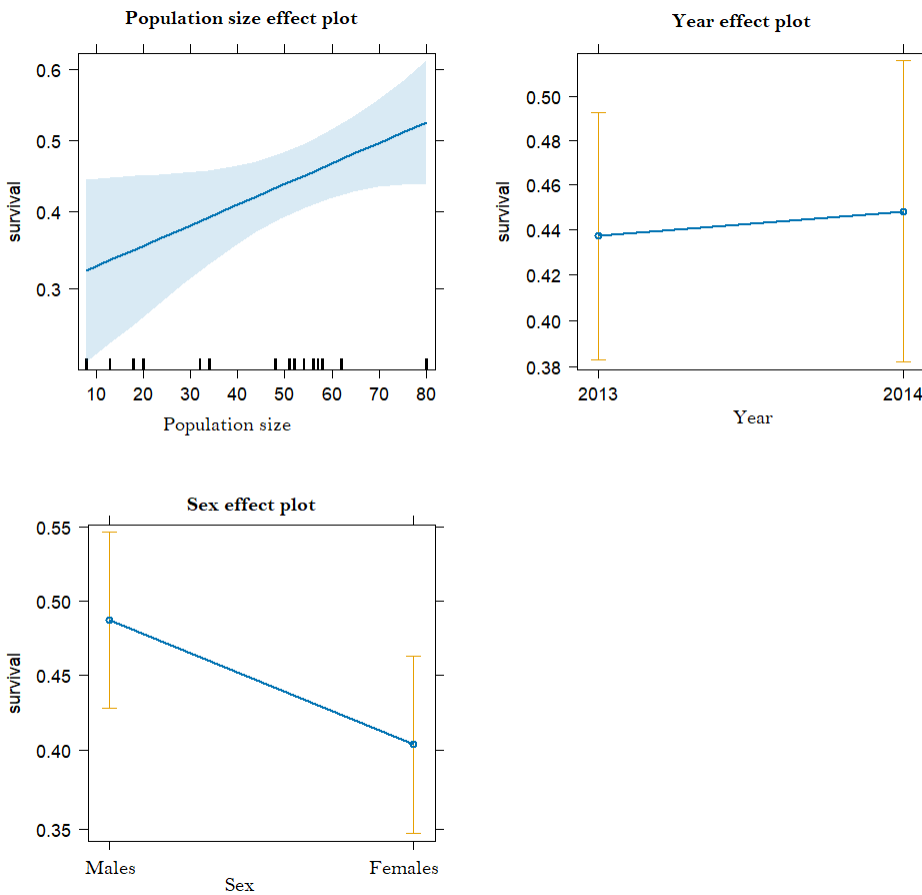


Figure 5: The effect of year, population size, and sex on survival

Changes in the sex-ratio of recruits

The next step was to examine whether the sex-ratio of recruits deviated from $P=0.50$ one year after manipulation, therefore I applied a generalized linear mixed model with a binomial family. I considered the number of male and female recruits as a response variable and year as a predictor variable. I did the analysis separately for male and female parents. The results indicated that the sex-ratio did not change neither for male (p value= 0.91) nor female (p value= 0.82) parents. Year effect was far from statistically significant. The output of models for male and female parents respectively presented in Appendix 6 and 7.

Figure 6 shows the number of recruits in 2013 and 2014 for male and female parents in the five study sites. As the graph illustrates in 2014 after manipulation of the sex-ratio in Handnesøy both male and female parents produced roughly the same number of male and female recruits. In Linesøya and Røvass, male parents produced approximately the same number of male and female recruits, however, female parents produced slightly more males. In Løkta, both parents produced slightly more female recruits, and in Røvass, female parents produced slightly more male recruits, but male parents produced more or less the same number of male and female recruits.

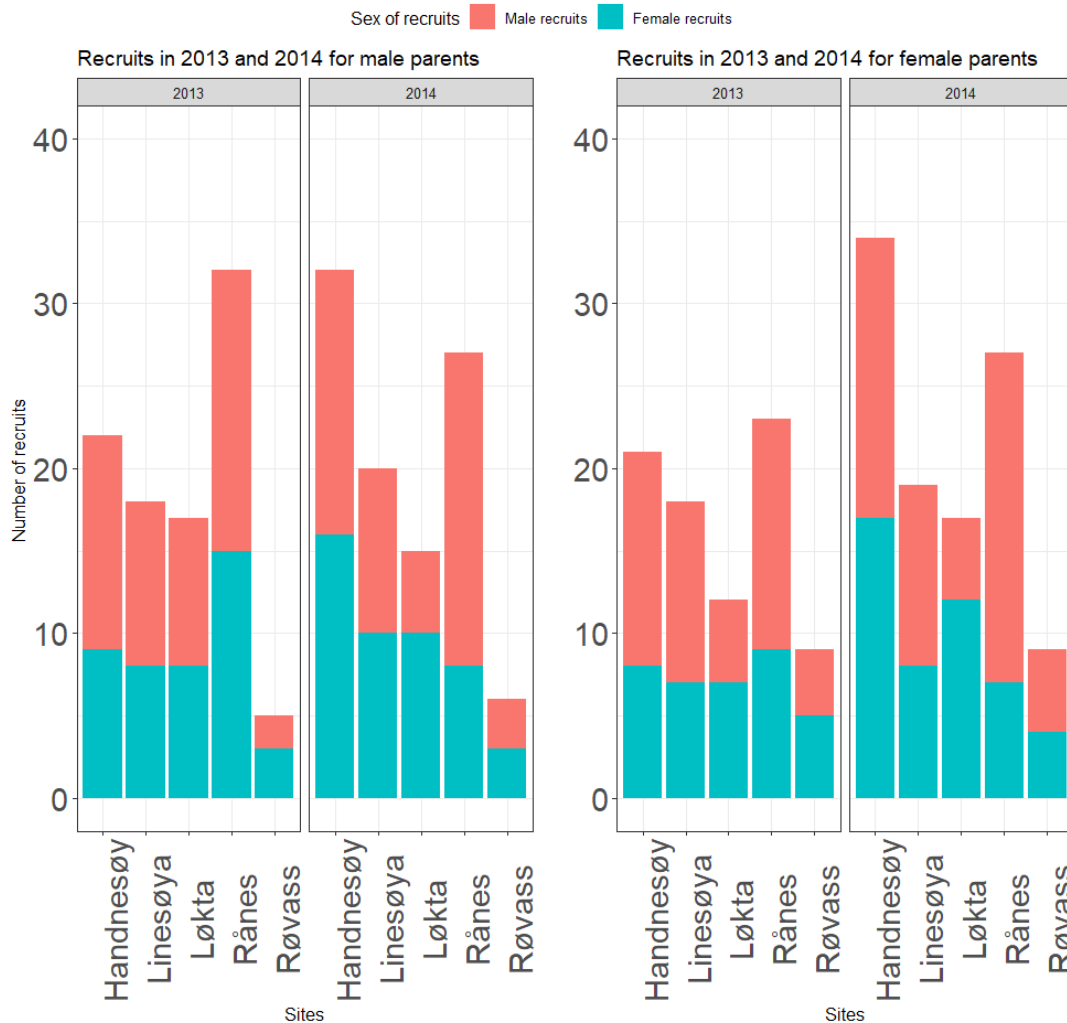


Figure 6: Recruits number for male parents (left) and females (right) in 2013 and 2014 for the 5 different sites.

Discussion

After a manipulation of the sex-ratio, I investigated how female-skewed populations of house sparrows responded with regards to size, growth rate, survival rate of parents, and whether parents were able to manipulate the sex-ratio of offspring towards rarer sex to increase their fitness. The results indicated that one year after removing half of the males from the study sites, the population sizes bounced back to the same level as they were before manipulation with equal adult sex-ratios. However, the growth rate did not increase, nor did the survival. Moreover, the sex-ratio of recruits also did not deviate from 0.5. Therefore, one likely explanation for recovering the population after manipulation could be that more males immigrated to the populations, which the study design did not allow to measure. Thus, few empirical studies from wild species with an experimental design have been carried out with the potential to disentangle whether parents adjust their investment in the number of recruits and sex-ratios to a perturbation in sex-ratio. Accordingly, the present study contributes valuable insight from a small passerine species with relevance for conservation biology.

intuitively, as sex-ratio was experimentally changed from 1:1 to 1:2 in 2014 it was expected that the female-bias among adults should still be present one year later, in 2015. However, this was not the case as the adult sex-ratios in the study populations 2015 in were roughly back to 1:1 as indicated in Figure 7, and actually, in two study sites (Råens and Stokkyøya) they are more male-skewed (see also Appendix 11 for numbers of males and females in 2014 and 2015 respectively).

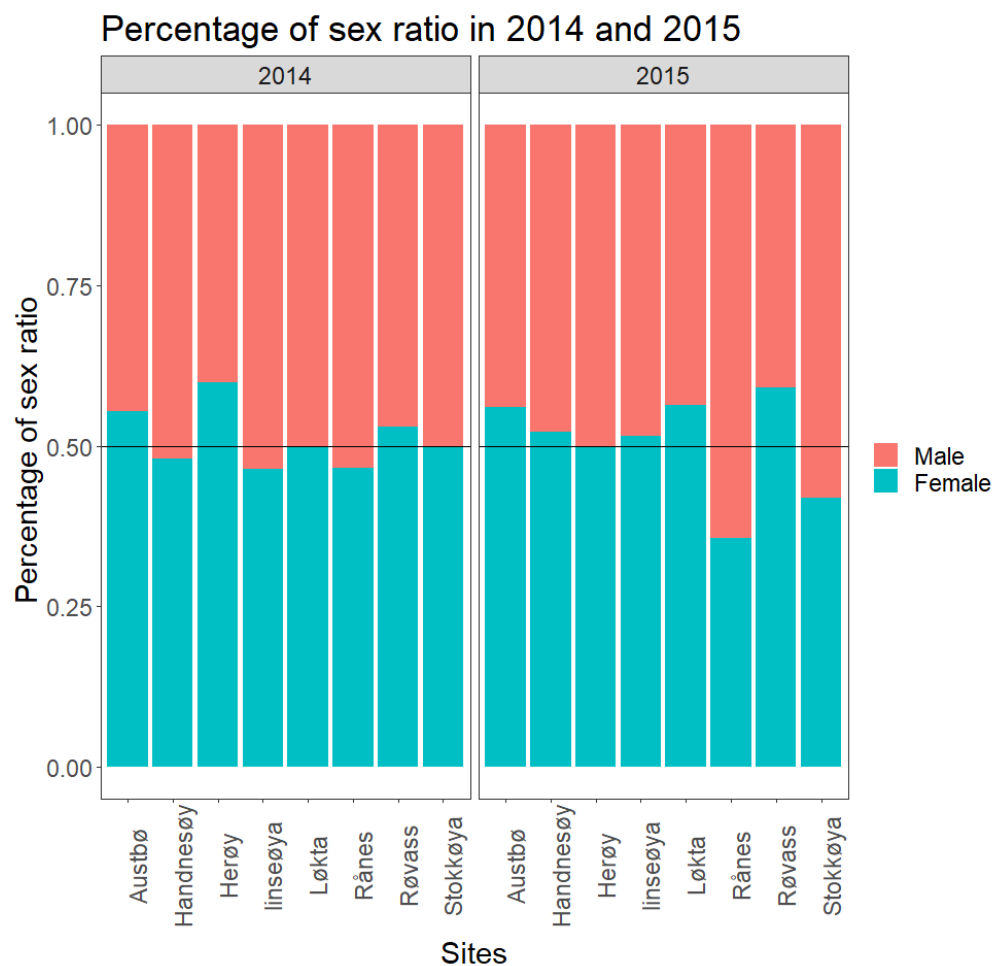


Figure 7: Percentage of adult sex-ratio in 2014 before manipulation, and adult sex-ratio one year later (2015) in the 8 different study sites. The solid line indicates 0.5 sex-ratio.

Manipulation of the sex-ratio had no effect on the number of recruits that female parents produced. However, male parents on average produced more recruits after the manipulation in 2014. The number of male parents that produced zero recruits declined substantially after the experiment compared to before (Figure 5) which potentially could explain why male parents produced more recruits. In species where the competitive ability of males relies on their age and size, a higher female ratio in the population gives an opportunity to smaller and younger males to reproduce in other words more inferior males have breeding success (Kodric-Brown, 1988). Therefore, probably in 2014 more males have a chance to have a mate after removing half of the males, that they did not have before.

Additionally, the age of females had no effect on the number of recruits produced. However, there was a weak tendency, older males produced on average more recruits than one-year-olds ($P=0.11$). There are some evidence that in avians, reproductive success and survival change with the age of individuals, and generally it increases with advancing age, though in some species, performance might decline as the birds age (Martin, 1995). In most bird species, first-time breeders have lower performance in comparison to older individuals (Desrochers & Magrath, 1993; Forslund & Larsson, 1992; Wheelwright & Schultz, 1994). Thus, increasing age affects reproductive success through physiological maturation, increased foraging ability, higher success in acquiring mates and high-quality breeding sites, better parental ability, and social dominance mechanisms (Martin, 1995). However, our result shows only the reproductive success of males increases with age. There are also some studies that the reproductive success of only males increased with age. In brown thornbills and bluethroats older males have higher reproductive success owing to increased feeding of nestlings by older males especially in the few days after hatching (Geslin et al., 2004; Green, 2001). Green (2001) also manifested in Australian brown thornbills (*Acanthiza pusilla*) only the reproductive success of males improved with age. Geslin et al. (2004) showed both sexes in French bluethroats (*Luscinia svecica*) improved reproductive success with age but males improved more. Hatch and Westneat (2007) and Stubberud et al. (2017) showed that in house sparrows both sexes improved their reproductive success with increasing age. There are also more studies that confirmed that reproductive success in avians increases with age (Forslund & Pärt, 1995; McCleery et al., 2008; Rockwell et al., 1993).

One likely consequence of removing half of the males led to polygyny and a secondary female would not get enough assistance from male is that more females raised their offspring without a male mate and therefore had to compensate this by increasing the maternal care, or alternatively, that the level of polygyny increased after the manipulation and a secondary female would receive less assistance from males for raising chicks. Since the common notion is that secondary females who raise their nestlings alone or without male assistance, work harder and have lower survival as a result of that (Alatalo & Lundberg, 1984; Alatalo et al., 1982; Gustafsson, 1989). However, the present study showed that the probability of survival of female house sparrow parents was not affected by the manipulation of the sex-ratio. In support of our study also Wheelwright et al. (1992) studied the polygyny effect on the survival of savannah sparrow, also Kempnaers (1995) measured the survival of primary and secondary females in blue tits, both found only weak support that polygyny affect the survival of females. Same as Garamszegi et al. (2004) also found in collared flycatchers that the survival of secondary females did not affect negatively.

However, both before and after the experiment the results showed that the survival probability of female parents was lower than male parents. Other studies also indicate female survival rates appear to be lower than males (Githiru & Lens, 2006; Liker & Székely, 2005; Promislow, 1992; Searcy & Yasukawa, 1981; Sillett & Holmes, 2002). There are two possible explanations that could explain the lower survival of females in avians. First, incubation is mostly undertaken by the females, which put them at greater risk of predation (Donald, 2007). Sargeant et al. (1984) showed most of the preys from predation on nesting waterfowls by Red Fox were females. Even for cavity-nesting birds, which have lower predation rates, the proportion of nest predation that result in the mortality of females might be high (O'Donnell, 1996). Second, in most bird species, females are more dispersive than males (Clarke et al., 1997; Greenwood & Harvey, 1982) and they leave mostly the natal area and disperse to more unfamiliar territories, which exposed them to higher risk (Steiffetten & Dale, 2006) and some of the dispersers might die during dispersal (Dale, 2001).

The present study found a positive effect of population size on the survival of parents, thus, the bigger the population size, higher survival probability. This result contrasts with the expected pattern where the assumption is that intraspecific competition over vital resources increases at higher population sizes. This would lead to the classical negative-density dependence mechanism that is commonly found as a regulatory mechanism in wild populations (Wangersky, 1978). However, one likely explanation for that might be that house sparrow populations with bigger population sizes, had better environmental conditions that could support higher population sizes, thereby the survival is higher and also most populations might be under carrying capacity, so the negative density dependence would not affect them.

As a consequence of the bias in sex-ratio introduced by the experiment, one could have expected that the mothers adjusted this if they were able to manipulate the primary sex-ratio (Trivers & Willard, 1973). Based on evolutionary theory, females should manipulate the sex of their offspring in response to the characteristics of the raising environment (Trivers & Willard, 1973) though it is very controversial (Ewen et al., 2004; West & Sheldon, 2002). However, the result from the present study revealed that the sex-ratios in the local populations did not affect the sex-ratio of recruits (Appendix 10). The general trend approximately shows no changes in the sex-ratio. In support of our study, Bensch et al. (1999) also found the sex-ratio of the community has no effect on offspring sex-ratio in Great Reed Warbler.

Conclusion

A year after removing half of males from eight house sparrow population, it rebound to the same level with a roughly equal sex-ratio of males and females. Manipulation of the sex-ratio almost has no effect on recruit production, though males produced more recruits, generally, it did not increase recruit production significantly. The result shows females generally have lower survival than males. Moreover, it illustrates, the sex-ratio of the community has no effect on the sex-ratio of recruits. Accordingly, the most likely explanation why both the sex-ratio and the population sizes returned to the levels before the experiment could be a numeric response due to immigration of males. However, unfortunately the design of the experiment did not allow me to control this effect.

For future studies it is important to investigate the mating status of both males and females, before and after manipulation, to perceive how the experiment affected polygyny, and how polygyny could affect

the survival of recruits and also parents. Moreover, environmental conditions could act as confounding factors and affect our experiment, for example, weather conditions could affect survival or recruit production differently among years. Thus, a set of control populations with no manipulation of sex-ratio would, contribute to disentangle the environmental effects from the experimental effects.

Bias in sex-ratio which differs from the typical sex-ratio of the species has implications for conservation biology. Change in the adult sex-ratio could possibly have a strong effect on N_e (Nunney, 1993). Also, in small and threatened populations the sex-ratio may deviate from the typical 0.5 due to demographic stochasticity (Engen et al., 2003) increasing the chance of the whole population going extinct (Wedekind, 2002). Bias in sex-ratio also affects sexual selection (Clutton-Brock et al., 1997; Jiggins et al., 2000; Jirotkul, 1999) moreover, any deviation from the equality of sex-ratio increases the inbreeding rate and loss of genetic variation (Wedekind, 2002). Accordingly, the present study contributes with important insight into the population processes that might compensate for perturbations in sex-ratio in small populations, suggesting that introduction of individuals from the underrepresented sex could be an appropriate mitigation. lastly, Manipulation of the sex-ratio away from a 1:1 sex-ratio in the first generation results in reduced N_e (Wedekind, 2002). In other words, when the sex-ratio is manipulated to be unequal in order to boost population growth rates, it results in a genetic bottleneck for at least one generation (Wedekind, 2002). Though by continuing manipulation of the sex-ratio from the second or later generation, N_e manipulated population could be higher than the unmanipulated, if the number of individuals increased (Wedekind, 2002). We have to consider all of these effects carefully before performing our management strategies.

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Appendix

Appendix 1: The output of the reproduction model for male parents.

Male parents			
AIC	572.1		
Random effect			
Groups	Variance	Standard Dev.	
Individuals	0.42	0.64	
Sites	0.014	0.118	
Fixed effect			
Groups	Estimates	Standard error	P value
Intercept	-0.66	0.16	0.00004
Year 2014	0.53	0.16	0.0001
Age 2	0.28	0.18	0.11
Correlation of fixed effect			
	Intercept	Age 2	
Year 2014	-0.41	0.208	
Age 2	-0.28		

Appendix 2: The output of the reproduction model for female patents.

Female parents			
AIC	629		
Random effect			
Groups	Variance	Standard Dev.	
Individuals	0.77	0.87	
Sites	3.113×10^{-12}	1.764×10^{-6}	
Fixed effect			
Groups	Estimates	Standard error	P value
Intercept	-0.79	0.16	9.43×10^{-7}
Year 2014	0.09	0.17	0.57
Age 2	0.07	0.19	0.68
Correlation of fixed effect			
	Intercept	Age 2	
Year 2014	-0.34	-0.289	
Age 2	-0.25		

Appendix 3: Adjusted predictors of year and age for male and female parents.

	Factors		Predicted	95% CI
Male parents	Year ¹	2013	0.52	[0.38, 0.71]
		2014	0.88	[0.62, 1.25]
	Age ²	1	0.52	[0.38, 0.71]
		2	0.68	[0.46, 1.02]
Female parents	Year	2013	0.45	[0.33, 0.62]
		2014	0.50	[0.34, 0.73]
	Age	1	0.45	[0.33, 0.62]
		2	0.49	[0.32, 0.74]

1. Factor year for both male and female parents, adjusted for age = one year old
2. Factor age for both male and female, adjusted for year = 2013

Appendix 4: The output of the survival model.

Parents (Males and females)			
AIC	943.9		
Random effect			
Groups	Variance	Standard Dev.	
Individuals	0.19	0.4366	
Sites	1.629×10^{-9}	4.036×10^{-5}	
Fixed effect			
Groups	Estimates	Standard error	P value
Intercept	-0.6771	0.3416	0.0475
Population size	0.0117	0.0056	0.0364
Year 2014	0.0445	0.1779	0.8023
Sex (female)	-0.3366	0.1662	0.0429

Appendix 5: Adjusted predictors of year, sex, and population size.

factors		Predicted	95% CI
Sex ¹	Males	0.48	[0.42, 0.55]
	Females	0.40	[0.33, 0.47]
Year ²	2013	0.48	[0.42, 0.55]
	2014	0.49	[0.41, 0.57]
Populatin size ³	8	0.36	[0.24, 0.50]
	18	0.39	[0.28, 0.51]
	20	0.39	[0.29, 0.51]
	34	0.43	[0.35, 0.52]
	51	0.48	[0.41, 0.55]
	54	0.49	[0.42, 0.56]
	57	0.50	[0.43, 0.56]
	80	0.57	[0.47, 0.65]

1. Factor sex adjusted for population size = 51.35, and year = 2013.
2. Factor year adjusted for population size=51.35 and sex = male.
3. Factor population size adjusted for year= 2013 and sex = male.

Appendix 6: Sex-ratio deviation from equality for male parents.

Female parents			
AIC	195.6		
Random effect			
Groups	Variance	Standard Dev.	
Individuals	0	0	
Sites	0	0	
Fixed effect			
Groups	Estimates	Standard error	P value
Intercept	0.17	0.20	0.41
Year 2014	0.030	0.28	0.91
Correlation of fixed effect			
	Intercept		
Year 2014	-0.71		

Appendix 7: Sex-ratio deviation from equality for female parents.

Female parents			
AIC	196.3		
Random effect			
Groups	Variance	Standard Dev.	
Individuals	0.081	0.28	
Sites	0.086	0.29	
Fixed effect			
Groups	Estimates	Standard error	P value
Intercept	0.23	0.27	0.38
Year 2014	-0.06	0.30	0.82
Correlation of fixed effect			
	Intercept		
Year 2014	-0.63		

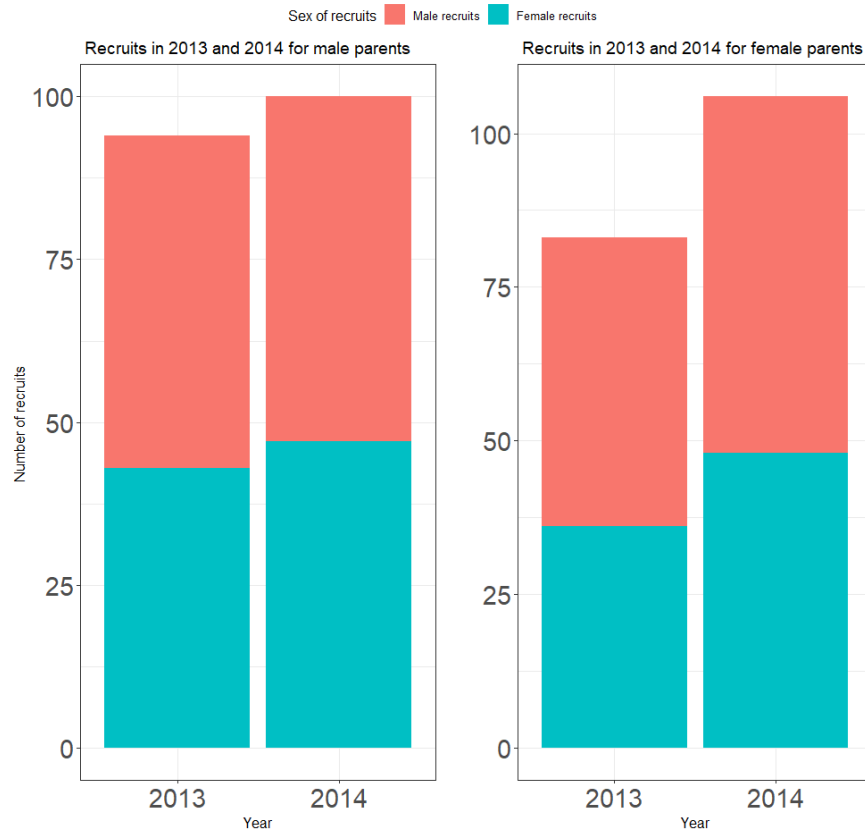
Appendix 8: Models comparison based on AIC for the reproduction analysis.

Fixed factors in the model	Random factors	AIC	
		Male parents	Female parents
<ul style="list-style-type: none"> • Year • age • population size • population size * year 	<ul style="list-style-type: none"> • Sites • individuals 	575.1	632
<ul style="list-style-type: none"> • Year • age • population size 	<ul style="list-style-type: none"> • Sites • individuals 	573.2	630
<ul style="list-style-type: none"> • Year • age (Best model)	<ul style="list-style-type: none"> • Sites • individuals 	557.3	629
<ul style="list-style-type: none"> • year 	<ul style="list-style-type: none"> • Sites • individuals 	572	627

Appendix 9: Models comparison based on AIC for the survival analysis.

Fixed factors in the model	Random factors	AIC
<ul style="list-style-type: none"> • Population Size • Year • Sex • Population size * year • Population size * sex • Sex * year 	<ul style="list-style-type: none"> • Sites • individuals 	948.3
<ul style="list-style-type: none"> • Population size • Year • Sex • Population size * sex • Population size * year 	<ul style="list-style-type: none"> • Sites • individuals 	947.3
<ul style="list-style-type: none"> • Population size • Year • Sex • Population size * year 	<ul style="list-style-type: none"> • Sites • individuals 	945.4
<ul style="list-style-type: none"> • Population size • Year • Sex • Year * sex 	<ul style="list-style-type: none"> • Sites • individuals 	945.8
<ul style="list-style-type: none"> • Population size • Year • Sex <p>(Best model)</p>	<ul style="list-style-type: none"> • Sites • individuals 	943.9

Appendix 10: The sex-ratio of recruits before and after manipulation.



Appendix 11: The Sex-ratio of the population in 2014 before the removal of half of the males and in 2015.

Sites	2014 before the manipulation of the sex-ratio		2015	
	Males	Females	Males	Females
Røvass	8	9	9	13
Handnesøy	40	37	32	35
Løkta	22	22	24	31
Austbø	29	36	22	28
Herøy	4	6	5	5
linseøya	37	32	30	32
Stokkøya	21	21	25	18
Rånes	39	34	27	15



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