Viability of an endangered population of ortolan buntings: The effect of a skewed operational sex ratio

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ARTICLE INFO

Article history:
Received 4 August 2005
Received in revised form 1 March 2006
Accepted 17 March 2006
Available online 6 May 2006

Keywords:
Population viability
Demography
Operational sex ratio
Unpaired males
Ortolan bunting

ABSTRACT

Population viability analyses (PVAs) are based on basic demographic parameters such as breeding success, juvenile and adult survival. However, no PVAs have included the operational sex ratio (OSR). The Norwegian population of ortolan buntings (Emberiza hortulana) is characterized by a strongly skewed OSR (almost half of all males are unpaired). We assessed the effect of a skewed OSR on annual growth rate (\( \lambda \)). Based on empirical data the deterministic growth rate was negative (\( \lambda = 0.82 \)), and mean time to extinction was 21.8 years. Model parameters had to be increased substantially compared to the empirical mean values to achieve \( \lambda = 1.0 \) (clutch size from 4.25 to 8.06, juvenile survival from 17.6% to 33.5%, adult survival from 62.9% to 80.8%, and proportion of males breeding from 52.4% to 99.8%). Using low, mean and high empirical parameter estimates, we examined 36 scenarios for population development. Only five resulted in values exceeding \( \lambda = 1.0 \), of which four required an OSR of 1:1. Correlations between inter-annual population change and demographic parameters indicated that the proportion of males breeding matched the observed population trend best. Because breeding success, juvenile and adult survival were within the normal range seen among other bird species of similar body size, we suggest that the skewed OSR is the major factor limiting population growth. Skewed OSRs may be particularly common in small and isolated bird populations, because of female-biased natal dispersal, and should therefore be considered in all PVAs of endangered bird species.

1. Introduction

Population declines and range contractions are currently seen in a number of bird species worldwide (e.g. Tucker and Heath, 1994; Fuller et al., 1995; BirdLife International, 2000; Chamberlain and Fuller, 2000; Cumming et al., 2001), and has become an issue of great conservation concern. Human-caused changes in the environment, such as habitat destruction and conversion, are likely to be the ultimate causes for many of these declines, and one of the most serious threats confronting the long-term survival of many species (Holsinger, 2000; Young and Clarke, 2000). However, even though the human-related factors causing population decline have been identified in many cases (Newton, 2004), and measures to halt or reverse these impacts have been taken, some populations still decrease in numbers, suggesting that other factors could be preventing population growth. One of these factors could be intrinsic demographic problems. Thus, an understanding of how demography affects population dynamics and population growth rates is essential when trying to recover small and declining populations (Bro et al., 2000).

Basic demographic parameters such as breeding success, juvenile and adult survival have all been suggested as the proximate mechanisms that underlie the declines of many bird species (Newton, 2004). For example, breeding success has been suggested to be below levels needed to sustain
viable populations among grassland bird species in North America (Basore et al., 1986; Herkert et al., 2003), and also among some farmland passerines in Europe (Bradbury et al., 2000; Siriwardena et al., 2000), and juvenile and adult survival have been implicated in the declines of several species found in farmland habitat (Thomson et al., 1997; Peach et al., 1999; Siriwardena et al., 1999; Bradbury et al., 2000; Bro et al., 2000; Freeman and Crick, 2003; Robinson et al., 2004). Although knowledge of breeding success and survival are essential for understanding changes in population size (Paradis et al., 1998), other demographic parameters may be just as important. One such parameter might be the operational sex ratio (i.e., the ratio of males to females available for mating at any one time; see Krebs and Davies, 1996). Dale (2001a) argued that small and isolated bird populations are particularly prone to skewed sex ratios, because of female-biased natal dispersal, subsequently leading to a high proportion of unpaired males, and hence, reduced potential for population growth. To our knowledge the operational sex ratio has never been specifically assessed in population viability analyses, but a male-biased sex ratio has been seen in several bird populations that are fragmented or isolated (reviewed by Dale, 2001a; see also Walters et al., 1999; Bayne and Hobson, 2001; Zanette, 2001; Fraser and Stutchbury, 2004), indicating that the operational sex ratio should be given more attention in studies of declining populations.

The ortolan bunting (Emberiza hortulana), a long-distance migrant passerine, is one of several farmland birds that have suffered major population declines in much of Europe (Cramp and Perrins, 1994; Kutzenberger, 1994). As a result, it is listed as depleted (i.e., species with unfavourable conservation status; Tucker and Heath, 1994), but does not meet any European or global IUCN red list criteria (BirdLife International, 2004). Agricultural changes, such as amalgamation of fields and the consequent loss of breeding habitat together with reductions in crop diversity, have been implicated as the primary causes of the decline (Lang et al., 1990), but the use of mercury-treated seed grains might also have played a role (Ree, 1992). In addition, about 50,000 migrant ortolan buntings were estimated to be trapped each year in south-west France as a “culinary delicacy” in the early 1990s (Stolt, 1996), and trapping of ortolan buntings is still going on today. In Norway the ortolan bunting was a common farmland bird until around 1950, but has since declined dramatically (Haftorn, 1971), and is now classified as endangered on the Norwegian red list (Størkersen, 1999). Although the primary causes of decline have been halted to some extent the population is still decreasing, and current estimates of total breeding population size are 159–166 males, but fewer breeding pairs. Moreover, preliminary data on reproductive success, juvenile and adult survival suggest that the population should have an annual rate of increase of 0.2% (Dale, 2001b). This indicates that other factors than classical demographic parameters may be involved in the observed decline, and the large proportion of unpaired males may play a role (Dale, 2001b).

In the present six-year study we determined the current demographic basis for the decline of the ortolan bunting. Demographic parameters such as breeding success, juvenile and adult survival, in addition to the operational sex ratio, were incorporated into a population model to assess their effect on annual population growth. In addition, we performed a population viability analysis using mean empirical values in order to assess the viability and long-term persistence of the focal population.

2. Methods

2.1. Study area and population

The remaining population of the ortolan bunting in Norway is restricted to an area of nearly 500 km² in central Hedmark County (60°29′–60°53′N, 11°40′–12°18′E), although a minor sub-population exists approximately 60 km further south in Akershus County. The birds occur in about 40 well-defined habitat patches (raised peat bogs, forest clear-cuts on poor sand, land being cleared for cultivation, and one forest burn; Dale, 2001b), but always close to arable land, which is used for foraging (Dale, 2000; Dale and Olsen, 2002). Dispersal among habitat patches is frequently observed (Dale et al., 2005), but dispersal between neighbouring populations is probably limited, as the nearest population is located approximately 250 km further east, in Sweden. The Norwegian population lies at the edge of the species’ range.

2.2. Data collection

The demography of the ortolan bunting was monitored annually during the breeding season (May–June) from 1996 to 2004. The first three years of observations were mainly from a single locality, whereas the last six years included the entire known population in Norway. To avoid biases in demographic parameters between the two periods, only data from the latter was used for analyses unless otherwise stated. Data on adult survival was obtained by capturing males in mist nets with the aid of playback of song. For individual identification each male was given a unique combination of three colour rings and one numbered metal ring. In any year at least 55% of all adult males had colour rings, but for most years the proportion of colour-ringed males were between 70% and 84% (range 103–133 males). Resightings were confirmed through regular visits (1–3 days interval) to all habitat patches which have been used by ortolan buntings. In addition, all other potentially suitable habitat patches within the study area were visited frequently. Because females behave cryptically throughout most of the breeding season and do not aggressively respond to playback of song, the capture and subsequent resightings of females is difficult. Thus, little data on female survival is available, but is assumed to be similar to male survival. This assumption was based on the study by Dobson (1987) who showed that there were no significant differences between male and female survival in the majority of the fifteen species he examined, and a preliminary analysis of our own data showed that male and female survival rates did not differ (95% confidence interval: males 0.593–0.671, n = 581 male-years; females 0.378–0.625, n = 63 female-years). Resighting probability of returning males was very high. Data on movements between years, showed that for males recorded in at least two years, the time series were continuous without “holes” (e.g., not recorded in year y, but recorded in years y – 1 and y + 1), in 216 out of 217 cases. Hence, the use of mark-recapture modelling is not needed.
The mating status of each male in the population was classified into one of the four following categories: (1) males with a female (i.e. nest found, feeding behaviour, prolonged bouts of warning calls, or seen together with a female most of the breeding season), (2) males most likely with a female (i.e. reduced singing activity late in the breeding season, and/or warning calls, but the female or any sign of nesting activity was not observed directly), (3) males most likely without a female (i.e. seen with a female early in the breeding season, but no signs of being mated during the egg-laying, incubation or nestling period), and (4) males without a female (i.e. never observed with a female, and sang frequently throughout the breeding season). Although categories 2 and 3 are connected with uncertainties regarding male status, most males (90.2%) were assigned to either category 1 or 4.

During the nestling period as many nests as possible were located and both clutch size and brood size were recorded. Each nest was visited on a regular basis until nestlings had left the nest. Nestlings were ringed with one colour ring and one numbered metal ring, and returning male nestlings were recaptured and given two additional colour rings. In total 621 nestlings were ringed (includes 11 fledged nestlings), but nestlings from 1996 to 1998 and 2004 (n = 251) were excluded in survival analyses. Thus, juvenile survival was based on 370 nestlings, of which 185 were assumed to be males.

2.3. Model parameters and underlying assumptions

In the present study, we explicitly wanted to examine the annual growth rate ($\lambda$) in order to use it as a measure of population viability. For this purpose we used the computer program VORTEX (Lacy et al., 2003), which is an individual-based simulation model for population viability analyses (PVA). Population growth under the influence of stochastic fluctuations was calculated by random simulations repeated 1000 times, whereas the deterministic growth rate was determined from life table analysis. Although most data needed for analyses were empirically available, some assumptions had to be made for a few input parameters. First, since no data on maximum breeding age, or life expectancy, exists for the ortolan bunting, the value was arbitrarily set at 20 years to ensure that all males and females in the population would be modeled as reproductively active until death. Although studies have shown that reproductive success decreases with age (e.g. Robertson and Rendell, 2001; Laaksonen et al., 2002), we have no reason to believe that old males cannot mate and reproduce (see Holmes and Austad, 1995). Indeed, the oldest male in the focal population that has been observed breeding successfully was nine years old. Second, we assumed a 1:1 sex ratio at birth. For the PVA we also assumed that no catastrophes would occur during the 100 years of simulation, and that there was no inbreeding depression. Although two examples of close kin mating (brother and sister, father and daughter) have been observed, nestlings fledged successfully in both cases.

Estimates of total population size were based on the number of marked and unmarked males in each year. Due to the possibility of counting unmarked males twice because of extensive within-breeding season and between-patch dispersal by adult males (Dale et al., 2005), we operated with a low and high estimate in order to avoid the uncertainty of relying on a single value. Thus, males that were observed in the same territory for 15 days or more were considered likely to be the same individual throughout the breeding season, and were included in the low estimate. On the other hand, males that were observed in the same territory for 5–15 days could potentially have moved to a different locality after the last observation, increasing the likelihood of being counted as a new individual. These males were included in the high estimate. Single observations of unmarked males, or males observed less than five days within the same territory were considered to have moved to other territories and excluded from the estimate altogether. However, unmarked males showing feeding behaviour were included in the low estimate regardless of the time observed.

As initial population sizes for the PVA we used the low, mean, and high estimates of total population size for 2004. There was a deficit of females in the population (see Section 3), which we assumed to be due to female-biased dispersal. In VORTEX one does not have the option to model male and female population size separately. Therefore, the deficit due to dispersal was modeled as the proportion of females that did not breed in a given year, and this approach will lead to exactly the same results as if one could model female population size separately. Thus, the number of females incorporated into the population size estimates were equivalent to the number of adult males, but those that were assumed to have dispersed were modeled as non-breeders. In calculating the mean proportion of males breeding (equivalent to the operational sex ratio), we first assumed that all pairs that were observed in a given year would also breed. Because we used low and high estimates for both population size and the number of breeding pairs, this resulted in four different estimates of the proportion of males breeding in a given year. The mean value of each year were then used to calculate the overall mean value used for analyses.

As a measure of breeding success we used clutch sizes recorded during 1996–2004. Clutch size was used because we also wanted to incorporate mortality that occurs at the incubation stage into juvenile survival estimates. In total 190 clutches were included in analyses. Note that although Cramp and Perrins (1994) cited one study which reported a clutch size of seven (1.1% of all clutches), the largest clutch size observed in the focal population was five. To be conservative, we therefore set the maximum clutch size at six, which is also the highest value normally reported for the ortolan bunting (Cramp and Perrins, 1994). To define the proportion of individuals within various cohorts, we used the stable age distribution calculated by VORTEX for both males and females (see Miller and Lacy, 2003 for a definition of and methods for calculating this distribution). Carrying capacity was set at 2000 individuals in order to avoid habitat availability as a limiting factor. Environmental variation in carrying capacity was assumed to be unchanged during the simulated time period. Although some habitats are lost to new cultivation or other land uses, new breeding habitats are also created through clear-cutting of forest, and the attractiveness of some peat bogs may have increased through cultivation of new areas close to bogs. Thus, at present, habitat availability does not seem to be limiting (Dale, 2001b). Summary of the input parameters used for analyses are shown in Table 1.
In addition to modeling population persistence using the empirical mean demographic rates, we also undertook sensitivity analysis in which we increased or decreased several variables one by one while all other variables were held constant. For breeding success we modeled the population with clutch sizes in steps of one from 1 to 6. Juvenile and adult survival were stepwise changed by three percentage points from the empirical mean value, with extremes of 6% below and 15% above, whereas the proportion of males breeding was decreased to 30% and increased up to 100%. We also calculated the specific value of each parameter that was needed to achieve $\lambda = 1.0$.

To examine the possible range of growth rates intrinsic to the population, the low, mean and high empirical estimates of juvenile and adult survival, and the proportion of males breeding, were modeled for all different combinations of each parameter. In addition, we included an operational sex ratio of 1:1 because this is expected in most natural populations, making the resulting values comparable to other studies. However, low and high estimates of clutch size were omitted from analyses because preliminary results showed that this parameter had least effect on population growth, and also because annual fluctuations in clutch size were low ($4.25 \pm 0.28$; range 3.75–4.83). We therefore used the mean clutch size as a standard variable in all analyses. A total of thirty-six different combinations were analysed.

Finally, we tested whether the yearly mean empirical values of each parameter could explain the observed change in population size from one year to the next using correlation analysis. We assumed that the magnitude of the correlation coefficients of the four demographic parameters, would indicate their relative importance in explaining the observed population decline.

### 2.4. Sensitivity analysis

In addition to modeling population persistence using the empirical mean demographic rates, we also undertook sensitivity analysis in which we increased or decreased several variables one by one while all other variables were held constant. For breeding success we modeled the population with clutch sizes in steps of one from 1 to 6. Juvenile and adult survival were stepwise changed by three percentage points from the empirical mean value, with extremes of 6% below and 15% above, whereas the proportion of males breeding was decreased to 30% and increased up to 100%. We also calculated the specific value of each parameter that was needed to achieve $\lambda = 1.0$.

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### 3. Results

Based on the empirical data in Table 1 the deterministic calculations performed by VORTEX showed that population growth rate was negative ($\lambda = 0.82$) even in the absence of any random fluctuations. When stochastic events were included in the model the corresponding growth rate was 0.81. This resulted in a probability of extinction within 100 years of 1.0, and mean time to extinction was 21.8 years (range: 21.6–22.1 years).

The effect of increasing breeding success to a mean clutch size of six was only of minor importance to population growth ($\lambda = 0.91$; Fig. 1a). For breeding success to achieve $\lambda = 1.0$ the mean clutch size had to be raised to 8.06, an almost twofold increase from the empirical mean value of 4.25. Increasing juvenile survival by 15%, on the other hand, had a stronger positive effect on population growth ($\lambda = 0.99$; Fig. 1b). To achieve $\lambda = 1.0$ the empirical mean value of 17.6% had to be increased to 33.5%. For adult survival a 15% increase resulted in a slightly lower growth rate than juvenile survival ($\lambda = 0.97$; Fig. 1c). The empirical mean value of 62.9% had to be increased to 80.8% to reach $\lambda = 1.0$. The only parameter that resulted in a positive growth rate using the maximum preset values was the proportion of males breeding. By increasing the proportion to 100% the growth rate was slightly above 1.0 ($\lambda = 1.01$; Fig. 1d). To achieve $\lambda = 1.0$ the corresponding value was 99.8%. However, this is still an almost twofold increase from the empirical mean value of 52.4%.

The current range of possible growth rates based on low, mean and high empirical values of survival and the proportion of males breeding, in addition to the value reflecting an operational sex ratio of 1:1, are shown in Fig. 2. When we used the low estimate of juvenile survival as a constant variable, none of the different scenarios were able to bring $\lambda$ above 1.0 (range: $\lambda = 0.60–0.89$; Fig. 2a). However, when the mean
value of juvenile survival was used as a constant variable we found one scenario in which \( k > 1.0 \) (range: \( k = 0.70–1.10 \); Fig. 2b). For the high estimate of juvenile survival the corresponding number of scenarios that exceeded \( k = 1.0 \) was four, in which three were associated with scenarios that included an operational sex ratio of 1:1, and only one that was associated with values based on empirical observations (range: \( k = 0.78–1.26 \); Fig. 2c).

There were no relationships between inter-annual population change and clutch size (Spearman rank correlation: \( r_s = 0.20, n = 6, p = 0.65 \)), juvenile survival (\( r_s = 0.37, n = 6, p = 0.41 \)), and adult survival (\( r_s = 0.37, n = 6, p = 0.41 \)). However, the proportion of males breeding contributed to explaining the observed population trend, although not significantly so due to small sample sizes (\( r_s = 0.60, n = 6, p = 0.18 \)). This indicates that the observed changes in population size from one year to the next (mostly decline) is more likely an effect of a skewed operational sex ratio, than by any of the other three demographic parameters.

4. Discussion

The ortolan bunting, in common with a number of other passerine species that occur on farmland, has experienced large population declines. Analyses of long-term field data from Norway showed that the deterministic growth rate was negative, and that the population is likely to go extinct within a short period of time. One important reason to make deterministic projections is to obtain a general idea of whether or not the rates of reproduction and survival are minimally adequate to allow for population growth (Miller and Lacy, 2003). The present results suggest that the current causes of the decline are more likely an effect of limiting demographic rates, than by stochastic fluctuations alone. Among the demographic parameters investigated, the operational sex ratio had the largest impact on population growth, suggesting that the male-biased sex ratio observed in the focal population is the major force driving the decline. We stress the importance of including operational sex ratios in population studies of declining bird species, in particular those that have small and isolated populations (Dale, 2001a).

4.1. Breeding success

4.1.1. Clutch size

The mean clutch size of 4.25 is close to the maximum number of five observed in the focal population, and also close to mean clutch sizes of the ortolan bunting reported elsewhere in Europe (see Cramp and Perrins, 1994). In addition, the observed distribution of clutch sizes matches to some degree those found in other studies (see Cramp and Perrins, 1994). Compared to other closely related species with a similar
population trend, i.e. reed bunting (*E. schoeniclus*), yellowhammer (*E. citrinella*), and corn bunting (*E. calandra*), the mean clutch size in our study was similar or even higher (Yom-Tov, 1992; Bradbury et al., 2000; Siriwardena et al., 2000), indicating that clutch size is within the normal range seen among other bunting species. Also, an increase of the mean clutch size to the maximum number of six failed to move \( k \) above 1.0, further supporting the view that female fecundity is already high and unlikely to be the primary cause of the decline. Furthermore, to achieve \( k = 1.0 \) the mean clutch size had to be raised to 8.06, a value that has never been observed in the ortolan bunting. Correlation analysis also showed that there was no relationship between inter-annual population change and clutch size, again suggesting that fecundity does not contribute to the decline.

### 4.1.2. Nest mortality

Mortality that occurs at the incubation and nestling stages may be a significant factor determining breeding success and the subsequent number of new recruits into the population.
Our mean estimate of post-fledging mortality (67.8%), here that the mortality rates shown in Table 1 reflect the true range were comparable with those in previous years. We thus argue between 68–73% of all nests, and the different mortality rates differences in predation or weather conditions could have oc-

North America (Anders et al., 1997; King et al., 1996; Porneluzi and Faaborg, 1999; Pietz and Granfors, 2000; Herkert et al., 2003), and losses up to 80–90% is typical of many neotropical migrants occupying fragmented, urban, or agricultural land-scapes (Robinson and Wilcove, 1994; Brawn and Robinson, 1996). Low breeding success until fledging has also been sug-
gested to have driven the decline in the linnet (Carduelis canna-

bina) in Britain (Siriwardena et al., 2000), and of being too low to maintain a stable population of the yellowhammer on lowland farmland (Bradbury et al., 2000). Our data, however, show that only a small proportion of eggs and nestlings are lost to either predation, starvation or severe weather conditions (mainly heavy rainfall) (see Table 1). Although a sampling bias (i.e. local differences in predation or weather conditions) could have occurred due to small sample sizes during the first five years of study (13–37% of all nests were found), in 2004 we found between 68–73% of all nests, and the different mortality rates were comparable with those in previous years. We thus argue that the mortality rates shown in Table 1 reflects the true range of the focal population, and that they are normal or even below values usually seen in ground-nesting species (see Ricklefs, 1969). Because mortality is already low the opportunity for any substantial increase in survival is absent, and an increase in survival will therefore have only a marginal effect on popu-

lation growth rate.

4.2. Post-fledging mortality

Our mean estimate of post-fledging mortality (67.8%), here defined as mortality that occurs after fledging until the return as first year breeder, is substantially lower compared to many other species of similar body size (see Weatherhead and Forbes, 1994). Also, when we compared total juvenile mortality (i.e. mortality imposed at the incubation stage and onwards until the return as first year breeder) with the same dataset, our estimate was still lower for all but two cases (n = 65). It should be noted, however, that natal dispersal can be exten-

sive, thus some locally studied populations may have overes-
timated mortality rates (Weatherhead and Forbes, 1994). Although Siriwardena et al. (1998) found higher first-year sur-
vival rates in a study of twenty-eight passerines, these esti-
mates were based on survival rates of young birds ringed after independence, and excludes nesting mortality and mor-
tality that occurs immediately after fledging. Thus, their val-
ues cannot be compared directly with ours. It seems that our estimates of juvenile mortality are well within, and even below, the range normally seen in small passerines. As such, an increase of total juvenile survival from 17.6% to 33.5%, which is required to achieve $k = 1.0$, is probably unrealistic and not normal for small long-distance migrant passerines. A study by DiQuinzio et al. (2001) on the saltmarsh sharptailed sparrow (Ammodramus caudacutus) found annual return rates for juveniles ranging from 0% to 44%, hence showing that survival may be high in some years, but they argue that the mean values (11.6–29.7% depending upon year and site) fall at the upper end of documented return rates for migrants and well within typical return rates for residents. In support of the view that juvenile survival in our population is reason-ably high, and therefore most likely not the major limiting demographic parameter, we found no relationship between inter-annual population change in abundance and juvenile return rates, indicating that population trend is unaffected by changes in juvenile survival rates. Moreover, Weatherhead and Forbes (1994) found that most migratory species that exhibited high juvenile returns were from isolated popul-
ations, although extrapolating these results to the study popu-
lation should be taken with great caution. Nonetheless, it is possible that the juvenile survival estimate found in this study could be somewhat higher, partly because a substantial number of ortolan buntings are trapped each year in France during migration (Stolt, 1996). Although both adults and juve-
niles are susceptible to trapping, juveniles might be more na-
vie than adults, thus experiencing higher mortality.

4.3. Adult survival

Compared to other passerines of similar body size (both sed-
entary and migratory species) the mean adult survival rate (62.9%) was high (see Botkin and Miller, 1974; Saether, 1989; Dobson, 1990; Johnston et al., 1997; Siriwardena et al., 1998; Siriwardena et al., 1999; Peach et al., 2001 for reviews). How-
ever, the compared data sets are mostly based on mark-
recapture studies faced with the problems of distinguishing between permanent emigration and mortality, and may thus underestimate survival rates. Although one can argue that we are faced with the same problems, data on movements be-
tween years showed that we had an almost 100% resighting probability (Dale et al., 2005). Nonetheless, this suggests that adult survival is unlikely to be the limiting factor for popula-

tion growth. This is further supported by the finding that to achieve a positive growth rate in the population, mean adult survival had to be raised above 80.8%. To our knowledge such an estimate has never been recorded for a long-distance mi-
grant passerine of small body size. Moreover, tropical passe-
rines, which are thought to have a higher survival rate than species in northern temperate regions, rarely have survival rates above 80% (Johnston et al., 1997; Peach et al., 2001). The fact that there was no relationship between inter-annual popula-
tion change and adult survival again show that this parameter is unlikely to have driven the recent decline.

4.4. Operational sex ratio

One striking feature of the focal population was the skewed operational sex ratio with almost twice as many males as fe-

males. Several explanations may account for this apparent discrepancy. First, there may be a skewed sex ratio at birth. Numerous studies have shown that individual birds make adjustments of primary sex ratios that appear to be adaptive (e.g. Komdeur et al., 1997; Bradbury and Blakey, 1998; Nager et al., 1999; Whittingham and Dunn, 2000), but this does not affect the population-level sex ratio. Furthermore, in the study population a male-biased sex ratio would be maladap-
tive, because there already is an excess of reproductive males. We therefore believe that the assumption of a 1:1 sex ratio at birth is reasonable, and that the skewed operational sex ratio is due to some other cause. Second, adult mortality could dif-
fer between sexes due to differences in ecology (Siriwardena
et al., 1998). Although slightly higher mortality rates have been found for females than males in some species, very few species-specific examples have been statistically significant (Dobson, 1987; Siriwardena et al., 1998). Moreover, even if there is a sex-biased mortality in the focal population, it is unlikely to produce a sex ratio with almost twice as many males as females, which is the current situation. Furthermore, sex-biased mortality is expected to be more common in sexually size-dimorphic species than in sexually size-monomorphic species (Ellegren et al., 1996) such as the ortolan bunting. A third possibility, proposed by Dale (2001a), is that a male-biased sex ratio may be the consequence of female-biased natal dispersal. In small and isolated populations some females may disperse away from the local population through natal dispersal, subsequently being lost from the breeding pool. As a result, this will lead to a skewed operational sex ratio with a high proportion of unpaired males. A similar trend has been observed among other species with a high degree of isolation (see Dale, 2001a). In the ortolan bunting, we found that only 52% of all males paired with a female, and such a value is likely to be detrimental for total reproductive output and the subsequent recruitment of new individuals into the population. Our data also showed that the proportion of males breeding had a large influence on population growth rate. Increasing the number of males that breed to 100%, which is usually assumed to be the case in most natural populations (Dale, 2001a), resulted in a stable growth rate ($\lambda = 1.01$). Also, sensitivity analyses showed that this maximum value was needed to achieve $\lambda > 1.0$ in four of the five scenarios that gave a positive growth rate. Finally, we found a positive trend in the relationship between interannual population change and the proportion of males breeding. These results suggest that the skewed operational sex ratio, through the proportion of males breeding, could be an important determinant of population growth rate in the focal population, and hence, population viability.

5. **Conclusions**

All PVA models are more or less simplified versions of real life, and thus, susceptible to errors at a number of stages. To obtain meaningful data from any PVA-programme, one has to have extensive knowledge of the focal species’ biology, in addition to a lot of data, so that it represents the wild population as accurately as possible. In this study we think that both criteria are fulfilled. Although some assumptions have been made in the model, most parameters (at least the critical ones) were based on extensive field data. We therefore believe that the simulations reflect the demographic situation of the focal population well. At least for two of the four parameters investigated (i.e. breeding success and adult survival) it seems reasonable to conclude that they are not the cause of the current decline, because the estimated values falls within, or even above, the range seen among other species of similar body size. We suggest that the proportion of males breeding is the principal factor limiting population growth. Even so, increasing the proportion of males breeding to 100% only resulted in $\lambda$ being slightly above 1.0, thus making the population potentially unstable in the long run when stochastic events are taken into consideration. In fact, the correspond-
increase female immigration. Direct actions to prevent females from emigrating seems difficult, especially in highly mobile animals such as birds. However, creating suitable habitat patches around the population may reduce the number of females that are lost from the core areas, because these patches may act as “conspecific male traps” that attracts females to settle. In the long term, natural selection might increase female philopatry and reduce dispersal distances, but we have no information on the time span involved, or, indeed, if there is enough heritable variation in dispersal behaviour for selection to act on. In highly isolated populations (which is the case for the Norwegian population) natural immigration of females is not likely to occur. The only conservation measure available then is the introduction of females from other populations. However, such actions are connected with uncertainties as to whether females will stay in the site of introduction, and whether the females will return in future years. Moreover, this is still just a temporary solution, and will have no long-term effect on the operational sex ratio. In summary, the scope for management actions to offset the negative effects of female emigration from small populations seems to be disappointingly small. Thus, management actions need to be implemented before the population size decreases below a threshold value where this kind of Allee effect starts to operate.

Acknowledgements

We thank V. Bunes, P. Christiansen, J.P. Cygan, A.K. Darrud, T. Granerud, H. Gregersen, B. Hessel, H. Johansen, A. Lambrechts, B. Lelaure, A. Lunde, N. Manceau, A.K. Narmo, B.F.G. Olsen, T. Olstad, T. S. Osiejuk, K. Ratynska, T.I. Starholm, C. Sunding and K. Sørensen for assistance in the field, and J. Swenson for comments on the manuscript. The study was financially supported by Selberg legacy/WWF Norway, Mr. and Mrs. Sørli’s Foundation, the Norwegian Directorate for Environment and Mrs. Sørli’s Foundation, the Norwegian Directorate for Nature Management and the Environmental Authorities of Hedmark and Akershus Counties.

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