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A population viability analysis on the declining population of Little Owl (*Athene noctua*) in Denmark using the stochastic simulation program VORTEX

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When a bird population is facing extinction, ecologically artificial conservation actions such as feeding and captive breeding may be considered as temporary efforts to rescue the population remains until environmental conditions for a self-sustaining population have been restored. Population viability analysis can be used to evaluate different management options for endangered bird populations. Here we use the program VORTEX to explore different management strategies using the Danish population of Little Owl (*Athene noctua*) as a model species. The Little Owl is declining in several countries, including Denmark, where lack of food during the breeding season has been identified as the main reason for the decline. Four scenarios were run, simulating 25 years of population dynamics: (1) "do nothing" scenario, (2) captive breeding scenario where individuals are supplemented to the population, (3) food supplementation or habitat improvement scenario and (4) scenario combining captive breeding and food supplementation/habitat improvements. In scenarios where no management actions were taken the population went extinct within 12 years. When supplementing individuals continuously the population remained extant but the population size remained small. Food supplementation/habitat improvements can restore the population, though there must be capacity to secure food/habitat for a minimum of 100 individuals to minimize genetic losses. By combining food supplementation and the release of captive bred individuals, the population has a chance of being restored and become independent of human aid. This study exemplifies how management scenarios can be used to guide managers to make informed decisions.

1. Introduction

According to the IUCN 12% of the world's avian species are threatened (Baillie *et al.* 2004). It is therefore of utmost importance to assess the viability of endangered populations, determine the factors that make them vulnerable and evaluate the potential management strategies that can potentially save them from further decline or extinction. A Population Viability Analysis (PVA) is a tool used to predict population trajectories (Shaffer 1990), especially when it comes to its extinction risk. A PVA uses information on population life history traits and sometimes its genetics and the environmental stochasticity to determine the population structure and fitness (Gilpin & Soulé 1986). When using accurate input data, the PVA is accurate in its predictions on a species future (Brook *et al.* 1997, Brook *et al.* 2000). A retrospective PVA study on the population of Lord Howe Island Woodhen (*Gallirallus sylvestris*) found that the future predicted by PVAs were optimistic, but became accurate when including density dependency and the correct carrying capacity (Brook *et al.* 1997). PVAs have also been used to assess management options of small populations. A population of only four Red-cockaded woodpeckers (*Picoides borealis*) in the USA was subject to a PVA, showing that the population could recover if woodpeckers were translocated to this population over a period of 10 years (Haig *et al.* 1993). By 1997, 54 translocations had taken place, resulting in a population increase from 4 to 99 woodpeckers (Franzreb 1997). Several programs are available for PVAs, one of them being VORTEX, a Monte Carlo simulation. VORTEX can simulate deterministic forces on a population, along with environmental, demographic and genetic stochastic events (Lacy 1993) and is best used on long lived species, like mammals, birds and reptiles (Thirstrup *et al.* 2009, Bach *et al.* 2010, Lacy *et al.* 2013).

The Little Owl (*Athene noctua*) is in decline over most of Western and Central Europe (Gouar *et al.* 2011, Nieuwenhuyse *et al.* 2008, Pellegrino *et al.* 2014, 2015). Globally, the species is listed as "Least Concern" on the IUCN redlist due to its large range (BirdLife International 2012), whilst it is listed as having "an unfavorable conservation status" on the Species of European Conservation Concern list (Ozinga & Schaminée 2005). The global range of the Little Owl has its northwestern boundary in Denmark and extends to Northeastern China to the east and to the Mediterranean Sea and Northern Africa in the south (Nieuwenhuyse *et al.* 2008). In Denmark, the species is considered "Endangered" on the Danish red list due to a massive decline in the population since the 1970s (Wind & Pihl 2010). Low offspring survival due to food limitation in the breeding season caused by agricultural intensification has been identified as the main reason for the population decline in Denmark (Thorup *et al.* 2010). To properly manage the Danish population there is thus an urgent need to analyze how many "normally" reproducing pairs (attained through artificial feeding or restoration of prey populations in the foraging habitats) are needed in the population to make it self-sustainable. Further, it is important to determine which management actions (e.g., food supplementation/habitat restoration leading to improved breeding success vs. captive breeding) are likely to succeed and reverse the population decline. This can be done through a PVA.

In this paper the viability of a conservation reliant bird population, the Little Owl in Denmark, is determined under different action scenarios. This population is likely to be rescued only through captive breeding, by improving living conditions for the owls or by a combination of the two, all of which will be tested using PVA. The Little Owl in Denmark can thus be used as a model case of a population rescue analysis, and the scenarios created here can thus be utilized in other bird populations facing decline due to habitat disruption.

2. Materials and methods

2.1. Study species and study area

The Little Owl is a sedentary and monogamous species, with no extra-pair copulations (Müller *et al.* 2001). It is an opportunistic generalist predator that feeds on a wide variety of species, including small mammals, invertebrates and birds (Laursen 1981, Nieuwenhuyse *et al.* 2008) and appears to be dependent on a broad composition of alternative foraging habitats that offer alternative foraging opportunities in different seasons and weather conditions (Sunde *et al.* 2014). The Little Owl is an obligate cavity breeder, nesting in hollow trees (Jacobsen 2006, Nieuwenhuyse *et al.* 2008), but in the absence of old trees, all presently known Danish pairs breed and roost in farmhouse buildings and nest-boxes. When the owlets leave the nest they are unable to fly (Nieuwenhuyse *et al.* 2008) and are exposed to a high rate of accidents and predation (Pedersen *et al.* 2013). In Denmark, a survey determined that 43% of juvenile Little Owls

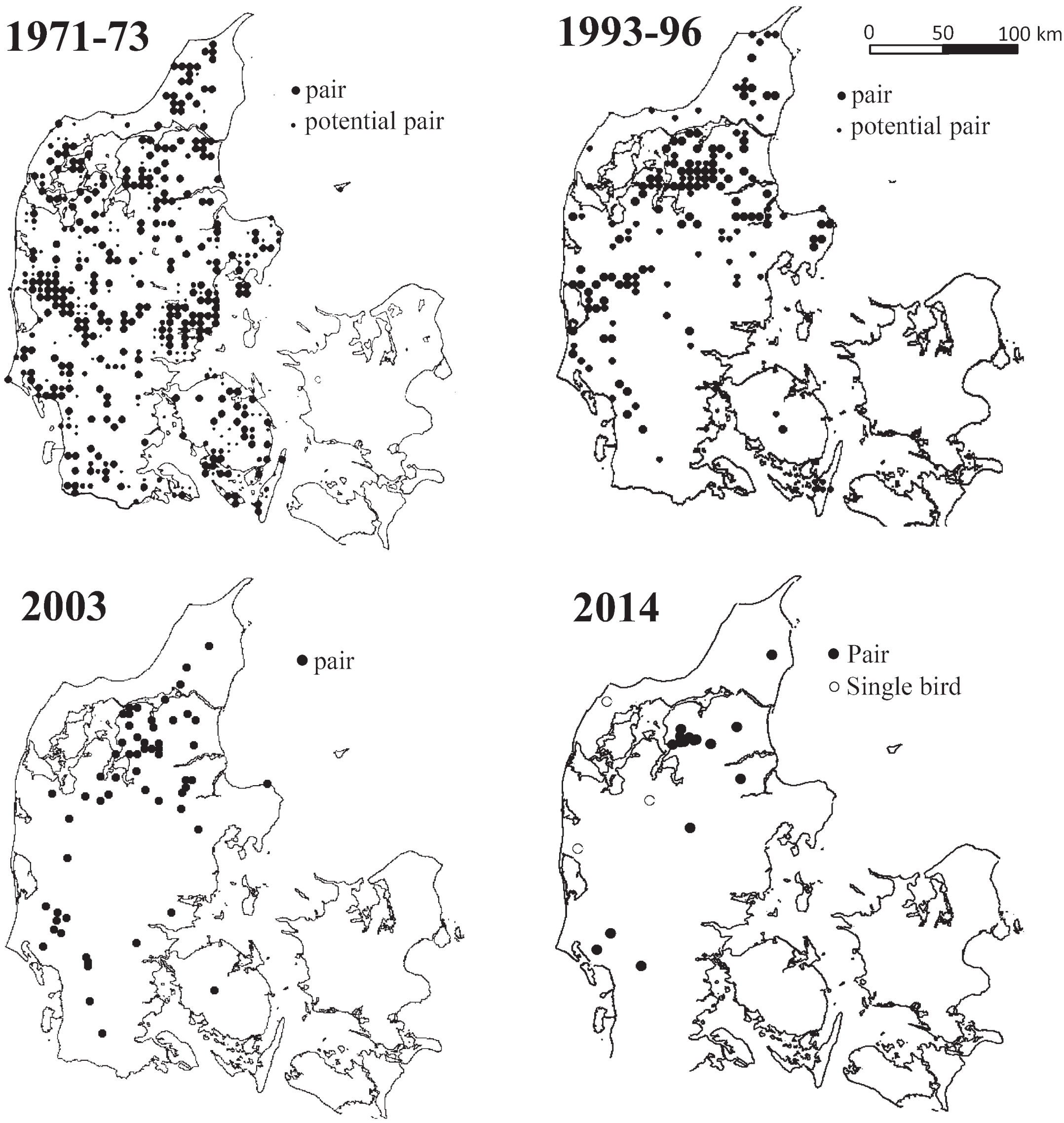

Fig. 1. The spatial distribution of little owl during the past 40 years. Large dots in maps from 1971–1973 and 1993–1996 indicate breeding pairs, while smaller dots indicate possible breeding pairs. In the map of 2003, all dots represent the presence of Little Owls. In 2014, all dots represent the presence of either a breeding pair or a single bird.

were killed by predators, while 17% were killed by cars and 12% were killed by machinery (Jacobsen 2006). In Germany, the juvenile mortality caused by predators reached 69.3% in one population and 24% in another, while only 15% and 13% of juveniles were lost to predation in a Swiss and French population, respectively (Nieuwenhuyse *et al.* 2008). Breeding pairs mostly remain on the same territory (Sunde *et al.* 2009). In Danish Little Owls, natal dispersal averages 22 km, with a maximum distance of 71 km (Bønløkke *et al.* 2006). This effectively isolates the Danish population from the nearest population 300 km to the south in Germany.

Since the 1970s, when the species was found on both Funen and all over Jutland (Dybbro 1976, Grell 1998) with an estimated 1,000 breeding pairs, numbers have dropped continuously to 40–

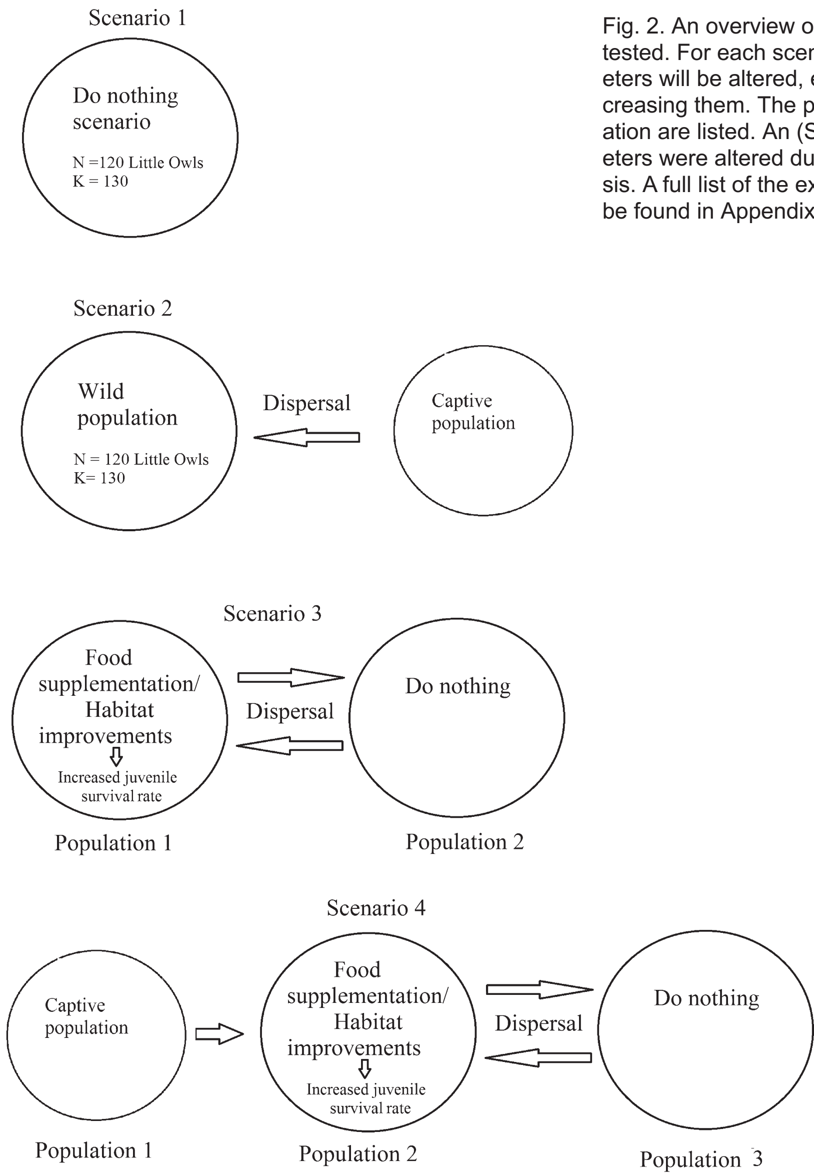

Fig. 2. An overview of the four scenarios tested. For each scenario, a number of parameters will be altered, either by decreasing or increasing them. The parameters under alteration are listed. An (S) indicate that the parameters were altered during the sensitivity analysis. A full list of the exact alterations made can be found in Appendix 2.

46 known breeding pairs in 2010 (Fig. 1) (Eskildsen & Vikstrøm 2011). The remaining population is situated in the northwestern part of Denmark, primarily in Himmerland, but with few pairs in the area of Sallinge and Ringkøbing (Fig. 1). In 2014 nine locations with successful breeding have been found, two of them had six fledged young, three had only two fledged young, two had three fledged (Mette H. H. Hansen, pers. comm.). By 2005–2007, in the last population stronghold, the population density was 0.05 pairs / km^2 (Sunde *et al.* 2009) as compared to 0.04–2.04 pairs / km^2 in the Netherlands, and up to 0.5 pairs / km^2 in Germany (Nieuwenhuyse *et al.* 2008). This places the Danish population amongst the lowest in densities.

2.2. Scenarios

We created a model including four different scenarios, all run in VORTEX 10.0.8.0 (Lacy *et al.* 2005). These scenarios simulate what will happen to the Danish population if nothing is done, or under different management regimes (Fig. 2). As the

Table 1. Estimated parameters used in the simulations. SD is the standard deviation. [1] According to Jacobsen (2006), 2.47 ± 1.15 SD fledglings per brood is the average. Thorup *et al.* (2010) state a trend where 0.05 fewer fledglings appear every year. Subtracting this number from the 2006 average, 2.12 fledglings per brood can be expected in 2013. [2] Dispersal not included in scenario 1 and 2. [3] High estimate.

Parameter	Estimate	References
Number of iterations	1,000	
Adult mortality (aged 1-death)	32% (SD 10)	Thorup *et al.* 2013
Juvenile mortality (aged 0–1)	85% (SD 10)	Thorup *et al.* 2013
Environmental correlations in mortality rates	0.5	Default value
Mating structure	Monogamous	Nieuwenhuyse *et al.* 2008, Thorup *et al.* 2010
Breeding age	1 year	Thorup *et al.* 2010
Maximum age of reproduction	11 years	Calculations based on formula in Lande 1988
Density dependency	No	Nieuwenhuyse *et al.* 2008
Mean no. of fledglings/brood	2.12[1]	Jacobsen 2006, Thorup *et al.* 2010
SD (mean no. fledglings)	1.15	Jacobsen 2006
Maximum no. of progeny	8	Jacobsen 2006
Ratio of breeding pairs successful in getting fledglings	66%	Jacobsen 2006
Sex ratio at birth (male:female)	50:50	Thorup *et al.* 2010
No. of males in breeding pool	100%	Assume all attempt to breed
No. of females in breeding pool	100%	Assume all attempt to breed
Catastrophe, cold winter	5% occurrence Mortality 75% of normal	Poulsen 1940, Poulsen 1957
Min. age of dispersal[2]	1 year	Pedersen *et al.* 2013
Max. age of dispersal	11 years	Calculations based on formula in Lande 1988
Probability of dispersal	5%	Sunde *et al.* 2009
Dispersing sex	Males and female	Niuwenhuyse *et al.* 2008
Population size	120 indivisuals[3]	Eskildsen & Vikstrøm 2011

Danish population of Little Owl is small and found within a limited geographic area, it will be simulated as one large population consisting of 60 breeding pairs (1). Then, different management strategies were tested in order to explore which management option was likely to restore the population. First, a captive breeding strategy was tested where Little Owls obtained from populations outside Denmark were supplemented to the Danish population (2). This would both increase the population size and the genetic variation, and it was tested whether this in itself would be enough to rescue the population. Then, simulations determined whether aiding a limited number of breeding pairs through food supplementation or habitat improvements was a viable mean of saving the population (3). A two population scenario was simulated, where one experienced food supplementation or habitat improvements and thus experienced a drop in juvenile mortality. This was done to determine if all or only a part of the population needed to receive help in order to result in positive population growth. Finally, a combination scenario was created, including both captive breeding and food supplementation/habitat improvements (4). Within each of the four scenarios, a number of runs were performed (overview in Fig. 2, whereas all runs are listed in Appendix 1). For each run, different parameters will be altered to determine the factors that make the population most vulnerable.

2.3. Simulations

The basic scenario included one population consisting of 120 individuals and a carrying capacity (*K*) of 130 individuals. Besides running a basic scenario with the values listed in Table 1, several runs were conducted within each scenario. A total of 1,000 iterations were completed for each run. The runs within each scenario were chosen to test the overall population response to alterations in specific life history traits or environmental changes. If one life history trait proved to have a noteworthy influence on the population as a whole, this parameter will be especially important when making management decisions. Runs with both increased and decreased *K* were tested. The maximal age of reproduction was also altered, as were the mortality rates (summary of all runs within each scenario can be found in Appendix 1).

2.4. Estimation of parameters

Population viability models predict the probability of extinction based on the given input values. The model can thus never be more precise than the input values allow them to be. When input values differ from real value this must be taken into consideration when interpreting the results. The exact population size for the Little Owl in Denmark is not known, but is likely to count less than 20 pairs. Published data names a larger population size of close to 60 breeding pairs (Eskildsen & Vikstrøm 2011), which is used within these simulations. Apart from the optimistic population size, all other input values have been based upon those of the fairly well studied Danish population of Little Owl. The estimated basic parameters used in the simulations can be found in Table 1. The timeframe for the simulations is 25 years. As the environment is assumed stable within the period simulated, a relatively short timeframe will make the data obtained more reliable. To include environmental stochasticity we included a catastrophe in the simulations. This catastrophe symbolized cold winters, a factor known to increase the mortality rates (Poulsen 1940, Poulsen 1957). The mortality rates was thus lowered to 75% of the normal rate in years affected by catastrophes. There was a 5% risk of catastrophe in any given year.

VORTEX provides a large amount of output. We included PE (percent extinct), a value that sums up the percentage of simulations where the population went extinct, N, the mean final size of the extant population, TE being the mean time that went by before the population went extinct and GD, the percentage of genetic diversity that remained in the extant population after 25 years.

2.5. Carrying capacity

Estimating the carrying capacity (*K*) for the Little Owl population in Denmark is a somewhat theoretical problem. As the population is declining and close to no breeding pairs are able to reproduce at sufficiently high rates to replace themselves the *K* can effectively be seen as being zero. The *K* will increase as a result of management interventions or changes in the environment. Another problem when estimating *K* lies within Little Owl behavior and their ability to find appropriate territories. Little Owls disperse over short distances, and might not be able to reach appropriate territories, thus lowering the actual carrying capacity. Also, they might not be able to select appropriate territories, as they settle during winter-time and cannot predict the productivity of a given area in the future.

A *K* of zero is of no use in a simulation program such as VORTEX as it would result in immediate extinction, and thus a standardized number will be determined. At present, *K* will be proportional to the number of breeding pairs one chooses to supplement with either food or restored feeding habitats. As the present habitat does not support population growth, *K* is set at a standard value of 130 individuals, only slightly higher than the 120 individuals modeled in the simulations. *K* will be altered during a number of scenarios, and the *K* used will thus symbolize the number of breeding pairs that society is willing to pay for or set aside habitat for.

2.6. The release of captive bred Little Owls and food supplementation/habitat restoration

In scenarios two and four, captive breeding was included. This is done be adding a captive population to each of the scenarios. The captive population will experience a drop in juvenile mortality and an increase in the mean number of offspring produced. Dispersal of a fixed number of individuals will happen from this captive population into the wild population. It is possible to specify which age classes that disperse into the wild, thus we simulated both the dispersal of all age classes and the dispersal of young individuals only (1–3 years). The dispersers have a 75% chance of surviving dispersal (Alonso *et al.* 2011 found that 71.4% of Little Owls who received pre-release training survived release into the wild).

Scenarios three and four included food supplementation or alternatively, improvements of the quality of foraging habitats (long term goal for a self-sufficient population) resulting in the same effect on offspring survival. Food supplementation is simulated by a decrease in the juvenile mortality rates from 85% to 14% (Thorup *et al.* 2010). A study on food supplementation in Germany found a juvenile survival rate of 98.6% in juveniles receiving food (Perrig *et al.* 2014). Food supplementation/habitat improvements might not be able to prevent mortality caused by non-natural causes such as car coalitions. However, a study by Jacobsen (2006) including 75 dead juvenile Danish Little Owls found that 17% were indeed killed by cars. Thus road mortality does not seem to be the main cause of death amongst juvenile Little Owls in Denmark. The adult mortality was not altered when receiving food. Though the adult mortality has dropped by a few percent during the past few years (Thorup *et al.* 2013), the adult mortality rate appears to have been stable during long time periods and is thus not likely to decrease (Thorup *et al.* 2010). As it might not be economically feasible to feed or improve habitats for the entire population, two wild populations were simulated, of which one received the conservation actions (resulting in 14% juvenile mortality) and the other did not (85% mortality). Free dispersal was possible between the two "populations" as would be the case in a situation where conservation targeted and non-targeted pairs are mixed among each other in the landscape. Within scenario three, the initial number of individuals aided by these management actions was varied from 10 to 50 individuals. Also, the maximum number of individuals receiving food or having their habitats improved was varied by altering the carrying capacity for the conservation targeted population segment. The carrying capacity of this population therefore represents the number of Little Owls society is willing to rescue. In all cases, food supplementation or habitat improvements were maintained throughout the 25 years.

2.7. Genetic parameters

A lethal equivalent is a unit of deleterious genetic variation, defined as a set of alleles, that, when dispersed amongst a group of individuals, would be lethal in one individual (Kalinowski & Hendrick 1998). Since the number of lethal equivalents is unknown for the Little Owl, the program's standard settings of 6.29 lethal equivalents are used (Lacy 1993). According to Frankham (2010), this number underestimates the deleterious consequences of inbreeding and he suggests a value of 12 lethal equivalents per diploid genome, which will be modeled as well. The total genetic load that is due to recessive lethal alleles is set to 50% according to the default value (Miller & Lacy 2005). Whenever a population is subjected to inbreeding depression this will affect the fecundity and the first year survival (Lacy 1993). Inbreeding depression is included in all runs unless specified otherwise.

In the initial population, VORTEX assumes that all individuals are unrelated. Also, each individual is assigned two unique alleles at a hypothetical locus (Lacy 1993). Allele frequencies on the Little Owl in Denmark obtained from Pertoldi *et al.* (2012) were used as starting allele frequencies.

2.8. Sensitivity testing

A sensitivity test will help examine whether an unknown parameter value is of great importance to the population dynamics or not, by examining a range of values (Lacy 1993). The sensitivity parameter is defined from the following formula, with ΔX being the change in the observed response variable, and *param* being the parameter under examination:

$$S_X = (\Delta X / X) / (\Delta param / param) \quad (1)$$

If nothing else is noted, only one parameter is changed at a time. The exceptions are mortality rates, which are always changed for both males and females in a given analysis. Apart from testing juvenile and adult mortality rates, the mean number of progeny was tested. Also, the genetic parameters inbreeding lethality and the number of lethal equivalents were subjected to sensitivity analysis.

Table 2. Results of the simulations in the “Do nothing” scenario. All simulated populations face extinction within a timeframe of less than 13 years. Probability of extinction (PE) is the part of simulations where the population goes extinct, SD is the standard deviation of a given parameter, *N* extant is the mean population size of the extant populations. GD is the remaining genetic diversity of extant populations, and TE is the mean time of extinction. *N* is the initial population size (*N* = 120 individuals when nothing else is stated), max age repro is the maximum age f dispersal and *K* is the carrying capacity. Results are included for the basic settings and when the maximal age of reproduction or the *K* was altered. The length of the runs were 25 years.

Do nothing scenario	PE	*N* extant	GD (SD)	TE
Basic settings	1	0.00 (0.00)	0.000 (0.000)	11.5
No catastrophe	0.999	2.00 (0.00)	0.625 (0.000)	12.2
N = 40, max age repro = 6	1	0.00 (0.00)	0.000 (0.000)	6.7
N = 40	1	0.00 (0.00)	0.000 (0.000)	8.5
Max age repro 4	1	0.00 (0.00)	0.000 (0.000)	7.0
Max age repro 6	1	0.00 (0.00)	0.000 (0.000)	9.0
Max age repro 9	1	0.00 (0.00)	0.000 (0.000)	10.8
K = 125	1	0.00 (0.00)	0.000 (0.000)	11.5
K = 250	1	0.00 (0.00)	0.000 (0.000)	11.8
K = 500	1	0.00 (0.00)	0.000 (0.000)	11.5
K = 1000	0.998	3.00 (0.00)	0.667 (0.000)	11.5

3. Results

3.1. Scenario 1: “Do nothing strategy”

Based on the “do nothing scenario” the population of Little Owl in Denmark will not survive the coming 25 years on its own merit. In our simulations the populations went extinct within 6.7 to 12.4 years (Table 2). Neither changes in *K*, nor the maximal age of reproduction had any great impact on the time of extinction (Table 2).

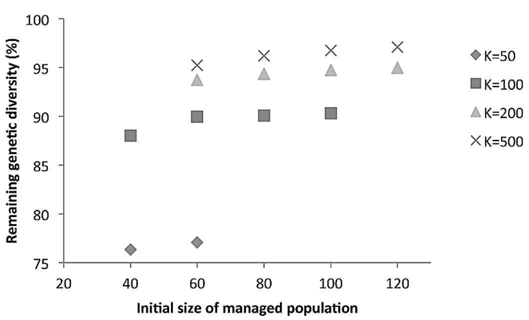

Fig. 3. The remaining amount of genetic diversity plotted against the initial number of individuals receiving food/high quality foraging habitat (scenario 3). The figure includes results on the effect of *K* (managed population) on the remaining genetic diversity. The length of the run was 25, and these are the results after year 25.

3.2. Scenario 2: Captive breeding scenario

When including captive breeding and release of birds in the age range 1–3 years, the risk of extinction in the wild ranged from 22.1% to 59.0% in the wild population when the initial size of the captive population was 20 individuals (Table 3). It dropped to 1.5%–16.8% if the captive population

Fig. 4. The risk of extinction of the captive population in scenario 4. The length of the simulations were 25 years. The risk of extinction is plotted against the number of individuals extracted from the population each year. The initial population size (*N*) and the carrying capacity (*K*) of the captive population was varied. As the results are similar regardless of the initial size of the managed population (Fig. S3), data is only shown for *N*(managed) = 80.

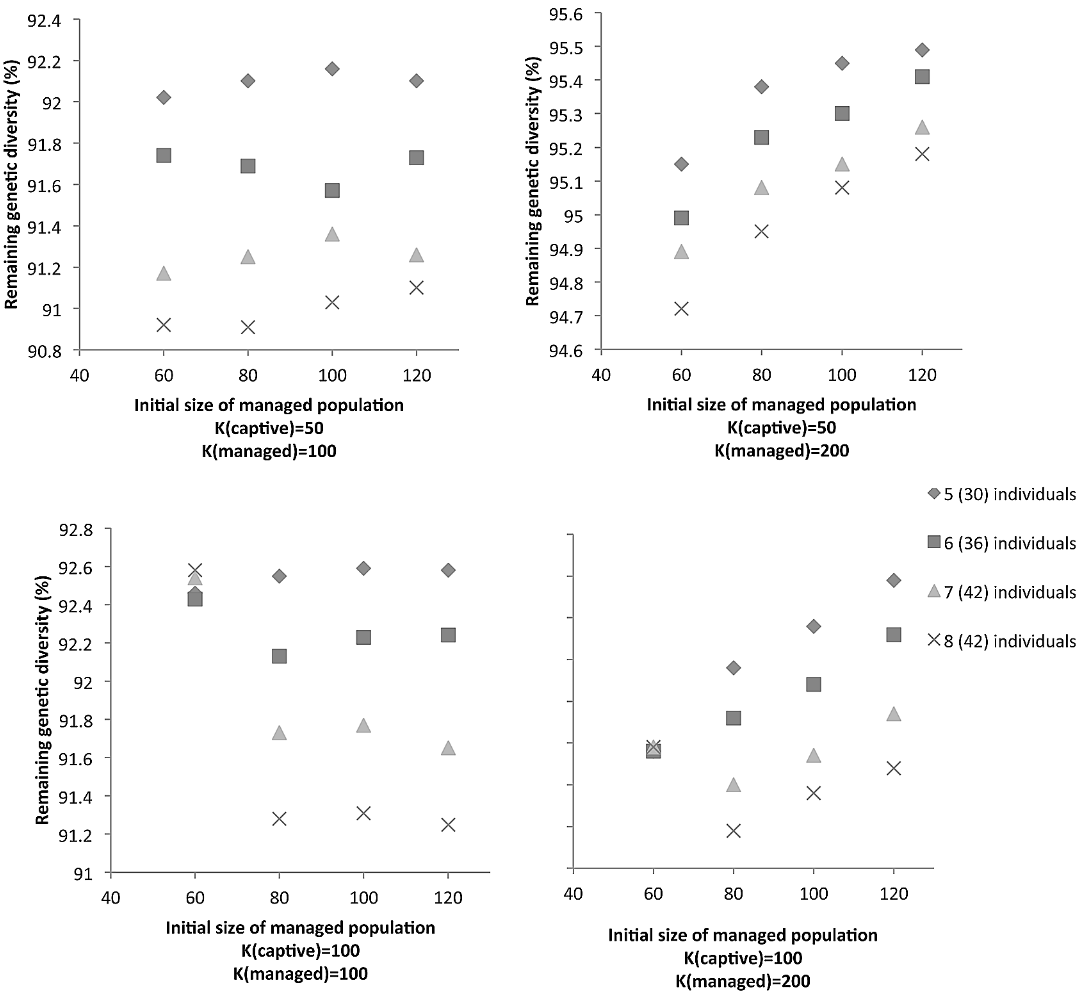

Fig. 5. Results from the wild managed population in scenario 4. The remaining genetic diversity is plotted against the initial size of the managed population. The number of individuals released into the wild each year (or as long as the captive population remained extant) is included; first, the number of individuals of each sex in the age classes 1–3, in parenthesis the total number of individuals released into the wild. Both the carrying capacity (*K*) of the managed and the captive population were varied. The initial population size of the captive population was 20 individuals. The length of the simulations were 25 years.

were founded by 40 individuals (Table 3). If releasing birds of all age classes, the risk of extinction dropped to 9.7%–21.2% if the initial size of the captive population was 20, while an initial population size of 40 individuals lowered the risk of extinction to 0.4%–13.4% (Table S2). The wild population never exceeded 24.17 (SD 7.69) individuals when extant, and at least 12% of the genetic diversity would be lost (Table 3). Both the wild and the captive population had a greater risk of going extinct when more individuals were transferred from captivity to the wild (Table 3). When extant, the captive population always held more individuals after 25 years than the wild population.

3.3. Scenario 3: Food supplementation/ habitat improvements to a limited number of breeding pairs

With a capacity to feed/improve habitat for 50 individuals, the risk of extinction was 11.1%. When this capacity was raised to 100 individuals or

Table 3. Results of the captive breeding scenario. The table includes data on PE; the percent of the simulated populations that went extinct, *N* extant; the mean final population size of the extant population, GD; the mean amount of genetic diversity remaining in the population at the end of the simulations, and TE; the mean time that passed before populations went extinct. No. dispersing is the number of individuals of each sex in the age class 1–3 dispersing from the captive into the wild population, the number in parenthesis is the total number of individuals released into the wild. *K* is the carrying capacity of the captive population. If nothing else is stated, *N*(wild) is 120 individuals. The length of the run was 25, and these are the results after year 25.

		No. dispersing	PE	*N* extant (SD)	GD (SD)	TE (mean)
N(captive) = 20						
K = 50	Wild	5 (30)	0.244	13.74 (4.88)	0.7921 (0.0673)	16.3
	Captive		0.284	42.62 (11.83)	0.7986 (0.0638)	11.9
	Wild	6 (36)	0.378	15.91 (6.18)	0.7965 (0.0673)	15.8
	Captive		0.448	40.44 (13.42)	0.7973 (0.0623)	11.5
	Wild	7 (42)	0.529	18.36 (7.37)	0.7979 (0.0761)	15.8
	Captive		0.599	38.66 (13.79)	0.7957 (0.0681)	10.6
	Wild	8 (48)	0.660	18.58 (8.40)	0.7969 (0.0697)	15.4
K = 100	Captive		0.746	35.29 (15.81)	0.7941 (0.0691)	9.0
	Wild	5 (30)	0.221	14.49 (4.51)	0.8400 (0.0508)	15.8
	Captive		0.223	97.50 (9.28)	0.8622 (0.0372)	9.5
	Wild	6 (36)	0.336	17.47 (5.78)	0.8419 (0.0598)	15.1
	Captive		0.348	97.53 (9.74)	0.8602 (0.0424)	9.0
	Wild	7 (42)	0.435	20.32 (6.16)	0.8477 (0.0512)	14.9
	Captive		0.444	96.47 (11.66)	0.8602 (0.0401)	8.0
	Wild	8 (48)	0.590	23.06 (7.68)	0.8450 (0.0595)	14.6
	Captive		0.607	94.84 (14.72)	0.8577 (0.0414)	7.5
N(captive) = 40						
K = 50	Wild	5 (30)	0.036	13.85 (4.83)	0.8080 (0.0630)	20.4
	Captive		0.074	43.23 (11.03)	0.8143 (0.0600)	20.5
	Wild	6 (36)	0.068	16.37 (5.84)	0.8126 (0.0675)	20.3
	Captive		0.134	40.99 (12.72)	0.8129 (0.0612)	19.4
	Wild	7 (42)	0.105	18.91 (7.42)	0.8166 (0.0708)	20.5
	Captive		0.212	38.48 (14.44)	0.8092 (0.0715)	19.2
	Wild	8 (48)	0.168	20.45 (8.45)	0.8186 (0.0644)	21.1
	Captive		0.326	36.79 (15.48)	0.8073 (0.0643)	19.1
K = 100	Wild	5 (30)	0.002	14.93 (5.13)	0.8699 (0.0380)	17.6
	Captive		0.001	98.18 (7.35)	0.8934 (0.0259)	8.0
	Wild	6 (36)	0.009	18.14 (5.86)	0.8772 (0.0376)	16.5
	Captive		0.009	98.86 (6.71)	0.8930 (0.0265)	10.4
	Wild	7 (42)	0.015	21.06 (6.51)	0.8840 (0.0291)	17.7
	Captive		0.015	98.34 (7.2)	0.8924 (0.0269)	11.9
	Wild	8 (48)	0.016	24.17 (7.69)	0.8857 (0.0304)	16.7
	Captive		0.017	97.67 (8.67)	0.8914 (0.0265)	10.6
N(wild) = 40						
K = 100	Wild	5 (30)	0.006	14.51 (4.81)	0.8699 (0.0360)	16.6
	Cap		0.003	98.57 (6.39)	0.8934 (0.0243)	12.0
	Wild	6 (36)	0.002	17.62 (5.75)	0.8767 (0.0349)	14.7
	Cap		0.002	98.1 (7.02)	0.8932 (0.0254)	11.5
	Wild	7 (42)	0.012	20.74 (6.68)	0.8806 (0.0356)	16.2
	Cap		0.014	98.18 (7.71)	0.8934 (0.0257)	11.2
	Wild	8 (48)	0.016	23.91 (6.94)	0.8869 (0.0291)	16.1
	Cap		0.017	97.81 (8.85)	0.8925 (0.0268)	10.6
N(captive) = 20						
K = 50	Wild	5 (30)	0.244	13.74 (4.88)	0.7921 (0.0673)	16.3
	Captive		0.284	42.62 (11.83)	0.7986 (0.0638)	11.9
	Wild	6 (36)	0.378	15.91 (6.18)	0.7965 (0.0673)	15.8
	Captive		0.448	40.44 (13.42)	0.7973 (0.0623)	11.5

Table 3, continued

		No. dispersing	PE	*N* extant (SD)	GD (SD)	TE (mean)
	Wild	7 (42)	0.529	18.36 (7.37)	0.7979 (0.0761)	15.8
	Captive		0.599	38.66 (13.79)	0.7957 (0.0681)	10.6
	Wild	8 (48)	0.660	18.58 (8.40)	0.7969 (0.0697)	15.4
K = 100	Captive		0.746	35.29 (15.81)	0.7941 (0.0691)	9.8
	Wild	5 (30)	0.221	14.49 (4.51)	0.8400 (0.0508)	15.8
	Captive		0.223	97.50 (9.28)	0.8622 (0.0372)	9.5
	Wild	6 (36)	0.336	17.47 (5.78)	0.8419 (0.0598)	15.1
	Captive		0.348	97.53 (9.74)	0.8602 (0.0424)	9.0
	Wild	7 (42)	0.435	20.32 (6.16)	0.8477 (0.0512)	14.9
	Captive		0.444	96.47 (11.66)	0.8602 (0.0401)	8.0
	Wild	8 (48)	0.590	23.06 (7.68)	0.8450 (0.0595)	14.6
	Captive		0.607	94.84 (14.72)	0.8577 (0.0414)	7.5
N(captive) = 40						
K = 50	Wild	5 (30)	0.036	13.85 (4.83)	0.8080 (0.0630)	20.4
	Captive		0.074	43.23 (11.03)	0.8143 (0.0600)	20.5
	Wild	6 (36)	0.068	16.37 (5.84)	0.8126 (0.0675)	20.3
	Captive		0.134	40.99 (12.72)	0.8129 (0.0612)	19.4
	Wild	7 (42)	0.105	18.91 (7.42)	0.8166 (0.0708)	20.5
	Captive		0.212	38.48 (14.44)	0.8092 (0.0715)	19.2
	Wild	8 (48)	0.168	20.45 (8.45)	0.8186 (0.0644)	21.1
	Captive		0.326	36.79 (15.48)	0.8073 (0.0643)	19.1
K = 100	Wild	5 (30)	0.002	14.93 (5.13)	0.8699 (0.0380)	17.6
	Captive		0.001	98.18 (7.35)	0.8934 (0.0259)	8.0
	Wild	6 (36)	0.009	18.14 (5.86)	0.8772 (0.0376)	16.5
	Captive		0.009	98.86 (6.71)	0.8930 (0.0265)	10.4
	Wild	7 (42)	0.015	21.06 (6.51)	0.8840 (0.0291)	17.7
	Captive		0.015	98.34 (7.2)	0.8924 (0.0269)	11.9
	Wild	8 (48)	0.016	24.17 (7.69)	0.8857 (0.0304)	16.7
	Captive		0.017	97.67 (8.67)	0.8914 (0.0265)	10.6
N(wild) = 40						
K = 100	Wild	5 (30)	0.006	14.51 (4.81)	0.8699 (0.0360)	16.6
	Cap		0.003	98.57 (6.39)	0.8934 (0.0243)	12.0
	Wild	6 (36)	0.002	17.62 (5.75)	0.8767 (0.0349)	14.7
	Cap		0.002	98.1 (7.02)	0.8932 (0.0254)	11.5
	Wild	7 (42)	0.012	20.74 (6.68)	0.8806 (0.0356)	16.2
	Cap		0.014	98.18 (7.71)	0.8934 (0.0257)	11.2
	Wild	8 (48)	0.016	23.91 (6.94)	0.8869 (0.0291)	16.1
	Cap		0.017	97.81 (8.85)	0.8925 (0.0268)	10.6

more, the risk of extinction was 0.2% or less. The main determinant of the final population size when providing food/high quality habitat was the *K* of the population receiving food/high quality habitat (Fig. S2). Thus the final population size will be limited by the number of individuals managers choose to provide with either food or high quality foraging habitat. The final population size will reflect this *K* regardless of the number of individuals initially receiving help (Fig. S2). The population within the managed area will function as a population source to the surrounding habitat. The amount genetic diversity lost will also depend on the *K* of the managed population. With a capacity to feed/provide habitat for 500 individuals, less than 5% of the genetic diversity will be lost (Fig. 3). Less than 10% will be lost when there is capacity to provide for 100 individuals, whereas a capacity to feed/provide habitat for 50 individuals results in a loss of more than 20% of the genetic diversity (Fig. 3). If the initial population size was 40 individuals instead of 120 individuals, the risk of extinction was 1.1% if *K* = 100 and 14.1% if *K* = 50. If decreasing the maximum age of reproduction to the age of 6 years, these numbers would increase to 2.5% and 26.2% respectably (data not shown).

3.4. Combination scenario

When combining captive breeding and food supplementation/habitat improvements the risk of extinction in the wild population was 0%. The risk of extinction in the captive population depended on the initial number of individuals used to found the population, the carrying capacity of the captive population and the number of individuals extracted from the captive population to be released into the wild. The risk of extinction increased when extracting more individuals (Fig. 4). When founding the population of 20 individuals, the risk of extinction ranged from 11.7% to 62.7% depending on the number of individuals extracted. If increasing the initial population to 40 individuals, the risk of extinction dropped considerably (Fig. 4). The carrying capacity of the captive population had only limited effect on the risk of extinction.

The wild managed population had a final *N* equal to the *K* of the managed area (Fig. S4), thus a *K* of 100 individuals produced a final population size of approximately 100 individuals and a *K* of 200 produced a population counting close to 200 individuals. The number of individuals released from captivity into the wild had no influence on the final population size. The remaining genetic diversity was affected by the number of individuals released into the wild as well as the initial number of individuals supplied with food or access to high quality foraging habitat (Fig. 5). When the *K* of the wild managed population was 100 individuals, 8%–10% of the genetic diversity would be lost regardless of the *K* of the captive population (Fig. 5). If increasing the *K* in the wild to 200 individuals 4%–6% of the genetic diversity would be lost.

With an initial population size of 40 individuals in the wild, the population would still remain extant during all 25 years in *N*(captive) = 40 and *K*(captive) = 100. The wild population would reach the *K*, and less than 5% of the genetic diversity was lost (data not shown).

3.5. Sensitivity analysis

The sensitivity analysis found that increasing the number of lethal equivalents or the severity of the inbreeding depression had only limited impact on the risk of extinction (Table S1). The population would remain extant when juvenile mortality dropped below 28%, whereas increases in the juvenile mortality resulted in rapid extinction, as did increasing the SD on mortality (Table S1, Figure S1). If increasing the mean number of progeny produced, the population was still at great risk of extinction. The time of extinction would however be prolonged (Table S1).

4. Discussion

According to the IUCN, a population can only be considered demographically viable if the estimated risk of extinction is 5–10% or less over a 30-year period (IUCN Standards and Petitions Subcommittee 2011). Our modeling suggests that the Danish population of Little Owl cannot be considered demographically viable in the absence of management interventions, and is likely to go extinct within the next 6–12 years. The improvement of a single life history trait could only reverse the negative population trend when simulating juvenile mortality rates corresponding to a level of food supplementation or habitat improvements. When food was provided/habitat restored, the population had a chance to become self-sustained. In these cases, the final population size depended on the number of breeding pairs being fed or the *K* of the improved foraging habitat. Habitat/food must be secured for at least 50 breeding pairs to maintain more than 90% of the original genetic diversity. Captive breeding could only create a demographically viable and self-sustained wild population if the captive population was founded by 40 individuals and had a *K* of 100 (risk of extinction < 2%), but the wild population would never hold more than 25 individuals. Whenever the captive population went extinct, the wild population would go extinct shortly after. Thus the wild population would only persist as long as it was provided with captive bred individuals. When combining food supplementation or habitat improvements with captive breeding, a viable wild population was created. Even if the captive population went extinct before 25 years had passed, the wild population remained extant throughout all 25 years.

Even when considering worst case scenarios of only 20 breeding pairs, the population still have a chance of recovery. To obtain this recovery, high quality foraging habitat or food must be supplied, potentially combined with captive breeding.

4.1. Captive breeding, food supplementation and habitat improvements

If commencing captive breeding and release, a suitable source population must be located. Genetic data places the Danish Little Owls in a northwestern European cluster ranging from Portugal to Austria (Pellegrino *et al.* 2014, 2015). Even though Little Owl populations are in decline over a broad range of its distribution, thriving populations still exist. Local populations in nearby Germany could be a potential source population. In captive breeding, a genetic goal is to maintain 90% or more of the original genetic diversity within the wild population over a 200 year period (Soulé *et al.* 1986). To obtain this goal even within a 25 year period, a vast amount of individuals must be supplemented. A viable captive population must also be obtained. This requires an initial population of 20 breeding pairs in captivity and a capacity to hold 100 individuals. If fewer individuals are used on the captive population, it is likely to go extinct before 25 years have passed. Young individuals should preferentially be transferred from captivity to the wild after receiving training in predator avoidance.

A problematic aspect of captive breeding and release is that unless the factor causing the original population decline has been identified and dealt with, the captive population will end up as a source population while the wild population will be a population sink. This is the case with the California Condor (*Gymnogyps californianus*). The California Condor exists today solely due to a captive breeding program (Walters *et al.* 2010). The entire population was brought into captivity in the 1980s to be bred and subsequently released. Today, the majority of the California Condor population is still found in captivity, and the wild population is a population sink (Walters *et al.* 2010). The wild population is yet unable to sustain itself and grow, partly due to the fact that the original cause of the decline was not dealt with before the release (Walters *et al.* 2010). Further, as the present population is created from only 14 individuals, genetic issues are also present (Ralls & Ballou 2004). But in other situations, captive breeding and release have created self-sustained populations. Eagle Owls (*Bubo bubo*) were reintroduced to Germany, with nearly 1500 owls released during the period 1964–1985 (Radler & Bergerhausen 1988), and limited releases continuing until the early 1990s (Dalbeck & Heg 2006). The reintroduction was a success, and the population has increased to a total of 800–1,000 pairs (Dalbeck & Heg 2006).

If captive breeding is initiated without habitat improvements or artificial feeding, the Danish population will likely become a population sink and never become self-sustained. If combined with habitat improvements, the wild population will remain extant during the next 25 years, even in cases where the captive population goes extinct. The population will be boosted both in numbers and genetically as long as the captive population persists, but by the time the captive population has gone extinct, a viable population will have been created in the wild. A captive breeding program thus only has to exist for about 10 years in order to secure a viable wild population. The Danish agricultural landscape has changed over the past decades, leaving the Little Owls with habitats less suited for raising young (Thorup *et al.* 2010, Thorup *et al.* 2013). Food supplementation must be considered a temporary solution to keep the population alive while awaiting habitat restoration. In practice, the supplementation could consist of supplying each breeding pair with 1–3 dead mice or newly hatched chickens every day during the breeding period (Thorup *et al.* 2010). Food supplementation will increase not only juvenile survival rates but also the weight and overall physical condition of nestlings (Perrig *et al.* 2014). Historically, the Little Owl lived in agricultural landscapes, close to mosaic landscapes consisting of grassland and cropland (Jacobsen 2006). As opportunistic feeding generalist, a high structural complexity in availability of microhabitat seems to be essential during foraging (Sunde *et al.* 2014). As breeding little owls primarily forages within 150 m from the nest (Sunde *et al.* 2009), each pair requires 1–3 ha of high-quality foraging habitat to reproduce well. The simulations suggest that the final population size of the Danish Little Owl will depend largely on the carrying capacity of the land being managed to include high quality foraging areas. In sum, a few hundred hectares of restored foraging habitats scattered around breeding locations should suffice to sustain a viable breeding population of Little Owls. Abandoning or shifting the timing of drugs against intestinal parasites of livestock in areas inhabited by Little Owls may be a simple but very important action to improve insect abundance in Little Owl habitats, as these drugs limits the food availability for Little Owls. In Switzerland, a more diverse agricultural landscape has been created by using cross compliance; a method requiring farmers to comply with environmental standards in order to qualify for subsidies (Aviron *et al.* 2009). The method has been in use since 1993, and the biodiversity has increased within sites of cross compliance compared to control sites. Organic farming generally supports a higher species diversity and abundance than conventional agriculture (Beecher *et al.* 2002, Braae *et al.* 1988), but it will not necessarily secure the short grass habitats that Little Owls depend on for foraging. Habitat restoration can reverse population decline, and has led to an increase in population size of the Azores Bullfinch (*Pyrrhula murina*) from 40 pair to 1,600 individuals over a 40 year period as 230 ha of forest was restored (Birdlife International 2010, Monticelli *et al.* 2010).

4.2. Population viability analysis and its use in making management decisions

A PVA is often used to calculate a minimum viable population size, but can also and more importantly pinpoint the factors to which a given population is most vulnerable and evaluate different management strategies (Kohlmann *et al.* 2005, Pfab & Witkowski 2000). The caveat of PVAs are that they require a large amount of data collected over several years to produce solid results (McCarthy *et al.* 2003). This is often problematic when it comes to endangered species with small population sizes. A lot of scientific data do however exist on the Danish population of Little Owl, making it a good model population for PVA. Further, the sensitivity analysis did not find the population to be especially sensitive towards any of the modelled parameters in themselves. One aspect to be considered regarding the population viability analysis on the Little Owl is that the results that are likely to be optimistic in all runs with an initial population size of 120 individuals. However, runs with the more realistic population size of 40 individuals indicate that there is still hope for the Danish population if management actions are taken. The results do however show that a population of only 40 individuals is likely to go extinct within only 6 years if no management actions are taken.

The Little Owl is far from the only avian species facing population decline and potential extinction. All over the world, humans intervene with nature to secure the survival of wild avian populations. There are many possible ways to manage a declining population and choosing the best strategy for a given species is not always simple. Here, we present an evaluation of different management strategies prior to their implementation using PVA. Population viability analyses are excellent tools when having to evaluate and determine which strategies to implement. In the case of the Red-billed Curassow (*Crax blumenbachii*) a PVA was used to evaluate the release of captive bred individuals post-release (Sao Bernardo *et al.* 2014). Here, the chosen and already implemented management strategy proved to be unviable, and PVA was used to simulate and suggest management actions that could make the population viable. The Leadbeater's Possum (*Gymnobelideus leadbeateri*) in southeastern Australia has been subject to a comprehensive PVA considering its future survival under different management regimes (Lindenmayer & Possingham 1996), as has the endemic South African plant (*Euphorbia clivicola*; Pfab & Witkowski 2000). Both provided strategies for the future management in order to lower the risk of extinction. In an assessment of a PVA on the Peregrine Falcon (*Falco peregrinus anatum*) in the USA, it was found that acting upon the management actions suggested on behalf of the PVA simulations indeed did result in the anticipated population changes (Wootton *et al.* 2014).

4.3. Conclusions

In order to properly manage small and declining populations, PVAs can be a useful tool in determining which strategies are likely to reverse the population decline. The goal of all population management is to create a self-sustained population with a high chance of persistence. In the case of the Little Owl in Denmark, the population is likely to go extinct soon in the absence of management interventions. The release of captive bred individuals in itself will not create a self-sustained population. But the simulations suggest that it is possible to create a population that can persist and become self-sustained. This is the case when the habitat is improved, or when habitat improvements are combined with the release of captive bred individuals. In either case, the chosen management option must be initiated soon and at best before further population decline.

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Sårbarhetsanalys av den minskande populationen av minervauggla i Danmark

Artificiella bevarandeåtgärder såsom utfodring och uppfödning i fångenskap kan tillämpas för att på kort sikt rädda utrotningshotade populationer, tills förhållandena för en självbärande population har återställts. Sårbarhetsanalys (PVA) är ett verktyg för utvärdering av olika bevarandestrategier. Här använder vi programmet VORTEX för att utforska olika förvaltningsstrategier, med fokus på den danska populationen av minervauggla (*Athene noctua*) som modellorganism. Minervaugglan minskar i antal i flera länder, däribland Danmark. Brist på mat under häckningssäsongen är den främsta orsaken till nedgången.

Vi simulerade 25 års populationsdynamik enligt fyra olika scenarier: (1) inga åtgärder vidtas, (2) uppfödning i fångenskap och påföljande tillförsel av individer till den vilda populationen, (3) fåglarna matas eller livsmiljön förbättras, (4) en kombination av uppfödning i fångenskap och födotillskott (eller förbättring av livsmiljö). I scenarier där inga förvaltningsåtgärder vidtogs dog populationen ut inom 12 år. Kontinuerlig tillförsel av individer (scenario 2) höll populationen vid liv, men populationsstorleken förblev liten. Förvaltning i form av födotillskott och/eller förbättringar i livsmiljön (scenario 3) kan återställa populationen, men det måste finnas kapacitet att säkra omständigheterna för minst 100 individer för att minimera genetiska förluster. En kombination av åtgärder (scenario 4) kan eventuellt återställa populationen och göra den oberoende av mänsklig hjälp. Denna studie är ett exempel på hur förvaltningsscenarier kan användas för att vägleda naturförvaltningen att fatta välgrundade beslut.

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Appendix 1. A description of the different scenarios and associated parameter values.

Scenario 1. Do nothing

Category 1, one population: The basic model of one population of *N* = 120 individuals and a simulation time frame of 25 years. Basic input values as described in table 1. The carrying capacity is set at 130 individuals (SD 10).

- Run 1: Basic settings as described above and in table 1.
- Run 2–4: As run 1, but with different maximal age for reproduction:
- Run 2: 6
- Run 3: 9
- Run 4: 12
- Run 5–8: As run 1, but with different carrying capacities:
- Run 5: *K* = 125
- Run 6: *K* = 250
- Run 7: *K* = 500
- Run 8: *K* = 1,000
- Run 9: *N* = 40
- Run 10: No catastrophe
- Run 11: *N* = 40, max. age of reproduction = 6 years

Sensitivity testing for one population based on run 1:

Genetic parameters
- No inbreeding
- Inbreeding with 25% lethality
- Inbreeding with 75% lethality
- Number of lethal equivalents raised to 8 and 12 respectively

Demographic parameters
- Decrease in the juvenile mortality rates for both males and females to first 14%, then 28%, then 77%, followed by an increase to 92% and 98% respectively. Increase SD in mortality to 20.
- Mean number of progeny produced: increased with 10%, 20%, 30%, 50% and 100%, respectively.

Scenario 2: Captive breeding

Run 12–39. In the captive breeding scenario two populations exist, a wild and a captive. The wild population has the same parameter values as those of scenario 1, run 1. The captive population has the same parameter values, except for the juvenile mortality (14% SD 10), the mean no. of offspring (2.49 ± 1.15), and the no. of individuals successful in getting a brood (80%). Dispersal happens from the captive to the wild population. Each year, a fixed number of individuals disperse. There is a 75% chance of surviving dispersal. Dispersal continues during all 25 years or as long as the captive population remains extant. Cold winters do not affect the captive population. The *N* of the captive population is set at 20 individuals. Runs 24–35 are identical to runs 12–23, except *N* of the captive population is set at 40 individuals.

- Run 12: 5 owls of each sex in the age class 1–3 years disperse (30 owls/year), *K*(captive) = 50.
- Run 13: 6 owls of each sex in the age class 1–3 years disperse (36 owls/year), *K*(captive) = 50.
- Run 14: 7 owls of each sex in the age class 1–3 years disperse (42 owls/year), *K*(captive) = 50.
- Run 15: 8 owls of each sex in the age class 1–3 years disperse (48 owls/year), K(captive) = 50.
- Run 16: 5 owls of each sex in the age class 1–3 years disperse (30 owls/year), *K*(captive) = 100.
- Run 17: 6 owls of each sex in the age class 1–3 years disperse (36 owls/year), *K*(captive) = 100.
- Run 18: 7 owls of each sex in the age class 1–3 years disperse (42 owls/year), *K*(captive) = 100.
- Run 19: 8 owls of each sex in the age class 1–3 years disperse (48 owls/year), *K*(captive) = 100.
- Run 20: 2 owls of each sex in the age class 1–11 years disperse (44 owls/year), *K*(captive) = 50.
- Run 21: 3 owls of each sex in the age class 1–11 years disperse (66 owls/year), *K*(captive) = 50.
- Run 22: 4 owls of each sex in the age class 1–11 years disperse (88 owls/year), *K*(captive) = 50.

- Run 23: 5 owls of each sex in the age class 1–11 years disperse (110 owls/year), *K*(captive) = 50.
- Run 36: 5 owls of each sex in the age class 1–3 years disperse (30 owls/year), *K*(captive) = 100, *N*(wild) = 40.
- Run 37: 6 owls of each sex in the age class 1–3 years disperse (36 owls/year), *K*(captive) = 100, *N*(wild) = 40.
- Run 38: 7 owls of each sex in the age class 1–3 years disperse (42 owls/year), *K*(captive) = 100, *N*(wild) = 40.
- Run 39: 8 owls of each sex in the age class 1–3 years disperse (48 owls/year), *K*(captive) = 100, *N*(wild) = 40.

Scenario 3: Food supplementation or habitat restoration

Includes two populations; the first receiving food/access to restored habitat, while the second does not receive any such aid. An overview of all runs can be found in Table A1. All basic values are described in table 1. Deviations from values in Table 1 are: The juvenile mortality for both sexes within population 1: 14% (SD 10), and dispersal happens from age 1–3, both sexes disperse. Probability of dispersal 5%.

Scenario 4: Combination scenario

An overview of the runs within scenario 4 can be found in Table A2. “Captive” is the population held in captivity and is the source of all released individuals. “Managed” and “Do nothing” together represents the wild population. If not stated otherwise, these populations will initially hold 120 individuals when combined. “Managed” is the part of the population that receive either access to high quality foraging habitat or are supplied food, while “Do nothing” represents the part of the population that lives outside the high quality foraging area/food supply area. In all populations, the maximum number of progeny is 8, and the mean number of offspring/brood is 2.12 (SD 1.15) in the wild populations and 2.47 (SD 1.15) in the captive (Jacobsen 2006, Thorup *et al.* 2010). In the wild, 66% of breeding pairs are expected to produce a brood (Jacobsen 2006), while it is assumed that 80% will be able to produce a brood in captivity. Dispersal is used to simulate the release of individuals from the “Captive” population into the wild. All dispersal will happen into the “Managed” population. There is a 75% chance of surviving dispersal (Alonso *et al.* 2011). A fixed number of individuals will disperse (No. disperse) rather than a percentage. Only individuals in the age classes 1–3 will disperse. The specific number of individuals dispersing can be found in Appendix 1. Dispersal will also happen between the two wild populations. Here, 3 individuals of each sex/age class will disperse between populations any given year, with a 75% chance of survival. The mortality rate of all adult birds was set at 32% (SD 10), whereas the juvenile survival rates were 14% (SD 10) in the “Captive” and “Managed” population, and 85% (SD 10) in the “Do nothing”. Runs 89–121 are identical to runs 56–88 except for *N*(Captive) equals 40, and runs 122–187 are identical to runs 56–121 except the *K* of the managed wild population is set at 200.

Appendix 2. An overview of the parameters altered during the runs of scenario 3. The total initial population size in the wild is 120 individuals in runs 40–51, and 40 individuals in runs 52–55. and $N_{managed}$ is the amount of these individuals that initially receive access to food/high quality foraging habitat. *K* of the unmanaged part of the population is 130 (SD 10). Run 52–55 represent worst case scenarios, with a total initial population size of 40 individuals (20 breeding pairs). * In run 53 and 55, the maximum age of reproduction is lowered to 6 years.

Run	$N_{managed}$	$K_{managed\ population}$ (SD 10)
40	60	500
41	60	200
42	60	100
43	60	50
44	80	500
45	80	200
46	80	100
47	100	500
48	100	200
49	100	100
50	120	500
51	120	200
52	40	100
53	40	100 *
54	40	50
55	40	50 *

Appendix 3. An overview of the runs within scenario 4, the scenario combining food supplementation/habitat improvements with a captive release program.

Run	Population	*N*	*K*	No. disperse
56	Captive	20	50	5
	Managed	60	100	
	Do nothing	60	130	
58	Captive	20	50	6
	Managed	60	100	
	Do nothing	60	130	
59	Captive	20	50	7
	Managed	60	100	
	Do nothing	60	130	
60	Captive	20	50	8
	Managed	60	100	
	Do nothing	60	130	
61	Captive	20	100	5
	Managed	60	100	
	Do nothing	60	130	
62	Captive	20	100	6
	Managed	60	100	
	Do nothing	60	130	
63	Captive	20	100	7
	Managed	60	100	
	Do nothing	60	130	
64	Captive	20	100	8
	Managed	60	100	
	Do nothing	60	130	
65	Captive	20	50	5
	Managed	80	100	
	Do nothing	40	130	
66	Captive	20	50	6
	Managed	80	100	
	Do nothing	40	130	
67	Captive	20	50	7
	Managed	80	100	
	Do nothing	40	130	
68	Captive	20	50	8
	Managed	80	100	
	Do nothing	40	130	

Appendix 3, continued

Run	Population	*N*	*K*	No. disperse
69	Captive	20	100	5
	Managed	80	100	
	Do nothing	40	130	
70	Captive	20	100	6
	Managed	80	100	
	Do nothing	40	130	
71	Captive	20	100	7
	Managed	80	100	
	Do nothing	40	130	
72	Captive	20	100	8
	Managed	80	100	
	Do nothing	40	130	
73	Captive	20	50	5
	Managed	100	100	
	Do nothing	20	130	
74	Captive	20	50	6
	Managed	100	100	
	Do nothing	20	130	
75	Captive	20	50	7
	Managed	100	100	
	Do nothing	20	130	
76	Captive	20	50	8
	Managed	100	100	
	Do nothing	20	130	
77	Captive	20	100	5
	Managed	100	100	
	Do nothing	20	130	
78	Captive	20	100	6
	Managed	100	100	
	Do nothing	20	130	
79	Captive	20	100	7
	Managed	100	100	
	Do nothing	20	130	
80	Captive	20	100	8
	Managed	100	100	
	Do nothing	20	130	
81	Captive	20	50	5
	Managed	120	100	
	Do nothing	0	130	

Appendix 3, continued

Run	Population	*N*	*K*	No. disperse
82	Captive	20	50	6
	Managed	120	100	
	Do nothing	0	130	
83	Captive	20	50	7
	Managed	120	100	
	Do nothing	0	130	
84	Captive	20	50	8
	Managed	120	100	
	Do nothing	0	130	
85	Captive	20	100	5
	Managed	120	100	
	Do nothing	0	130	
86	Captive	20	100	6
	Managed	120	100	
	Do nothing	0	130	
87	Captive	20	100	7
	Managed	120	100	
	Do nothing	0	130	
88	Captive	20	100	8
	Managed	120	100	
	Do nothing	0	130	
189	Captive	40	100	5
	Managed	40	200	
	Do nothing	0	130	
190	Captive	40	100	6
	Managed	40	200	
	Do nothing	0	130	
191	Captive	40	100	7
	Managed	40	200	
	Do nothing	0	130	
192	Captive	40	100	8
	Managed	40	200	
	Do nothing	0	130	