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Behavioural flexibility in the mating system buffers population extinction: lessons from the lesser spotted woodpecker *Picoides minor*

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Summary

1. In most stochastic models addressing the persistence of small populations, environmental noise is included by imposing a synchronized effect of the environment on all individuals. However, buffer mechanisms are likely to exist that may counteract this synchronization to some degree.

2. We have studied whether the flexibility in the mating system, which has been observed in some bird species, is a potential mechanism counteracting the synchronization of environmental fluctuations. Our study organism is the lesser spotted woodpecker *Picoides minor* (Linnaeus), a generally monogamous species. However, facultative polyandry, where one female mates with two males with separate nests, was observed in years with male-biased sex ratio.

3. We constructed an individual-based model from data and observations of a population in Taunus, Germany. We tested the impact of three behavioural scenarios on population persistence: (1) strict monogamy; (2) polyandry without costs; and (3) polyandry assuming costs in terms of lower survival and reproductive success for secondary males. We assumed that polyandry occurs only in years with male-biased sex ratio and only for females with favourable breeding conditions.

4. Even low rates of polyandry had a strong positive effect on population persistence. The increase of persistence with carrying capacity was slower in the monogamous scenario, indicating strong environmental noise. In the polyandrous scenarios, the increase of persistence was stronger, indicating a buffer mechanism. In the polyandrous scenarios, populations had a higher mean population size, a lower variation in number of individuals, and recovered faster after a population breakdown. Presuming a realistic polyandry rate and costs for polyandry, there was still a strong effect of polyandry on persistence.

5. The results show that polyandry and in general flexibility in mating systems is a buffer mechanism that can significantly reduce the impact of environmental and demographic noise in small populations. Consequently, we suggest that even behaviour that seems to be exceptional should be considered explicitly when predicting the persistence of populations.

Key-words: buffer mechanisms, environmental noise, individual-based model, polyandry, population persistence.

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Introduction

Understanding mechanisms causing extinction of small populations is one of the major challenges of conservation biology (Shaffer 1987). A widely used tool for predicting extinction risk under different environmental conditions or management options is population viability analysis (PVA) (Akçakaya & Burgman 1995; Walsh, Akçakaya & Harcourt 1995; Brook *et al.* 2002). PVAs are usually based on stochastic population models, which allow the inclusion of two key factors influencing the risk of extinction of small populations: demographic and environmental noise. The strong effect of environmental noise on extinction risk is due to the synchrony induced by environmental fluctuations: if in unfavourable years the survival or reproduction of *all* individuals is reduced to more or less the same degree, the population might become so small that extinction due to demographic noise becomes likely (Wissel, Stephan & Zaschke 1994).

In most PVA models, environmental fluctuations are included by reducing survival and/or reproduction of all individuals simultaneously, for example by reducing the survival rate of all adults by 20% in bad years. However, buffer mechanisms might exist counteracting the synchronizing effect of environmental fluctuations (Grimm *et al.* 2005). Examples include: safe sites (or territories, home ranges) in the habitat where individuals are less affected by environmental variation (McLaughlin *et al.* 2002; Greene 2003); 'floaters', i.e. nonbreeding individuals in territorial species, which can rapidly occupy territories that have become vacant due to the death of a breeder (Walters, Crowder & Priddy 2002; Grimm *et al.* 2003); and in general, individual variability such that individuals differing in weight, age, social status or other correlates of fitness are not equally affected by environmental conditions (Uchmanski 1999, 2000).

A further potentially desynchronizing mechanism, which so far has received little attention in PVA models, is adaptive behaviour (Railsback 2001; Kokko, Harris & Wanless 2004): individuals adapt their behaviour to changes in their biotic and abiotic environment. Imperial eagles *Aquila adalberti*, for instance, mature at earlier ages when population density is low (Ferrer, Otalora & Garcia-Ruiz 2004), allowing the population to stay at carrying capacity longer. Here we explore the consequences of the flexibility of the social mating system for population persistence. In several generally monogamous bird species, the occurrence of social polygamous mating systems was described (Davies 1991). In these cases, an individual of one sex mates with two or more partners with separate nests during a single breeding season. The social mating system of species is closely related to their organization of parental care (Clutton-Brock 1991). Members of the sex less involved in parental care can spend more time and energy on intrasexual competition for extra mates. Furthermore, the occurrence of this behaviour is influenced by the operational sex ratio in the population, e.g. the ratio of fertilizable females to sexually active males (Emlen & Oring 1977).

Modelling studies suggest that strictly polygynous species may have advantages over those that are strictly monogamous (Engen, Lande & Sæther 2003; Sæther *et al.* 2004). However, it has never been investigated whether occasional polygamy within a generally monogamous species has an impact on persistence of the population. Furthermore, one could expect costs inherent in polygamous mating behaviour. Empirical investigations have found that the secondary mate in a polygamous mating usually receives less assistance in parental care than does the primary mate (Kempenaers 1995), resulting in lower survival rates and reproductive success (Bensch & Hasselquist 1994; Slagsvold & Lifjeld 1994; Garamszegi *et al.* 2004). Nevertheless, possible demographic costs of polyandry have not been previously considered.

We aim to investigate the impact of occasional polygamy on population persistence in a generally monogamous species. The life history of our theoretical study species is based on the biology of the lesser spotted woodpecker *Picoides minor*. The lesser spotted woodpecker is generally monogamous, but the facultative occurrence of social polyandry has been observed (K. Höntsch 1996 unpublished thesis; Wiktander, Olsson & Nilsson 2000; Rossmanith 2005). As individual behaviour has to be explicitly considered to investigate flexibility in the social mating system, we use an individual-based model (Walters *et al.* 2002; Grimm & Railsback 2005). For parameterization of the model, we use empirical data obtained from a lesser spotted woodpecker population situated in a German low mountain range near Frankfurt/Main (Taunus) (Rossmanith 2005).

Here we examine whether occurrence of polyandry in years with male-biased sex ratio has the potential to affect significantly the persistence of the population positively, i.e. to act as a buffer mechanism. We explore whether this effect exists (1) if the rate of polyandry is low, and (2) if we assume costs for secondary broods in terms of lower fecundity and higher adult mortality.

Methods

BIOLOGICAL BACKGROUND

The lesser spotted woodpecker is distributed across the Palaearctic region, from Great Britain and North-west Africa to Kamtschatka (Cramp 1985). This year-round resident has strong site fidelity. In general, lesser spotted woodpeckers establish monogamous life-long pair bonds and are single-brooding (Glutz von Blotzheim & Bauer 1994; Wiktander *et al.* 2000). However, social polyandry – where one female mates with two males and has two separate nests in one breeding season – was occasionally observed in two different populations in Sweden and Germany (Höntsch 1996 unpublished thesis; Wiktander *et al.* 2000; Rossmanith 2005). The percentage of all females that were polyandrous was 8·5% in Sweden (Wiktander *et al.* 2000) and 9·7% in Germany (Rossmanith 2005). Pairs that bred together in previous years, started breeding earlier in the season (Wiktander, Olsson & Nilsson 2001a; Rossmanith 2005). Owing to changes in food availability within the breeding season, an earlier onset of breeding translates into higher breeding success (Wiktander, Olsson & Nilsson 2001b; Rossmanith 2005).

FIELD STUDY

The model parameters are based on a field study of a marked lesser spotted woodpecker population in the Taunus low mountain range near Frankfurt/Main, Germany. The study area was situated in a heterogeneous landscape and consisted of deciduous and coniferous forests, old orchards, and grassland. In five study years between 1998 and 2003, 112 individuals were marked with colour rings for individual identification. The population was mapped to determine population size, sex ratio and mortality rates. At 34 breeding attempts, a variety of reproductive parameters (e.g. timing of breeding, nest predation, number of fledglings in successful nests, and brood sex ratio) was determined and mating system was investigated. For a further description of methods and results, see Rossmanith (2005).

THE MODEL

The model simulates the population dynamics of the lesser spotted woodpecker in annual time steps. Each individual in the population was followed from fledging the nest to its death and was characterized by the state variables of age, sex, mating status (unpaired/old paired/newly paired/polyandrous paired) as well as breeding start (early/late). Moreover, each paired individual knew the identity of the current partner and its characteristics.

Each time step started in spring and included the processes of mating, reproduction and deaths, which are described by the following 10 rules and shown in Fig. 1. Reference values of the parameters are given in Table 1.

- *Rule 1*: if both partners from the previous breeding season are still alive, they establish an old pair. With a minor probability *pDivorce* they split up and mating status becomes unpaired. Unpaired males mate with unpaired females and establish a new pair. If there is no unpaired female available, the mating opportunities of the unpaired male depend on the mating system scenario (monogamy/polygamy, see below).
- *Rule 2*: all old pairs have an early breeding start, while new pairs have an early breeding start with the probability *pStartEarly*, otherwise their breeding start is late. The breeding start is an attribute that influences the number of fledglings (see rule 6).
- *Rule 3*: the probability to fail because eggs do not hatch is *pFailure*.
- *Rule 4*: nest predation occurs with the probability *pPredation* and results in the death of all nestlings.
- *Rule 5*: when an individual dies during breeding time (probabilities to survive $pSurvBreed_{male}$ and $pSurvBreed_{female}$), its brood fails and its mate remains unpaired until the next breeding time.
- *Rule 6*: in successful nests, i.e. when eggs have hatched, no predation has occurred, and parents have survived the breeding season, nestlings fledge. The probabilities to produce a certain number of fledglings differ for early and late pairs (Table 1). The probability for a fledgling to be male is *pYoungMale* otherwise it is a female.
- *Rule 7*: fledglings have a certain probability to survive ($pSurvWinter_{juvenile}$) in the time between fledging and first breeding time.
- *Rule 8*: there is a maximum number of territories, i.e. a maximum number of individuals that can exist in the area, given in the parameter carrying capacity. Only if the number of birds is below the carrying capacity, fledglings can stay in the area, otherwise they emigrate.
- *Rule 9*: if an individual exceeds maximum age (= 10 years), it dies. Otherwise it has the probability of $pSurvWinter_{male}$ and $pSurvWinter_{female}$ to survive.
- *Rule 10*: at the end of the simulation year, the age of all individuals is updated.

To mimic demographic noise, all demographic parameters (Table 1) were interpreted as probabilities (Burgman, Ferson & Akçakaya 1993). In processes that are strongly influenced by environmental fluctuations between years (predation and survival rates), parameter values were drawn from a normal distribution (truncated at 0 and 1) at the beginning of each time step to account for environmental stochasticity. The normal distribution was defined by the mean and the SD derived from the field data over all years (Table 1).

Except for pre-breeding survival and its annual variation ($pSurvWinter_{juvenile}$ + SD), all parameter values were derived from data collected in our field study. Pre-breeding survival was estimated by pattern-orientated parameterization (Wiegand *et al.* 2003) using the model presented here, i.e. the model was simultaneously fitted to a set of four empirically observed patterns (adult sex ratio, ratio of old and new pairs, proportion of nest producing at least one fledgling, number of fledglings per successful nest, see Rossmanith 2005). Consequently, for the reference parameter set, we found population structure to be realistic.

The following model scenarios were contrasted:

- *Monogamous scenario*: unpaired males mate with females from the unpaired stock and form a 'new pair'. If no unpaired partners are available, the individual cannot reproduce within this time step.
- *Polyandrous scenarios*: males that remained unpaired after monogamous pair formation can mate with an already paired female. Yet, the existence of an unpaired male alone does not determine the proceeding of a polyandrous mating event. First, we assumed that only females with an early breeding start can initiate an additional brood with a second male, because the breeding conditions deteriorate with time (Rossmanith 2005). Secondly, polyandry has to be seen as an exceptional behaviour in woodpeckers and we assumed that it will only be realized in some cases. In fact, unpaired males were observed in the field even though early breeding females were available (Rossmanith unpublished data),

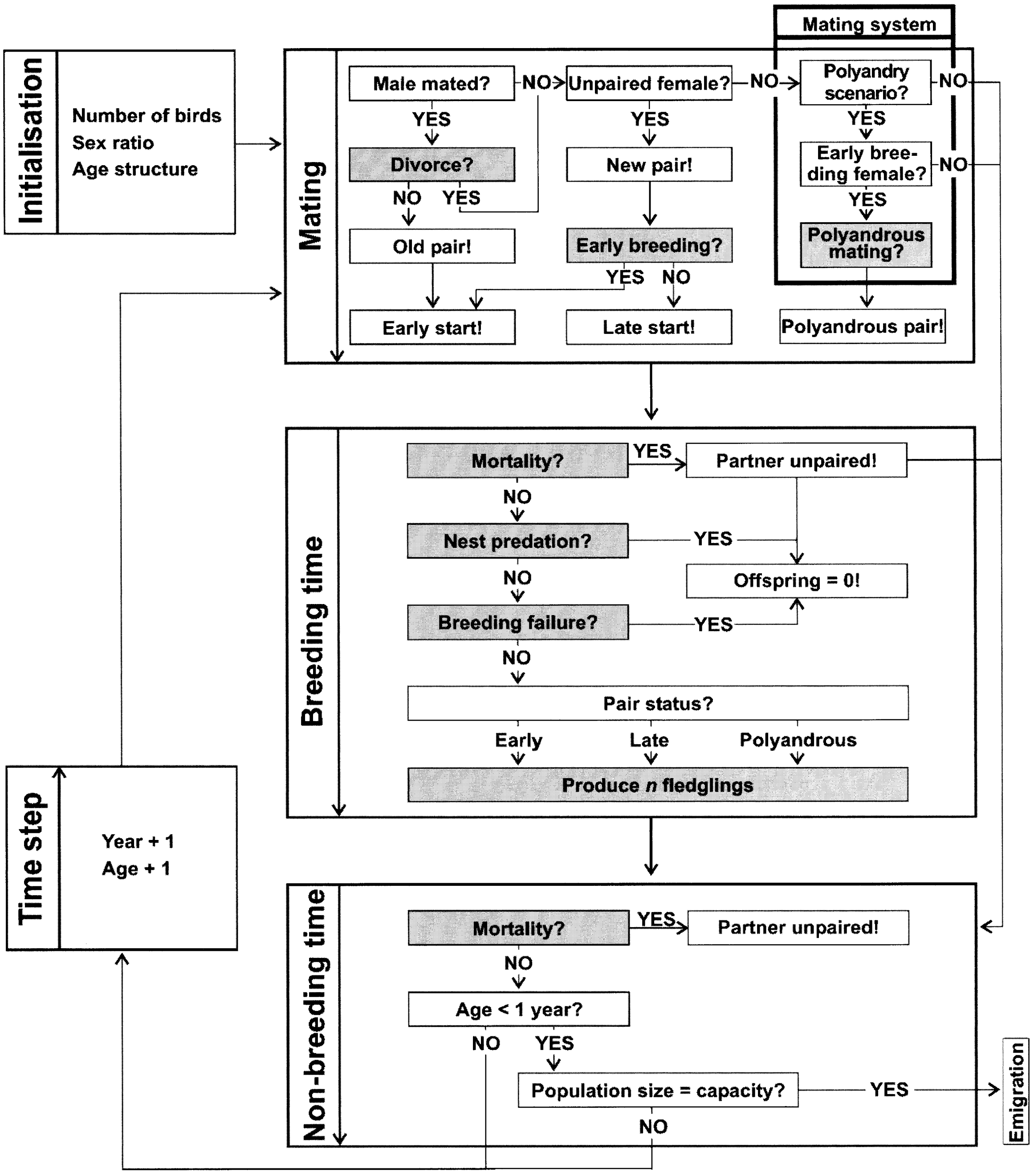

Fig. 1. Simplified float chart for the lesser spotted woodpecker simulation model. Grey boxes indicate stochastic processes in which the result is determined by a probability and a random number.

which demonstrates that polyandrous mating events occur only with a certain probability (*pPolyandry*). Thus, if *pPolyandry* equals 0, no polyandrous mating will occur. If it equals 1, all unpaired males finding an early breeding female will mate. However, an individual female can mate with two males and produce two broods at maximum.

In species with biparental care, polyandrous females have to share their parental care between two broods. Empirical investigations showed that especially the secondary partner suffers from reduced care of the polygamous mate, which yields in lower proportions of successful broods, smaller brood sizes or lower adult survival (Kempenaers 1995; Albrecht & Johnson 2002; Garamszegi *et al.* 2004). An unequal share of care by polyandrous females between their two broods has also been reported for the lesser spotted woodpecker study population (Rossmanith 2005). Here, females invested more care in the primary than in the secondary brood and secondary males tend to have lower reproductive success and survival during breeding time compared with males in primary and monogamous broods. However, as the exact costs of polyandry are not known, we used two polyandrous scenarios to test the impact of polyandry under different assumptions of costs for the secondary male:

- *'No-cost' scenario*: demographic parameters for reproductive success and mortality are the same for

Table 1. Default parameter set. Quality of the parameters: values based on empirical investigations with large (++) and small (+) sample sizes (Rossmanith 2005), parameter estimation by pattern-orientated modelling (±; Rossmanith 2005) and assumptions (–). A sensitivity analysis was conducted for the monogamous (mono) and the high-cost polyandrous (poly) scenario (SI)

			SI		
Stochastic parameters	Value	Quality	mono	poly	Description: probability
pDivorce	0·03	+	<1	–1	for old pairs to split up
pStartEarly	0·46	+	3	3	for new pairs to start early
pFailure	0·03	++	–2	–1	to fail in reproduction
pPredation	0·16	++	–6	5	to lose brood to predators
(± SD)	± 0·02	+	–4	6	
$pSurvBreed_{male}$	0·969	++	–3	–3	to survive during breeding time
$pSurvBreed_{female}$	0·966	++	–3	< 1	
$p(x)Fledg_{early\ pairs}$	0·09 [x = 2] 0·33 [x = 3] 0·33 [x = 4] 0·25 [x = 5]	+	57	27	for successful pairs with early breeding start to produce x fledglings
$p(x)Fledg_{late\ pairs}$	0·20 [x = 1] 0·20 [x = 2] 0·40 [x = 3] 0·00 [x = 4] 0·20 [x = 5]	+	16	14	for successful pairs with late breeding start to produce x fledglings
pYoungMale	0·54	++	8	28	for young to become male
$pSurvWinter_{male}$	0·582	+	–62	–97	to survive during nonbreeding season
(± SD)	± 0·060	+	<1	–3	
$pSurvWinter_{female}$	0·621	+	–7	–4	
(± SD)	± 0·207	+	–6	–6	
$pSurvWinter_{juvenile}$	0·50	+/–	–49	–54	to survive before first breeding
(± SD)	± 0·03	–	< 1	–1	
Parameters for polyandrous broods					
pFailure	0·15	–		< 1	for secondary broods to fail because eggs do not hatch
pSurvBreed	0·845	–		–4	for secondary males to survive during breeding time
p(2)Fledg	1·0	–		1	for successful secondary males to produce x fledglings
pPolyandry	Varied between 0 and 1	–		< 1	for unpaired male and early breeding, paired female to mate
Other parameters					
Capacity	250		6		maximum number of territories
StartSize	200		< 1		number of individuals at initialisation
MaxAge	10		< 1		maximum age

individuals from polyandrous as for those from monogamous broods.

- *'High-cost' scenario*: both, mortality of the secondary male during breeding time and failure of its brood caused by unhatched eggs was set five times higher. The number of fledglings in successful secondary nests is reduced to two juveniles. The reduction of breeding survival rate reduces the annual survival rate (calculated by *SurvBreed* ∗ *SurvWinter*) from 0·564 to 0·495.

The model was implemented as a computer program in C++ (Borland Builder 5·0) and simulations were conducted on a common personal computer. For each parameter set, the model was run 2000 times for 6000 time steps or until the population became extinct. From the distribution of extinction times, we calculated the intrinsic mean time to extinction T_m in years using the 'ln(1 – P_0) plot' described by Grimm & Wissel (2004). From T_m we also calculated the risk of extinction, $P_0(100)$, after 100 years. As viability criterion for the population, we here defined that $P_0(100)$ does not exceed 5%.

To check sensitivity of model outputs to changes in parameter values, each parameter was changed by ±10% of its default value (Table 1) while keeping all other parameters constant (Dunning *et al.* 1995; Wichmann *et al.* 2003). As number of fledglings per brood is a discrete value, we had to modify this value by one young. This equals a modification by 26% (early broods), 36% (late broods) and 50% (secondary polyandrous broods), respectively. Survival rates during breeding times were about 0·96. It is not possible to raise these values by 10%, as a probability cannot exceed 1. Therefore, we referred to mortality rates (1 – survival rate) in the sensitivity analysis. Sensitivity was calculated as the relative change of T_m divided by the relative change of the reduced parameter (SI–) and the enhanced parameters (SI+), respectively. For each parameter, the entire sensitivity (SI) was calculated by summing up SI+ and SI– (see Table 1). Thus, high values for SI indicate strong sensitivity. Moreover, the qualities of the data underlying the parameters are indicated in Table 1 as follows: data based on empirical investigations with large (++) and small (+) sample sizes, pattern-orientated parameter estimation (+/–) and assumptions (–).

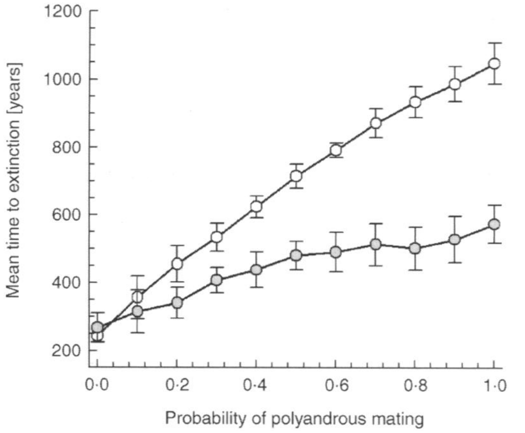

Fig. 2. Effects of the probability for an realized polyandrous mating event, *pPolyandry*, on the population's mean time to extinction, T_m, for the 'no-cost' scenario (white circles) and the 'high-cost' scenario (grey circles). *pPolandry* = 0 equals a strict monogamous mating system.

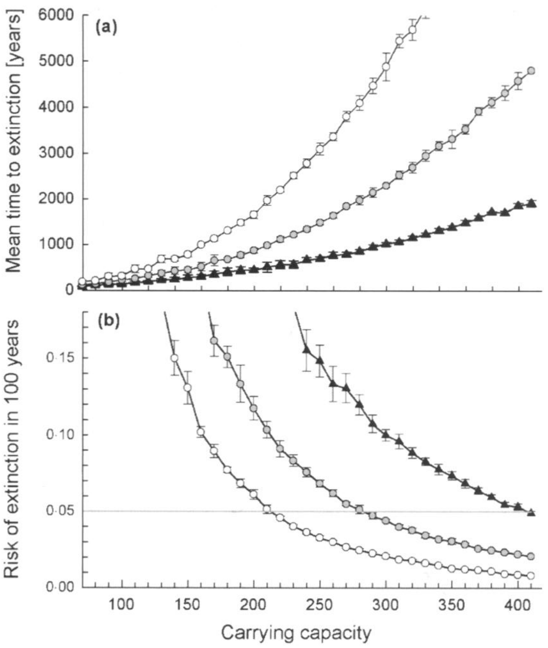

Fig. 3. Persistence of the population vs. carrying capacity for three different scenarios: purely monogamous (black triangles), polyandry with 'high cost' (grey circles) and polyandry with 'no cost' (white circles) (mean and SD for 15 replicate runs). (a) Mean time to extinction, T_m; (b) Risk of extinction within 100 years, $P_0(100)$; viability, here defined as $P_0(100) < 0{\cdot}05$, is indicated by the horizontal line.

Results

INFLUENCE OF POLYANDRY RATE ON POPULATION PERSISTENCE

When all potential polyandrous mating events were realized (*pPolyandry* = 1·0), the mean rate of polyandrous females was 20·2%. The proportion of polyandrous females in the population was similar to the rate found in the empirical investigation (9·7%, Rossmanith 2005) when the probability for a polyandrous mating event, *pPolyandry*, was 0·5.

With increasing *pPolyandry* and consequently with an increasing proportion of polyandrous females, the mean time to extinction increased in both polyandry scenarios (Fig. 2). The slope increased steeply in the 'no-cost' scenario (linear regression: $T_m = 296 + 780 * pPolyandry$, $r^2 = 0{\cdot}920$, $P < 0{\cdot}001$), and still strong in the 'high-cost' scenario ($T_m = 296 + 327 * pPolyandry$, $r^2 = 0{\cdot}560$, $P > 0{\cdot}001$).

INFLUENCE OF DIFFERENT MATING SYSTEMS ON POPULATION PERSISTENCE

For the following simulations, we set *pPolyandry* at 0·5 to receive a polyandry rate similar to the rate found in the field. To assess the relationship between polyandry and the influence of environmental fluctuations on the persistence of populations, we computed mean time to extinction and risk of extinction in 100 years for various carrying capacities (number of territories) (Fig. 3).

In the monogamous scenario, the increase of T_m with carrying capacity was flat (Fig. 3a), indicating high environmental noise (i.e. environmental fluctuations cause strong variations of the population's growth rate). In the 'no-cost' scenario, the increase of T_m was much steeper, indicating the polyandry might buffer environmental noise. The 'high-cost' scenario showed an intermediate result, but the buffer effect of polyandry was still considerable.

Consequently, the risk of extinction in 100 years decreased with carrying capacity in all three scenarios (Fig. 3b). Assuming strict monogamy, the minimum size for a viable population (risk of extinction smaller than 5% in 100 years) was 410 individuals. Assuming 'high-cost' polyandry, the minimum size decreased to 290; assuming polyandry does not include costs, the minimum size of a viable population was 220. Thus, considering different mating systems and costs, the carrying capacity for a minimum viable population differs strongly.

EFFECT OF MATING SYSTEM ON POPULATION DYNAMICS

To understand better the reason for the effect of polyandry on population persistence, we investigated the dynamics of the population in the monogamous and the polyandrous scenario with costs in more detail. First, we simulated 300 populations assuming a carrying capacity of 300 individuals. Population size was significantly higher in the polyandrous scenario than in the scenario with strict monogamy (Fig. 4a, unpaired *T*-test, $T = -4{\cdot}680$, $n = 300$, $P < 0{\cdot}001$). Moreover, the fluctuation in the number of individuals – given as the coefficient of variation – was lower in scenarios with a flexible mating system (Fig. 4b, $T = 3{\cdot}875$, $n = 300$, $P < 0{\cdot}001$). Consequently, in the polyandrous scenario, the population

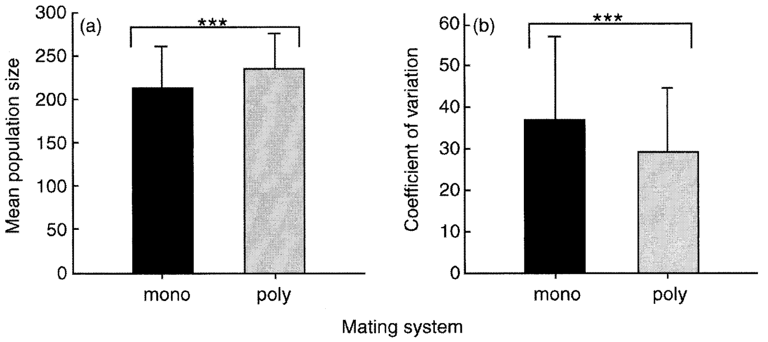

Fig. 4. Differences between the population dynamics of monogamous vs. 'high-cost' polyandrous scenario. (a) Mean population size over 100 years (mean and SD). (b) Coefficient of variation of the population sizes (mean and SD); $^{***}P < 0{\cdot}001$.

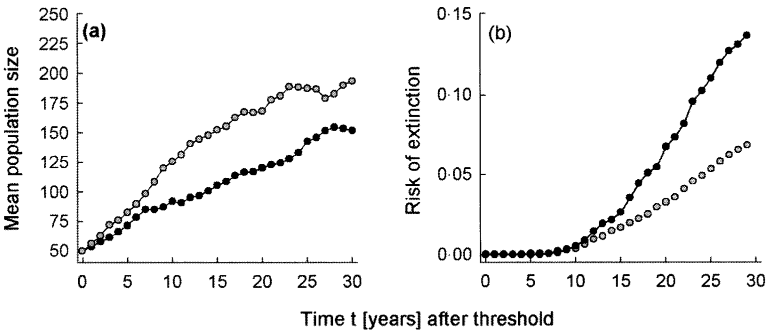

Fig. 5. Population development after the population reached a threshold of 50 individuals. (a) Recovery of mean population size by time *t* after the threshold. Only populations that survived the first 30 years were included. (b) Risk of extinction by time *t* after the threshold. Carrying capacity is 300; monogamous scenario (black) and 'high-cost' polyandrous scenario (grey) are compared. For the latter a probability for polyandrous mating, *pPolyandry*, of 0·5 and high costs for the additional male were assumed.

size was fluctuating with smaller amplitude around a higher mean number of individuals.

Because small populations suffer a higher risk of extinction due to demographic stochasticity, persistence of a population can be influenced by the probability of reaching a certain threshold. This probability is higher the more the population size fluctuates. We analysed the performance of the population after falling below the threshold of only 50 individuals. Populations had a higher ability to recover after falling under a certain threshold when polyandry was permitted. The increase in population size was stronger (Fig. 5a) and the risk of extinction within the next 30 years after reaching a critical threshold (here 50 individuals) was lower (Fig. 5b) in the polyandrous scenario. These results demonstrate that the population has a higher ability for recovery when females can mate polyandrously with remaining males.

SENSITIVITY ANALYSIS

The sensitivity analysis of the model shows that the parameters with lowest quality (parameters for secondary males and fluctuation of juvenile survival rate) only have a low sensitivity (Table 1). The most sensitive parameters are all based on empirical investigations on the lesser spotted woodpecker. The comparison of the sensitivities of monogamous and the polyandrous scenarios shows that male mortality and its fluctuation become more sensitive in the polyandrous scenario, while the mortality of females becomes less sensitive. This demonstrates that the number of males has a stronger influence on population growth rate in the polyandrous scenarios because a higher proportion of males are able to reproduce in years with a male-biased sex ratio. Therefore, factors influencing the sex ratio of the population such as brood sex ratio (*pYoungMale*) and mortality in fledglings, which are mostly male-biased, become more sensitive.

Discussion

We developed an individual-based population model to address the question whether occurrence of polyandry has the potential to affect the persistence of the population positively, i.e. to act as a buffer mechanism. The life history of our theoretical study species was based on the biology of the lesser spotted woodpecker, a generally monogamous species with facultative occurrence of social polyandry. We did not aim to present absolute values for viability or mean time to extinction, but to compare the persistence of the population under different mating system scenarios. The sensitivity analysis indicates that parameter quality is sufficient for the purpose of our comparative modelling study.

Our main result is that polygamous mating systems have a positive effect on the persistence of populations.

This supports results from mathematical models (Engen *et al.* 2003; Saether *et al.* 2004). In contrast to these models, we assumed that the mating system is flexible. In our study species, polyandry is an exception to the general behaviour, therefore we assumed that a female only mates with two males in years with male-biased sex ratio and when the female is breeding under good conditions (early breeding start). Moreover, we varied the probability for a realized polyandrous mating event and found that the positive effect for the population was still strong if the rate of polyandrous females was very low. This demonstrates that not only generally polygamous species persist longer when compared with monogamous species, but also species that only show certain flexibility in the mating system.

Presuming a rate of polyandry, which is similar to empirical findings in the lesser spotted woodpecker, we showed that polyandry has an important effect on the estimated minimum size of a viable population. This clearly demonstrates that the mating system has to be considered when investigating population viability.

Furthermore, we assumed that polyandry might be linked to costs in terms of lower survival and reproductive success for the secondary male in polyandrous broods. However, even in the scenario with high costs for polygamous mating, the flexibility in mating system increases population persistence considerably. This is surprising, as the costs for polyandry include a lower survival rate in secondary males. Male survival rate proved to be the most sensitive parameter and thus a decrease should have severe effects on population persistence. However, the lower survival rates in the polyandrous high-cost scenario only concern some males in the population and only in years with a surplus of males. Thus, mortality in these males affects population persistence to a minor extent and polyandry can still buffer population decline.

What are the mechanisms causing the buffer effect in the polyandrous scenarios? Polyandry occurs in years with male-biased sex ratio. In strictly monogamous systems skewed sex ratios have a negative effect as the proportion of reproductive individuals declines. When individuals practice social polygamy the proportion of reproductive individuals increases in the population. This has two effects: First, demographic noise, i.e. the bias in sex ratio due to stochasticity in demographic processes, is reduced. Second, a higher proportion of reproductive individuals increase the population's growth rate, which minimizes the effect of environmental fluctuations on the population (Grimm *et al.* 2003).

Theoretical models showed that under strong environmental noise persistence time increases only slightly with carrying capacity, while it increases exponentially without environmental noise (Wissel *et al.* 1994). Suffering strong environmental noise, the population is fluctuating strongly and might occasionally become so small that demographic noise leads to extinction. Thus, the slight increase of persistence time with carrying capacity in the monogamous scenario indicates strong environmental noise. In contrast, in polyandrous scenarios, the mean time to extinction increases more quickly with capacity, revealing a buffer effect that reduces environmental noise (Grimm *et al.* 2005).

Furthermore, even larger positive effects of occasional polygamy are possible if sex ratio adjustments occur. In birds, brood sex ratio can be biased in response to environmental conditions (Oddie 2000; Suorsa *et al.* 2003; Dyrcz *et al.* 2004; Szekely *et al.* 2004). In these cases, mating system flexibility can buffer the effect of environmentally caused biases in sex ratio and thus environmental noise.

Our analysis of the population dynamics of a monogamous species with facultative occurrence of polyandry demonstrated that flexibility in the mating system acts as a mechanism buffering demographic and environmental noise. Therefore, we suggest that PVAs should consider sex ratio by including (1) sex-specific survival rates as well as the brood sex ratio, and (2) a potential flexibility in the mating system, when empirical evidence is available. In doing so, reasonable costs for polygamous mating should be considered as well, as the costs will also influence the magnitude of the positive effects in persistence time.

The fact that even small proportions of polyandrous mating in the population had a strong effect on the population persistence further demonstrates that exceptions from the general behavioural patterns should not be ignored. Certain plasticity in the behaviour does not only occur in mating systems but should also be considered in space use (Wichmann *et al.* 2005) or age of maturity (Ferrer *et al.* 2004). Unfortunately, observations of behavioural exceptions are often not published, because they do not fit the general picture or are considered not 'significant'. However, flexibility enables the individuals to adapt their behaviour to new or changing conditions and thus is the basis for evolution. Consequently, when investigating the performance of a population under different environmental scenarios, researchers should consider certain flexibility in behavioural traits.

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