Inbreeding in red-cockaded woodpeckers: Effects of natal dispersal distance and territory location

Karin Schiegga,b,*, Susan J. Danielsa,2, Jeffrey R. Waltersa, Jeffery A. Priddyc, Gilberto Pasinelli.a,b

aDepartment of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0406, USA
bZoologisches Institut, Universität Zürich, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland
cDuke University, Nicholas School of the Environment, Marine Laboratory, 135 Marine Laboratory Road, Beaufort, NC 28516-9712, USA

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ABSTRACT

Inbreeding depression constitutes a significant threat to the viability of small populations. In addition to small size and isolation of populations, short distance dispersal may elevate risk of inbreeding, but empirical evidence is scarce. Inbreeding depression has been demonstrated in the highly endangered red-cockaded woodpecker Picoides borealis. It has been suggested that conservation efforts to support extant populations should aim at spatially aggregating territories to enhance dispersal success. This however may aggravate inbreeding risk because distance between territories and hence dispersal distances become short. We analysed empirical data from a long-term study of the demography of the red-cockaded woodpecker and found that inbreeding risk varied inversely with natal dispersal distance of the mother. Using an individual-based, spatially explicit population model that incorporates simulations of environmental and demographic stochasticity and an empirically derived, species-specific estimate of inbreeding costs, we demonstrated that inbreeding depression significantly elevated extinction risk in this species. On the other hand, even though dispersal distances in populations with spatially aggregated territories were shorter and the proportion of inbred individuals was higher than in other populations of the same size, such populations were still more persistent. Despite the overall adverse effect of inbreeding depression on viability of red-cockaded woodpecker populations, lowering interterritorial distances can be viewed as a valuable conservation tool. Given the small size and isolated location of most extant red-cockaded woodpecker populations however, our findings suggest that inbreeding depression represents a significant threat to the survival of this species.

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1. Introduction

Evidence is accumulating that inbreeding depression, i.e., reduced fecundity owing to matings among relatives (Gibbs, 2001) can severely impair reproductive output in wild populations of naturally outbreeding species of plants and animals (see Hedrick and Kalinowski, 2000; Keller and Waller, 2002 for recent reviews). It has been argued that non-genetic stochastic effects drive small animal populations to extinction before inbreeding depression becomes important (Lande,
Two previous modelling studies of population viability in red-cockaded woodpeckers identified inbreeding as a serious threat to small populations of this species and emphasized the need to incorporate inbreeding depression into population viability analyses (Haig et al., 1993b; Daniels et al., 2000). Inbreeding depression has been documented in the red-cockaded woodpecker (Daniels and Walters, 2000a; Schiegg et al., 2002a), but its impact at the population level has not been investigated previously.

Our objective is to quantify the impact of inbreeding depression on population viability of small red-cockaded woodpecker populations. Specifically, we ask the following questions: (1) Is the probability that offspring are inbred related to parental natal dispersal distance? (2) How large is the potential impact of inbreeding depression on long-term persistence of small red-cockaded woodpecker populations? (3) Does the spatial arrangement of territories influence probability of inbreeding? We address question (1) by analysing empirical data from a long-term study of a relatively large red-cockaded woodpecker population, and questions (2) and (3) using an individual-based, spatially explicit simulation model that incorporates the effects of environmental and demographic stochasticity as well as those of inbreeding depression.

2. Methods

2.1. Empirical data

2.1.1. Study system and inbreeding coefficients

We obtained empirical estimates of inbreeding in red-cockaded woodpeckers by constructing pedigrees using demographic data collected from the North Carolina Sandhills population, located in south-central North Carolina, USA. This population contains about 560 groups, 220 of which have been monitored since 1980. All adult birds and all fledglings in the monitored groups were marked with unique combinations of colour bands. All these groups were censused each year and breeding status was assigned based on behavioural observations following Walters et al. (1988). Measures of reproductive success such as clutch size, number of nestlings and number of fledglings were recorded in all groups each year. Territory sizes in this population average 84 ha (Walters et al., 2002b). For more details of population monitoring and censusing see Walters et al. (1988).

Inbreeding coefficients (F) were calculated based on the pedigree including all known individuals (7350 birds) in the study population between 1980 and 2000 using PROC INBRED in SAS (SAS Institute Inc., 1999–2001). The inbreeding coefficient is the probability that a randomly chosen locus contains alleles that are identical by descent (Falconer and Mackay, 1996). There is no evidence that helpers ever sire offspring in this species, and the frequency of extra-pair fertilizations by individuals outside the group is among the lowest yet recorded in birds (Haig et al., 1993a, 1994). All individuals at the beginning of data collection and those immigrating into the study area were considered unrelated; hence our estimates of inbreeding levels are conservative.
2.1.2. Dispersal behaviour and distance
We categorized birds that bred on their natal territory as philopatric (natal dispersal distance = 0), and birds that emigrated from the natal group before breeding as dispersers (natal dispersal distance > 0). The latter category included birds that were helpers on their natal territory for 1–8 years before dispersing to a nearby territory to breed, as well as birds that dispersed in their first year. Natal dispersal distance was calculated as the straight-line distance between centres of the natal and the first breeding territory (Pasiellini et al., 2004). Female red-cockaded woodpeckers cross on average only two territories during natal dispersal (median, n = 603, Daniels and Walters, 2000b) and the corresponding number for males is even lower (Daniels, 1997). We hence decided to use Euclidian distances rather than number of territories crossed in our analyses to ensure sufficient variation in the data set. Because dispersal distances in this species are so short (median dispersal distance, excluding philopatric individuals: males: 2089 m, interquartile range iqr = 974–4380, n = 488; females: 3689 m, iqr = 1687–5921, n = 958) and our study area is large (110,000 ha), we are confident that our data set is not substantially biased towards short dispersal distances (see also Pasiellini et al., 2004). This assumption is further corroborated by a high recovery rate of fledglings (2518 (44.2%) out of 6260 nestlings banded between 1980 and 2000 were resighted as adults within the study area, own unpublished data).

2.2. Model simulations

2.2.1. Model description
The model we employed allows for stochastic, spatially explicit, individual-based simulations and was built on the extensive demographic database from the Sandhills population described above. Model parameter values and algorithms used are described in detail in Letcher et al. (1998) and Schiegg et al. (2005).

Landscape size (32 × 24 km) was chosen to enable us to match the range of territory densities observed among existing populations (Letcher et al., 1998). Territories were at fixed locations, because in red-cockaded woodpeckers territories are centered on clusters of cavities constructed in live mature pines that are used for decades (Walters, 1991). When a territory was unoccupied for five consecutive years, it was considered unsuitable and could not be reoccupied thereafter (Copeyon et al., 1991). New territories were formed by budding, i.e., the splitting of an existing territory into two, which occurred with an annual probability of 1%. Budding is the primary means by which new territories are formed in real populations of red-cockaded woodpeckers, but occurs at very low rates (Hooper, 1983; Doerr et al., 1989; Conner et al., 2001).

A bird’s behaviour depended on its sex and status class (i.e., fledgling, disperser, helper, breeder, solitary male). In their first year, males either remained on their natal territory as helpers or dispersed, depending on an empirically derived proportion set by model parameters. All females dispersed in their first year, because female helpers are rare (Walters et al., 1988). Dispersal of first-year birds occurred in random directions and in a straight line. Birds could emigrate from the study area by crossing the landscape boundary, but we did not allow for immigration, because most existing red-cockaded woodpecker populations are isolated from one another (Conner et al., 2001). The percentage of unbanded birds found each year is only 5% in our study area (Daniels and Walters, 2000b), even though it encompasses only about one-half of the Sandhills population and is adjacent to additional territories along its eastern boundary. Dispersing males moved at a speed of 2.3 km yr⁻¹ and competed for breeding vacancies within their search radius (3 km) each time step (3 months) as they moved across the landscape. Dispersing females moved at a speed of 4.8 km yr⁻¹ and, like dispersing males, competed for breeding vacancies within their search radius (3 km) each time step as they traversed the landscape. Breeding females have been shown to actively avoid incest by leaving their territory in >90% of the cases in which a son attained the breeding position (Daniels and Walters, 2000a). This behaviour was included in the model by invoking female dispersing dispersal when a son replaced a female’s mate.

 Helpers attained breeding status by inheriting their natal territory or by competing successfully for a breeding vacancy in their vicinity (i.e., within their 3 km search range, Walters et al., 1988). In case of competition for male vacancies, the oldest resident helper wins, as it invariably occurs in the real population (Walters, 1990; Daniels and Walters, 2000a). If no resident helpers are present, helpers from nearby territories and dispersing birds compete for the vacancy and the closest bird wins. Among equidistant competitors, the oldest bird wins. Competition for vacancies among females was based on age alone.

Mortality parameter values varied with sex and status class based on Walters (1990). The number of fledglings produced on a territory each breeding season depended on the probability of nesting successfully and the probable number of young fledged if successful. These parameters were calculated as functions of breeder age and number of helpers (Walters, 1990) (for equations and input parameters see Schiegg et al. (2005)). Variation in brood size was produced by generating the number of fledglings produced by a breeding pair in a given year as the mean of a normal distribution with a standard deviation estimated from empirical data (see Letcher et al. (1998) for additional justification of model parameters).

Demographic stochasticity was simulated by applying annual survival probabilities, annual status transition probabilities of male fledglings, and probabilities of producing different numbers of offspring to each individual. Non-emergent transition probabilities occurred when a random number drawn from a uniform distribution [0;1] was less than the appropriate transition probability value. Mortality probabilities and probabilities of producing different numbers of offspring varied annually reflecting environmental stochasticity. The variance in these parameters was estimated from 14 years of data from the North Carolina Sandhills population, and was drawn randomly each year from the resulting distribution to determine that year’s probability value.

2.2.2. Simulation of inbreeding depression
To incorporate inbreeding depression into the simulation model, we estimated the number of lethal equivalents (Morton et al., 1956) using demographic data collected from the
Sandhills and corresponding inbreeding coefficients as described above. A lethal equivalent is defined as "a group of detrimental alleles that would cause on average one death if homozygous" (Frankham et al., 2002). The probability of survival is dependent on inbreeding as follows:

\[ S = e^{-(A-B+F)} \]  

where \( S \) is the probability of survival, \( e^{-A} \) is fitness in an outbred population, \( F \) is the inbreeding coefficient, and \( B \) is a measure of the increased deaths due to inbreeding, i.e., the number of lethal equivalents per gamete (Hedrick, 1992). We estimated values for \( A \) and \( B \) for survival from egg to age one year, using data from 1985 to 2000 and one observation per nest (\( n = 2278 \)). We excluded observations prior to 1985 because that was the first year in which inbreeding was detected. We categorized each nest (with known clutch size) in each year into one of seven levels of inbreeding (i.e., the kinship coefficient of the breeding pair) and calculated the proportion of eggs that survived to age one for each nest. We then averaged these proportions within each level of inbreeding and performed a regression on the means weighted by sample size (\(-\ln S = 1.49 + 4.93 F; \) adj. \( R^2 = 0.77, n = 2278 \)), following Keller and Arcese (1998). The slope of this regression model (\( B = 4.93 \)) is the estimated number of lethal equivalents per gamete. To incorporate this level of inbreeding depression into the simulation model, we assigned all costs of inbreeding (rounded to five lethal equivalents) to production of fledglings, for simplicity. Annual mean number of fledglings per pair was reduced for related pairs by a value \( r \) (Hedrick, 1992), where

\[ r = 1 - e^{-(A-B+F)} \]

and \( F \) is the coefficient of kinship of the breeding pair, equal by definition to the inbreeding coefficient of the offspring (Falconer and Mackay, 1996). We treated breeding pairs with kinship coefficients <0.0625 as unrelated (\( F = 0 \)), because most pairs in populations simulated over long time periods will be at least distantly related (Daniels et al., 2000), and reproduction of distantly related pairs was not found to be significantly different than that of unrelated pairs in the real population (Daniels, 1997).

In calculating kinship coefficients for breeding pairs during a model simulation, all individuals were assumed to be unrelated at the beginning of each run. Once a new pair was formed during the course of a simulation, a kinship coefficient was calculated using a recursive path analysis algorithm and stored for later years to speed calculations.

### 2.2.3. Model runs

We used six landscapes differing in territory number (25, 49 or 100 territories) and aggregation (scattered or clumped). Our aim was to mimic features of current populations in terms of size and territory distribution.

Spatial arrangement of territories was set using the \( k \) parameter of the negative binomial distribution. The scattered arrangement was achieved by distributing territories randomly in the landscape and this distribution was used to define maximum \( k \). Minimum \( k \) was set by maximal spatial clumping of territories. Exact values of \( k \) were calculated by overlaying a grid, 4 km to a side, over the landscape, counting territory centres in each cell and using a maximum likelihood estimate of \( k \) (Bliss and Fisher, 1953). This process was repeated for each particular number of territories used in the simulations. To create the clumped aggregation level, we selected a \( k \) value 25% of the distance between \( \log k_{\text{min}} \) and \( \log k_{\text{max}} \) (also see Letcher et al., 1998).

Runs started with all territories being occupied, either by breeding pairs (90%) or by solitary males (10%). The number of helpers was set equal to half of the number of territories. Helper males were added to the landscape by assigning them to territories containing breeding pairs selected at random. Territories could be selected more than once, hence nearly half the territories had one helper, and a few had more than one, which mimicked the natural situation (Walters et al., 1988). No dispersing birds or fledglings were present initially. Each simulation was run over 100 years and was replicated 100 times. The stochastic algorithms included make each run unique and ensure statistical independence among replicated runs of the same treatment.

Classification of dispersal behaviour and calculation of natal dispersal distances were performed as in the empirical data set. To evaluate the impact of inbreeding depression on extinction probability and time to extinction, we conducted two sets of runs for each landscape. One set included inbreeding depression effects as described above, whereas the other did not.

### 2.3. Model sensitivity and suitability

Previous sensitivity analyses of a former model version that did not include inbreeding depression showed that model predictions were stable when basic input parameters varied by ±10% (Letcher et al., 1998) and a formal validation procedure indicated high predictive accuracy of the model even for complex output parameters such as distributions of dispersal distances or age of breeding individuals (Schiegg et al., 2005). We performed additional sensitivity analyses with the model version used here on the effect of inbreeding depression on extinction risk by conducting 100 runs with the two landscapes representing the extreme conditions (100 territories, clumped; 25 territories, scattered). When increasing/decreasing the effect of inbreeding depression by 10%, predicted extinction risk deviated from the nominal case by less than 0.45% in both landscapes. We therefore consider the model to be insensitive to small errors in estimates of inbreeding depression.

Models used to assess population viability under various environmental scenarios (PVA models) have been criticised to be only of limited use, because such models do not cover the entire range of potential (behavioural) responses to changes in resource availability and quality (Sutherland and Norris, 2002). In fact, performance of some PVA models has been poor when environmental conditions other than those used for model parameterisation are simulated (Bradbury and Payne, 2001). Here we use the model to explore extinction risk in relation to variation of territory location and inbreeding levels, which are both expected to cause responses on the individual and ultimately on the population level that are accounted for by the model algorithms. We are therefore confident that the predictions made for each scenario can be meaningfully compared to each other.
2.4. Statistics

2.4.1. Dispersal behaviour and distance (empirical data)
Our approach was to test whether an individual’s inbreeding coefficient was related to natal dispersal distance of its parents. The distribution of inbreeding coefficients was skewed due to many zeros (6255 of 7350 birds (85.1%) censused during the study period with \( F = 0 \)), which is to a large extent caused by our assumption that all individuals were unrelated at the beginning of the study (see above). We therefore used probability of being inbred (i.e., whether an individual’s inbreeding coefficient was zero or not) as the dependent variable in logistic regression models. Because natal dispersal distance was zero by definition for the philopatric class (i.e., for helpers that inherited their natal territory) we first tested whether offspring of philopatric parents were more likely to be inbred than young whose parents had dispersed. This was done by logistic regression with parental dispersal behaviour (philopatric or disperser) as a class and year as a continuous predictor variable. To explore a potential sex-specific effect of dispersal behaviour, we also included gender of the parent and its interaction with dispersal behaviour as additional predictor variables. The dependent variable was the probability of offspring being inbred.

We then tested for an effect of parental natal dispersal distance on the probability that offspring were inbred by using parental natal dispersal distance (if >0) and year as continuous independent variables in another logistic regression model. Because natal dispersal distance is larger in females than in males (Walters et al., 1988; Pasinelli et al., 2004), we analysed the sexes separately. Model fit was checked using residual analyses and likelihood ratios (Chatterjee and Price, 1991). If natal dispersal distances of both parents were available, one dispersal distance was randomly selected and used in the analyses (PROC SURVEYSELECT in SAS, using simple random sampling (SAS Institute Inc, 1999–2001)). This resulted in a sample size of 487 male and 958 female dispersal distances recorded in the years 1980–2001. Sample sizes for males are smaller than for females because the philopatric class has been removed from this data set. Results did not change, however, if individuals with natal dispersal distance = 0 were included.

2.4.2. Extinction probability and time to extinction (model data)
We defined extinction probability as the proportion of the 100 replicated model runs in which the simulated population went extinct before the end of the simulation, i.e., before 100 years. Time to extinction was the number of years these populations persisted, i.e., had at least one breeding pair. The influence of territory number (continuous variable), spatial arrangement (two levels: scattered or clumped) and inbreeding (two levels: whether simulations were performed with or without inbreeding depression) on extinction probability and time to extinction were tested with generalized linear models. Model fit was assessed by residual analyses (McCullagh and Nelder, 1989). Sample size was 1200 (3 landscape sizes \( \times 2 \) clumping levels \( \times 2 \) inbreeding levels inbreeding yes/no \( \times 100 \) replicates).

2.4.3. Effects of territory number and arrangement on inbreeding probability and dispersal distance (model data)
We used the set of runs including inbreeding effects described above to evaluate effects of population size and territory aggregation on the number of inbred birds \( (F > 0) \). Because several populations went extinct within 30 years of simulation (see below), we only analysed data from year 20. Results did not change when we repeated the analyses using data from year 10 instead of year 20. We used the proportion of inbred individuals per simulation as the dependent variable resulting in a potential sample size of 600 (3 landscape sizes \( \times 2 \) clumping levels \( \times 100 \) replicates). Because 120 populations went extinct before year 20, final sample size was 480. We included a logit link to account for binomial data (trial/events structure in SAS terminology: number of inbred birds versus total number of birds). To model natal dispersal distances as a function of population size and territory arrangement, we used median natal dispersal distance (by excluding philopatric individuals) per treatment and run as the dependent variable in a general linear model. All analyses were done with SAS 8.02 (SAS Institute Inc, 1999–2001).

3. Results

3.1. Probability of being inbred as a function of parental natal dispersal behaviour and dispersal distance
Inbreeding coefficients ranged between \( F = 0–0.280 \). Dispersal behaviour of parents, i.e., whether a parent bred on the natal territory or dispersed before breeding, did not affect probability of offspring being inbred (logistic regression, likelihood ratio test, \( \chi^2 = 0.13, df = 1, p = 0.715 \)), nor were there sex-specific effects (sex \( \times \) dispersal behaviour: \( \chi^2 = 0.23, df = 1, p = 0.631 \), \( n = 1669 \)). Likelihood of offspring being inbred increased with year \( (\chi^2 = 174.36, df = 1, p < 0.001, n = 1669 \) ). Because our sample was biased towards offspring with \( F = 0 \) (1354 out of 1669 individuals), we repeated these analyses with a data set that contained all offspring with \( F > 0 \) (\( n = 315 \)) and an equal number of offspring with \( F = 0 \) that were randomly selected from all offspring with \( F = 0 \). There was still no relation between parental dispersal behaviour and probability of offspring being inbred (dispersal behaviour: \( \chi^2 = 0.56, df = 1, p = 0.454 \), sex \( \times \) dispersal behaviour: \( \chi^2 = 0.23, df = 1, p = 0.629, n = 630 \) ).

In contrast, an individual’s inbreeding coefficient did depend on the natal dispersal distance of its mother, but not of its father (Table 1). The farther the mother had dispersed from the natal territory the less likely it was that her offspring were inbred. Again, year was positively related to likelihood of offspring being inbred.

3.2. Long-term stability of small populations
Extinction risk of simulated populations was significantly higher when inbreeding depression was included than when it was not (estimate \( \pm SE = 2.87 \pm 0.28; \chi^2 = 107.72, df = 1, p < 0.001 \)). Increased population size \( (\sim 4.01 \pm 0.45; \chi^2 = 77.94, df = 1, p < 0.001 \) ) and territory clumping \( (2.84 \pm 0.28; \chi^2 = 106.31, df = 1, p < 0.001, n = 1200 \) in all cases, Fig. 1) diminished probability of extinction. In simulations without inbreeding, territory clumping decreased extinction risk of populations containing
100 territories from 77% to 2%. However, when inbreeding depression was included in the simulation process, clumping reduced extinction risk only from 100% to 78% (Fig. 1).

Inbreeding also significantly reduced time to extinction (estimate ± SE = 7.32 years ± 0.82; $F = 79.12, p < 0.001$), while increasing population size (20.41 years ± 0.51; $F = 1613.87, p < 0.001$) and territory clumping ($-24.95$ years ± 0.82; $F = 919.58, p < 0.001, n = 993$ in all cases) increased time to extinction. Populations with a high extinction risk, i.e., very small, inbred populations with scattered territory arrangement, mostly went extinct within the first 40 years of simulation (Fig. 2). That time to extinction in populations containing 100 clumped territories was shorter in the absence of inbreeding depression is an artefact, because the value for populations without inbreeding depression was derived from only two populations (see Fig. 1, clumped territory arrangement, population size = 100). We conclude that inbreeding depression severely hampered persistence of small red-cockaded woodpecker populations.

### 3.3. Probability of being inbred as a function of spatial arrangement of territories

Increasing spatial clumping of territories led to a significant reduction in median natal dispersal distance in the simulated populations irrespective of their size (estimate ± SE = $-0.59$ ± 0.07; $F = 64.40, p < 0.001, n = 480$). The proportion of inbred individuals was higher when territories were clumped rather than scattered (estimate ± SE = 0.14 ± 0.04; $\chi^2 = 12.66, df = 1, p < 0.001, n = 480$).

### 4. Discussion

#### 4.1. Natal dispersal distance and probability of inbreeding

In our natural study population birds that remained on their natal territory to breed were not more likely to produce inbred offspring than were birds that dispersed from the natal territory. This finding is surprising and attests to the effectiveness of incest avoidance behaviour (Walters et al., 1988; Daniels and Walters, 2000a). Daniels and Walters (2000b) documented that females leave their breeding site when a son inherits breeding status on the territory. While such behaviour reduces inbreeding risk among familiar individuals on the natal site, dispersing females do not avoid territories held by closely related males with whom they were previously unfamiliar (Daniels and Walters, 2000b). As a consequence, we found a negative relationship between natal dispersal distance of the mother and the probability of her offspring being inbred. To our knowledge this is the first time that a quantitative

### Table 1 – Logistic model of the probability of an offspring being inbred as a function of parental natal dispersal distance (distance, km) and time (year)

| Parameter | DF | Females (N = 958) | | | Males (N = 487) | | |
|-----------|----|------------------|---|------------------|---|------------------|
|           |    | Estimate ± SE    | $\chi^2$ | p     | Estimate ± SE    | $\chi^2$ | p     |
| Intercept | 1  | -460.10 ± 44.50  | 106.87   | <0.001| -393.91 ± 59.37  | 44.03   | <0.001|
| Distance  | 1  | -0.06 ± 0.03     | 5.11     | 0.024 | -0.05 ± 0.04     | 2.19    | 0.139 |
| Year      | 1  | 0.23 ± 0.02      | 106.46   | <0.001| 0.20 ± 0.03      | 43.80   | <0.001|

Sexes are analyzed separately. Modelled was the probability that inbreeding occurred.
relationship between natal dispersal distance and inbreeding probability has been established empirically. Presumably this pattern is a result of the spatially restricted dispersal of helpers, who do not move beyond their neighbourhood (Walters et al., 1988; Daniels, 1997). Previously Daniels and Walters (2000b) showed that the probability that a female dispersing from her natal territory will encounter a related male declines once a female crosses a sufficient number of territories, and that dispersal distance increases when territory density decreases.

The positive association between year and likelihood of offspring being inbred suggests that inbreeding probability increases with time. However, this effect may instead be a consequence of our assumption that all birds were unrelated at the beginning of data collection.

4.2. Persistence of small red-cockaded woodpecker populations

Comparing population simulations with and without costs of inbreeding revealed that inbreeding depression significantly enhanced extinction risk of small red-cockaded woodpecker populations. Inbreeding also affected time to extinction, although this effect was less pronounced (Fig. 2). Most populations that went extinct did so within 40 years of simulation and within this time frame, inbreeding did not greatly accelerate this process. Our model of population dynamics was unusual and perhaps unique in that it simultaneously incorporated effects of territory aggregation, environmental and demographic stochasticity, and an empirically derived, species-specific estimate of inbreeding costs. Thus, this study provides evidence that inbreeding elevates extinction risk of small populations beyond levels induced by environmental or demographic stochasticity. Our results support those of Brook et al. (2002), who evaluated the role of inbreeding in extinction by conducting population viability analyses on 20 threatened species of various taxa. Inbreeding markedly decreased median times to extinction by 25–31% for populations ranging in size from 50 to 1000 individuals. Further, Spielman et al. (2004) compared heterozygosities of 177 threatened species with those of taxonomically related non-threatened species and found that in the majority of comparisons heterozygosities were lowered in the threatened taxa. They concluded that species generally are not driven to extinction before genetic factors become important.

Our simulations may underestimate the impact of inbreeding depression on population viability of red-cockaded woodpeckers. First, we ignored the known effect of inbreeding on timing of egg-laying (Schlegg et al., 2002a). Second, effects of genetic drift, which may diminish genetic variability and hence additionally increase inbreeding risk, were not considered. Finally, fitness costs of moderate inbreeding (F < 0.0625), if any exist, were not considered. On the other hand, our model does not allow for potential effects of purging, whereby recessive deleterious alleles are removed through natural selection (Frankham et al., 2001). The impact of purging on extinction risk is controversial (Miller and Hedrick, 2001), however, and in their review of inbreeding depression in wild populations, Keller and Waller (2002) suggest that purging has only small effects on inbreeding depression in fragmented populations (see also Brook et al., 2002).

Five lethal equivalents as used in this study represent a substantial cost of inbreeding, higher than those reported for other species (reviewed by Keller et al., 2002). Costs of inbreeding included in the calculations, however, vary greatly among studies, as different life stages are used in survival estimates. Keller and Arce (1999) calculated 3.21 lethal equivalents from egg to age one in an insular population of song sparrows Melospiza melodia when estimated as one unit egg to age one as we did here. Yet, we were conservative in our assessment of the consequences of inbreeding depression, both in the calculation of lethal equivalents and in assigning those costs in model simulations. We conclude that inbreeding depression poses a high risk for small populations of red-cockaded woodpeckers, and we further suggest that inbreeding costs and, consequently, the threat of those costs to population viability, may be higher for this and perhaps other species than currently recognized.

Short distances between territories have repeatedly been shown to be essential for the (demographic) stability of small red-cockaded woodpecker populations (Letcher et al., 1998; Schlegg et al., 2002b; Walters et al., 2002a), but these studies did not include possible negative effects of territory aggregation arising from inbreeding depression. Our simulation model tends to overestimate natal dispersal distances in both sexes (Schlegg et al., 2005). Given that real distances are even shorter and are negatively related to inbreeding risk at least in females, as shown above, the association of territory clumping and inbreeding may even be stronger than predicted here. Our results hence suggest that territory aggregation increases inbreeding and thus the benefits of short interterritorial distances may be lessened. On the other hand, extinction risk was still reduced by a clumped territory arrangement. We therefore suggest that measures to lower the risk of inbreeding should be undertaken, when spatial aggregation of territories is used to sustain small red-cockaded woodpecker populations.

4.3. Inbreeding in cooperative breeders

Avoidance of inbreeding is generally thought to be one of the major forces in the evolution of dispersal (Pusey and Wolf, 1996; Perrin and Goudet, 2001). Our empirical data reveal how increasing natal dispersal distances enhances the chance of mating with an unrelated partner, thereby reducing the odds of incurring fitness costs due to inbreeding. Nevertheless, natal dispersal distances in red-cockaded woodpeckers and other cooperatively breeding bird species are very short in general (Zack, 1990; Emlen, 1991), suggesting the existence of benefits of short distance dispersal that outweigh costs of inbreeding. Benefits of short distance dispersal may include competitive advantages in obtaining breeding vacancies (Zack and Rabenold, 1989), which usually are scarce in cooperative breeders. Further, territory owners usually are less aggressive towards related neighbours (Watson et al., 1994), and may even share parts of the territory to gain inclusive fitness benefits by enabling a relative to breed (Perrin and Goudet, 2001). Also, short distance dispersal, by maintaining low levels of inbreeding, may increase inclusive
fitness benefits to helpers, which are essential for the maintenance of cooperative behaviour by kin selection (Stevens and Wiley, 1995). Finally, previous work revealed that lifetime production of fledglings declines with increasing dispersal distance in red-cockaded woodpeckers (Pasinelli et al., 2004).

4.4. Conclusions

Consideration of reductions in fitness due to inbreeding is still the exception rather than the rule in population viability analyses. We recommend including an estimate of inbreeding depression in stochastic models whenever possible and using sensitivity analyses to assess potential impacts of inbreeding on population persistence.

Our findings raise particular concern about the persistence of the red-cockaded woodpecker. Because most of the remaining populations contain fewer than 80 breeding groups (USFWS, 2003), immigration is rare or nonexistent (Conner et al., 2001) and dispersal is restricted, this species is especially prone to inbreeding accumulation. We hence recommend increasing efforts to reduce the potential for inbreeding in the management regime for the red-cockaded woodpecker, especially when spatial clumping of territories is used to facilitate dispersal within populations. For instance, the size of extant populations can be enlarged by creating artificial cavities (Walters, 1991) provided that suitable habitat is available. This strategy is already applied successfully in several populations (Watson et al., 1995; USFWS, 2003; Costa, 2004). Increasing connectedness between populations may be another option, but would require in most cases the reforestation of residential areas. Finally, we support the recommendation in the species’ Recovery Plan (USFWS, 2003) to translocate individuals between populations to reduce inbreeding levels.

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