Inbreeding in small populations of red-cockaded woodpeckers: insights from a spatially explicit individual-based model

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ABSTRACT

Inbreeding depression can be a critical factor affecting viability of small populations and may be especially dangerous in combination with demographic and environmental stochasticity. For species with fragmented habitats and declining, isolated populations, estimating the threat of inbreeding depression is an urgent conservation need. In previous work, we documented inbreeding depression in a wild population of red-cockaded woodpeckers, an endangered, co-operatively breeding species that was once widespread but is now restricted to remnant patches of mature pine savannas in the south-eastern United States. Here, we investigated how rapidly inbreeding accumulates in red-cockaded woodpecker populations of varying size and with varying rates of immigration, using a spatially explicit individual-based simulation model of population dynamics. With this approach, we were able to assess the accumulation of inbreeding in the presence of environmental and demographic stochasticity, while also accounting for effects of the complex social system and extremely restricted dispersal of our study species. We found several meaningful results: (1) most populations were declining, (2) substantial inbreeding accumulated in small, declining populations with limited immigration, due mainly to high percentages of closely related pairs (numbering from 40% to 100% of all pairs after 50 years) and (3) moderately high levels of immigration (two or more migrants per year, equalling four effective migrants per generation) were required to stabilise small declining populations and obtain a mean inbreeding level under 0.10. We conclude that inbreeding depression is a very serious threat to the viability of the many small, isolated and declining populations of red-cockaded woodpeckers.
INTRODUCTION

Loss of genetic variation is a fundamental process of small isolated populations. Such loss may affect population viability through inbreeding depression and/or reduced evolutionary potential (e.g. Frankel & Soulé, 1981; Shaffer, 1981; Allendorf & Leary, 1986; Lande & Barrowclough, 1987; Lacy, 1997; Frankham, 1998). Although researchers have debated the relative importance of genetic, demographic and environmental effects on short-term population viability (e.g. Lande, 1988; Pimm et al., 1988; Schemske et al., 1994), inbreeding depression can be a critical factor in population extinction and may be especially dangerous in combination with demographic and environmental stochasticity (Gilpin & Soulé, 1986; Mills & Smouse, 1994; Frankham, 1995a, 1998; Lacy, 1997; Haig, 1998). Moreover, some authors have recently argued that genetic and non-genetic factors should not be viewed separately in viability assessment (Mills & Smouse, 1994; Lacy, 1997).

Evidence of inbreeding depression in wild populations is continually accumulating (e.g. Bensch et al., 1994; Kempenaers et al., 1996; Pusey & Wolf, 1996; Keller, 1998). In fact, costs of close inbreeding may be common or even universal. Lacy (1997) argued that for mammals, all studies that used appropriate statistical methods on adequate sample sizes have reported evidence of inbreeding depression. Similarly, Daniels & Walters (1999) held that, in studies of inbreeding depression in birds, reduced hatching rate was found in every species for which it was assessed. For species with fragmented habitats and declining, isolated populations, estimating the threat of inbreeding depression to population viability is an urgent conservation need. The development of new, holistic approaches – assessing genetic, non-genetic and interactive effects simultaneously – is especially critical given current landscape conditions.

Processes of population genetics are well understood in theory (e.g. Wright, 1931, 1943, 1951, 1978), but application of genetic theory to wild populations remains challenging. We need to better identify impacts of the loss of genetic variation on individual fitness and population viability. Documentation of inbreeding depression in wild populations is one small but difficult step towards this goal. Other valuable approaches to this problem include investigation of genetic impacts in extinction of island species (Frankham, 1998), theoretical models of accumulation of deleterious mutations (Lynch & Gabriel, 1990; Lande, 1994) and population-viability models incorporating genetic and non-genetic factors (e.g. Mills & Smouse, 1994). However, we also need to better understand how genetic variation is
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actually lost in wild populations. We know that loss of variation is a complex process affected by population size, demography, social and spatial structure, immigration rates and selection (Wright, 1951; Allendorf, 1983; Chepko-Sade & Halpin, 1987; Soulé, 1987; Lacy, 1997; and many others), but most theoretical and simulation models to date are unable to assess such factors simultaneously. Identifying rates of loss in natural populations can be enhanced by: (1) long-term field studies of marked individuals to collect appropriate and accurate demographic data, and (2) modelling techniques that incorporate complex social behaviour, spatial factors and demographic and environmental stochasticity.

Here we explore the potential effect of inbreeding on the population viability of the endangered, co-operatively breeding red-cockaded woodpecker (Picoides borealis). We first review our previous findings of inbreeding depression in this species. We then simulate the accumulation of inbreeding in small populations over time, using an individual-based, spatially explicit model of population dynamics developed recently by our research group (Letcher et al., 1998). We explore effects of various immigration rates and initial population sizes on inbreeding levels. These simulations reflect inbreeding in natural populations as accurately as currently possible, because the model incorporates complex social behaviour, spatially restricted dispersal and subsequent non-random mating, and environmental and demographic stochasticity. Lastly, we compare simulated rates of inbreeding with those expected from random mating within the simulated populations, using Wright's (1931, 1951) mathematical inbreeding models and a previous estimate of the ratio of effective population size to census population size (Reed et al., 1993) for this species. This work is an important contribution to the study of viability of small populations for several reasons. As emphasised, we assess inbreeding levels in the presence of demographic and environmental effects, while including complex social and spatial factors. Also, we use pedigree analysis, a rare but important approach to the study of genetic variation in natural populations. Finally, our work is based on a uniquely powerful data set collected over 15 years from a large, individually marked population (Walters et al., 1988a; Letcher et al., 1998). This study is only a first step, however, in identifying the relationships among inbreeding depression, environmental and demographic effects and population viability. Future work will incorporate declining survival and productivity due to inbreeding depression directly into the population simulations.
Red-cockaded woodpeckers

Red-cockaded woodpeckers are endemic to mature pine woodlands and savannas of the south-eastern United States. Historically, an estimated 3 million or more red-cockaded woodpeckers were distributed continuously throughout the south-east (Conner et al., in press); today, there are roughly 9000 birds, many of which exist in small, isolated populations in remnant patches of natural pine ecosystems (James, 1995). Red-cockaded woodpeckers are permanent residents, restricted to mature pines because of their unusual habit of excavating nesting and roosting cavities in live, rather than dead or decaying, pines (Jackson & Jackson, 1986).

The presence of a critical resource – cavities – is considered the primary basis for co-operative breeding in red-cockaded woodpeckers (Walters et al., 1992). In this co-operative breeding system, roughly half of male fledglings remain on their natal territory as helpers; these birds assist in raising young in subsequent years and commonly inherit a breeding position on their natal territory (Walters et al., 1988a; Walters, 1990). Female fledglings rarely remain on their natal territory. Natal dispersal distances for both sexes are extremely short: male and female fledglings disperse an estimated median distance of one and two territories respectively (Daniels, 1997). Long-distance movements by females between populations have been documented (e.g. Walters et al., 1988b), although this behaviour appears to be rare.

Inbreeding depression and avoidance in red-cockaded woodpeckers

Red-cockaded woodpeckers are one of the few species in which both inbreeding-avoidance behaviours and inbreeding depression have been documented. In our study population in south central North Carolina, we found inbreeding-avoidance behaviours exhibited by sub-adult and breeding females. Female fledglings rarely remain on their natal territory, but they remain less often if there are closely related breeding males present in the following year (Daniels & Walters, in press). Similarly, breeding females disperse in over 90% of cases in which their sons became breeders on their territories (Walters et al., 1988a). In this same population, close inbreeding results in substantial fitness costs. Closely related pairs (kinship coefficient ≥ 0.125) produced 44% fewer yearlings per year than did unrelated pairs (Daniels & Walters, in press). This difference in overall reproduction was the result of two separate effects: reduced hatching rates and lowered survival of fledglings. The substantial cost of close inbreeding, supported by evidence of inbreeding avoidance, prompts concern about the
effect of inbreeding depression on the viability of the many small, isolated and declining populations of red-cockaded woodpeckers (Daniels & Walters, in press).

**The individual-based, spatially explicit simulation model**

Individual-based, spatially explicit models provide information about population dynamics by tracking the performance, fate and locations of individuals (DeAngelis & Gross, 1992; Judson, 1994; Dunning et al., 1995). Individual behaviour is dictated by a set of rules that reflect the known biology of the species. Thus, these models are unique in their ability to incorporate complex social behaviour and spatially heterogeneous environments (DeAngelis & Gross, 1992). For red-cockaded woodpeckers, an individual-based, spatially explicit approach is able to simulate the delayed and spatially restricted dispersal behaviour of helpers, their failure to reproduce in the first and sometimes subsequent years, and the effects of extremely short dispersal distances of both sexes on demography and kinship structure. Letcher et al. (1998) developed such a model for red-cockaded woodpeckers and used it to assess effects of territory dispersion on the viability of populations of various sizes. In this study, we use the same model to examine inbreeding processes in the presence of stochastic, social and spatial factors.

**METHODS**

**Study population and data collection**

Demographic data used to construct the model were collected between 1980 and 1994 from a marked population of red-cockaded woodpeckers in south central North Carolina. By 1982 virtually all groups (roughly 220) within the 110 000-ha study area were being monitored. Individuals were banded with a unique colour combination and reproduction of all groups was monitored, from clutch size to number of fledglings. Most birds were banded as nestlings, and each breeding season all group members were identified and their status (breeder, helper, floater) determined based on behavioural observations and/or relative age. Further information on the study species, study area and methods of data collection is given elsewhere (Walters et al., 1988a).

**Model description**

Here we briefly describe the individual-based, spatially explicit model of
population dynamics in red-cockaded woodpeckers: further details, including input parameter values and illustrations of the spatial arrangement of territories, are available in Letcher et al. (1998). In each simulation, territories are fixed in space and separated by non-breeding space that the birds must cross. Territories are lost if unoccupied for more than five consecutive years, and new territories may be created by territorial budding (Hooper, 1983), a process of territory splitting for which each territory has a 1% probability annually. Both features mimic territory dynamics observed in the North Carolina study population. The number of territories and the level of clumping (the measure of dispersion) of these territories are determined prior to each model run. The size of the landscape is fixed, and therefore the density of territories within the landscape depends upon the number of territories.

Males and females behave according to separate sets of rules. Female fledglings disperse, and male fledglings either remain as helpers or disperse. Dispersing birds move in a random direction, and continue in that direction at a specified rate until they die, obtain a breeding position, or leave the population. Each time-step (three months), dispersing birds and helpers remaining on their natal territory compete for any breeding vacancy within 3 km. Helpers remain on their natal territory as helpers until they fill a breeding vacancy or die, and the oldest helper inherits the natal territory if a vacancy arises. Males compete for empty territories as well as breeding vacancies, and the closest male within the search radius wins. Females compete for breeding vacancies in territories that contain a male, and the oldest female within the search radius wins. Females do not pair with fathers or sons. Only pairs on territories produce offspring, because red-cockaded woodpeckers are monogamous (Haig et al., 1993a, 1994). Reproduction consists of the probability of nesting successfully and the probable number of fledglings produced from successful nests; both are functions of breeder age and the number of helpers. Mortality rates are specific to each status class (breeder, helper, etc.), and birds die if a deviate from a random uniform distribution is less than the probability of mortality. Mean probabilities of mortality and fecundity change annually; these probabilities are drawn each year from a normal distribution with a mean and variance as observed in 15 years of data collected from the study population. Recent additions to the model (and therefore not described in Letcher et al., 1998) include territorial budding and environmental stochasticity as described above.

In summary, model input parameters estimated from the study population include stage-based mortality and fecundity. Behaviours that are ob-
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served in nature and simulated in the model include avoidance of close inbreeding by females, delayed dispersal and reproduction of male helpers, the helper search radius, and monogamy, among others. Other behaviors simulated in the model, such as dispersal speed, dispersal direction and the search radius for dispersing birds, are approximations based on experience and judgment rather than directly supported by data. Emergent properties of the model include dispersal distance, recruitment of fledglings and helpers into the breeding population, population growth rate and net gain or loss of territories, among many others.

Model runs
We performed two sets of model runs to explore the effects of population size and immigration rate on the accumulation of inbreeding in this species. The first set of runs included three population sizes, referred to by initial number of territories rather than individuals: 25, 49 and 100 initial territories. Each of these three simulations (25, 49 and 100 initial territories) was continued for an arbitrary duration of 50 years and replicated 20 times. 50 years is equivalent to 12.5 generations, because estimated generation length in this species is roughly four years (Reed et al., 1988a). The second set of runs included two population sizes: 25 and 49 initial territories, and five levels of immigration: 0.125, 0.25, 0.5, 2 and 4 migrants per year. All migrants were female floaters, 1.75 years of age, and were placed in a random location on the edge of the smallest square that bounds all territories within the model landscape. Migrants had to compete for breeding positions and did not always reproduce; the effective number of migrants was roughly half (52%) of the absolute number of migrants.

Initial conditions were the same for all runs. We used a moderate level of territory clumping. Of all initial territories, 90% were inhabited by a breeding pair, and the remaining 10% contained an unpaired male. The initial number of helpers was equal to half the number of territories; roughly half of the territories with breeding pairs received one helper and a few received more than one helper. Ages of initial breeders were randomly assigned but were designed to reproduce the age distribution of the study population in 1991, a typical year (J. R. Walters et al., unpublished data). No dispersing birds or fledglings were present initially, so that all dispersal and reproduction emerged during simulations.

Analyses of population persistence and demographic status
We described the persistence of populations of varying size and immigration rates by calculating the percentage of the 20 replicates in each treat-
ment that had at least one successfully breeding pair remaining after 50 years (percentage replicates surviving). We described the demographic status (declining, stable or increasing) of these populations by calculating mean annual growth rate, mean percentage of initial territories that were occupied within the last five years (percentage territories surviving) and mean number of pairs successfully breeding in year 50 in surviving replicates.

Analyses of inbreeding

We constructed a pedigree file for each run containing all individuals and their parents. We then calculated coefficients of kinship for successfully breeding pairs using the SAS procedure, PROC INBREED (SAS, 1997). The coefficient of kinship between two individuals is the probability that two gametes taken at random, one from each, contain alleles that are identical by descent from a common ancestor (Falconer, 1989). By definition, the kinship coefficient of a breeding pair is equal to the inbreeding coefficient of its offspring. We averaged kinship coefficients for all successfully breeding pairs first by year within each replicate, then by year among the 20 replicates. Only successfully breeding pairs were included in these averages because the pedigree contained only individuals and their parents, not all known pairs. In this way, we estimated the average kinship coefficient between successfully breeding pairs. We refer to this measure as mean kinship of pairs; it should not be confused with mean kinship as defined by Lacy (1995) and others, which refers to the mean of kinship coefficients between a given individual and all others in the population. Other variables estimated by averaging among replicates were percentage of all successfully breeding pairs that were closely related (kinship coefficient ≥ 0.125), moderately related (kinship coefficient 0–0.125) and unrelated (kinship coefficient = 0).

We compared the accumulation of inbreeding estimated by pedigree analysis with that expected from random mating within the simulated populations. Expected inbreeding based on random mating was calculated using Wright’s (1931, 1951) mathematical models for inbreeding over time,

\[
F_t = \frac{1}{2} N_e + \left(1 - \frac{1}{2} N_e\right) F_{t-1} \quad (8.1)
\]

\[
F_t = \frac{1}{2} N_e + \left(1 - \frac{1}{2} N_e\right) F_{t-1} \times (1 - m)^2 \quad (8.2)
\]

where \( F \) is the inbreeding coefficient, \( t \) is the generation, \( N_e \) is the effective population size and \( m \) is the proportion of \( N_e \) that are migrants. Effective population size was computed every generation (four years: Reed et al.,
1988a) by adjusting the simulated population size by 0.725, a ratio of effective to breeding population size \( N_e/N \) recommended by Reed et al. (1993) for this species. Thus, changes in simulated population sizes were incorporated into inbreeding estimated with Wright's models. Unpaired males and helpers were not included in the breeding population size nor in Reed et al.'s (1993) estimate of \( N_e/N \). Effective migration, for Wright's island (migration) model, was estimated as half the absolute number of migrants in each generation. Migrants are assumed to be unrelated to each other and to the recipient population, in both Wright's island model and our simulated pedigrees.

**RESULTS**

**Population status and persistence**

Mean annual growth rates, mean percentage of territories surviving 50 years, percentage of replicates surviving 50 years and mean number of successfully breeding pairs in year 50 are presented in Table 8.1 for all population treatments. Closed populations of 25 and 49 initial territories declined steadily in size, with average growth rates of 0.962 and 0.956 respectively. For these populations, only 30% and 75% of replicates survived 50 years. In contrast, the closed population of 100 territories was stable, with a growth rate of 0.994 and 100% of replicates surviving. For simulations including immigration, populations of 25 and 49 initial territories showed declines at all immigration levels of less than two migrants per year. With two or four migrants per year, these populations exhibited relatively stable average growth rates (≥0.990), and 80% to 90% of replicates survived 50 years.

**Inbreeding**

For closed populations of 25, 49 and 100 initial territories, mean kinship of successfully breeding pairs increased somewhat linearly through the simulated 50 years, with final values of 0.33, 0.20 and 0.09 respectively (Fig. 8.1). Variation in mean kinship of pairs declined as population size increased: standard deviations in the final year for 25, 49 and 100 initial territories were 0.14, 0.10 and 0.02 respectively (Fig. 8.1).

For the closed population of 25 initial territories, mean kinship of pairs as estimated from simulated pedigrees was less than expected inbreeding based on Wright's model (1931, 1951) and an \( N_e/N \) of 0.725 (Reed et al., 1993) (Fig. 8.1). This population was severely declining: mean number of successfully breeding pairs in remaining replicates was less than five (Table 8.1). For populations of 49 initial territories, pedigree analysis and Wright's
<table>
<thead>
<tr>
<th>Initial number of Territories</th>
<th>Migration Rate(^a) (migrants per year)</th>
<th>Population growth rate ((\lambda \pm SD))</th>
<th>Percentage territories surviving ((\text{mean} \pm \text{SD}))</th>
<th>Percentage Replicates surviving</th>
<th>Number of successfully breeding pairs remaining(^b) ((\text{mean} \pm \text{SD}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>25</td>
<td>0</td>
<td>0.915 ± 0.043</td>
<td>12.6 ± 21.1</td>
<td>30</td>
<td>45 ± 4.3</td>
</tr>
<tr>
<td>25</td>
<td>0.125</td>
<td>0.904 ± 0.037</td>
<td>7.4 ± 15.7</td>
<td>15</td>
<td>3.7 ± 3.8</td>
</tr>
<tr>
<td>25</td>
<td>0.25</td>
<td>0.929 ± 0.037</td>
<td>14.6 ± 24.1</td>
<td>50</td>
<td>2.3 ± 3.1</td>
</tr>
<tr>
<td>25</td>
<td>0.5</td>
<td>0.946 ± 0.040</td>
<td>26.8 ± 26.3</td>
<td>60</td>
<td>4.8 ± 2.9</td>
</tr>
<tr>
<td>25</td>
<td>2</td>
<td>0.990 ± 0.014</td>
<td>70.8 ± 36.0</td>
<td>80</td>
<td>10.5 ± 5.4</td>
</tr>
<tr>
<td>25</td>
<td>4</td>
<td>0.999 ± 0.007</td>
<td>88.4 ± 29.0</td>
<td>80</td>
<td>14.1 ± 5.1</td>
</tr>
<tr>
<td>49</td>
<td>0</td>
<td>0.956 ± 0.038</td>
<td>34.3 ± 29.2</td>
<td>75</td>
<td>11.9 ± 8.5</td>
</tr>
<tr>
<td>49</td>
<td>0.125</td>
<td>0.959 ± 0.038</td>
<td>36.5 ± 29.7</td>
<td>80</td>
<td>11.9 ± 8.6</td>
</tr>
<tr>
<td>49</td>
<td>0.25</td>
<td>0.969 ± 0.031</td>
<td>44.3 ± 26.5</td>
<td>90</td>
<td>12.6 ± 6.7</td>
</tr>
<tr>
<td>49</td>
<td>0.5</td>
<td>0.966 ± 0.036</td>
<td>39.3 ± 26.3</td>
<td>95</td>
<td>9.9 ± 7.3</td>
</tr>
<tr>
<td>49</td>
<td>2</td>
<td>0.990 ± 0.009</td>
<td>67.7 ± 21.0</td>
<td>90</td>
<td>17.7 ± 7.3</td>
</tr>
<tr>
<td>49</td>
<td>4</td>
<td>0.993 ± 0.009</td>
<td>70.6 ± 24.0</td>
<td>90</td>
<td>22.0 ± 8.5</td>
</tr>
<tr>
<td>100</td>
<td>0</td>
<td>0.994 ± 0.008</td>
<td>83.6 ± 23.5</td>
<td>100</td>
<td>46.8 ± 16.8</td>
</tr>
</tbody>
</table>

\(^a\)Migration rate is the absolute, not effective, number of migrants per year; all migrants are female.

\(^b\)Number of successfully breeding pairs remaining is substantially lower than percentage territories surviving because the latter includes unoccupied territories not yet labeled abandoned, territories occupied by solitary males and territories occupied by unsuccessfully breeding pairs.
Fig. 8.1. Mean kinship coefficient between pairs of red-cockaded woodpeckers calculated from simulated pedigrees (open circles, ± SD) compared to inbreeding coefficients based on Wright's mathematical model (closed circles) for populations of 25, 49 and 100 initial territories and no immigration.

model gave similar results, and for 100 initial territories pedigree kinship of pairs was higher than Wright's estimate of inbreeding (Fig. 8.1).

Figure 8.2 illustrates the mean percentage of successfully breeding pairs that were closely related, moderately related and unrelated, for 25, 49 and 100 initial territories with no immigration. Mean percentage of closely related pairs increased in all treatments, but rose much less rapidly in the population of 100 territories. Final values for mean percentage of closely related pairs were 100, 70 and 19 for 25, 49 and 100 initial territories respectively. No unrelated pairs remained after 50 years at any population size. Moderately related pairs contributed more than closely related pairs to
Fig. 8.2. Mean percentage of successfully breeding pairs of red-cockaded woodpeckers that were closely related (hatched), moderately related (dotted) and unrelated (open) in simulated closed populations of (A) 25, (B) 49 and (C) 100 initial territories.

the mean coefficient of kinship in simulated populations of 100 initial territories, but the reverse was true for simulated populations of 25 and 49 initial territories. Also, percentage of related pairs was much less variable across replicates of the largest population size, as expected.

Effects of immigration on the accumulation of inbreeding over time are presented in Fig. 8.3. Mean kinship of pairs, as estimated from simulated pedigrees, rises above 0.10 for all immigration rates of less than two migrants per year, and remains below 0.10 for immigration rates of two and four migrants per year for both population sizes. Variation among repli-
icates of mean kinship between pairs decreased with increasing immigration.

Inbreeding estimated using Wright's models was higher than pedigree kinship of pairs for populations of 25 initial territories and low immigration rates (Fig. 8.3.) In these simulations, very few pairs remained at the end of the runs and immigration events sharply reduced mean kinship between pairs. Expected inbreeding under Wright's model is slightly lower than pedigree kinship of pairs in simulations of two and four migrants per year. However, Fig. 8.3 indicates that these populations receiving two and four migrants per year reach an equilibrium level of inbreeding fairly rapidly; that is, within 20 to 30 years. Equilibrium inbreeding is similar between populations of 25 and 49 initial territories, which is consistent with Wright's (1951) theory.

The effect of immigration on the mean percentage of closely related pairs is presented in Fig. 8.4. For both population sizes, there was a substantial reduction in the mean percentage of closely related pairs only when the number of migrants was two or more per year. For immigration rates of two or more migrants per year, mean percentage of closely related pairs was less than 20% in both population sizes. For immigration rates of one migrant every two years or less, mean percentage of closely related pairs was 60% or greater after 50 years in populations of 25 initial territories and roughly 40% after 50 years in populations of 49 initial territories.

**DISCUSSION**

Perhaps the major strength of this study is in the approach: we used a spatially explicit individual-based model, based on abundant demographic data, to simulate the accumulation of inbreeding in small populations. Thus, we were able to incorporate spatial structure and complex social behaviour as well as demographic and environmental variation into population models. This novel approach gave several meaningful results: (1) most populations were declining; (2) substantial inbreeding accumulated in small, declining populations with limited immigration, due mainly to high percentages of closely related pairs (numbering from 40% to 100% of all pairs after 50 years); (3) moderately high levels of immigration (two or more migrants per year, equalling four effective migrants per generation) were required to stabilise small declining populations and obtain a mean inbreeding level under 0.10; and (4) inbreeding predicted by population-genetics theory was fairly similar to that of our simulated populations, and cases in which the two approaches differed were consistent with known
Mean Kinship Coefficient of Pairs

Time (years)
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Fig. 8.4. Mean percentage of successfully breeding pairs of red-cockaded woodpeckers that were closely related in populations of (A) 25 and (B) 49 initial territories with 0.125, 0.25, 0.5, 2 and 4 migrants per year.

biology. However, this last result has an important caveat: when estimating inbreeding based on population-genetics theory, we accounted for simulated declines in population size. These results are discussed below, followed by an exploration of their implications for conservation.

Declining population size

All populations of 49 initial territories or fewer declined in size unless the number of immigrants was two or more per year. Prior use of the simulation model (Letcher et al., 1998; J. R. Walters et al., unpublished data) identified the dispersion of territories within the model landscape as well as population size as primary factors influencing population growth. Letcher et al. (1998) concluded that severely reduced dispersal, especially that of helper males, has profound influence on the population dynamics of red-
cockaded woodpeckers. Such a constraint has strong implications for management and reinforces the need to use a spatially explicit model to investigate population processes. We used a moderate amount of dispersion, or territory clumping, in our simulations. Dispersion of territories in wild populations has not yet been measured but probably varies a great deal, and so we chose an intermediate value. The decline exhibited by several of our simulated populations is, sadly, a characteristic of many natural populations of red-cockaded woodpeckers at the present time (Costa & Escano, 1989; Conner & Rudolph, 1991; James, 1991, 1995).

**Accumulation of inbreeding**

A small, declining and isolated population of red-cockaded woodpeckers will rapidly accumulate extremely high levels of inbreeding, despite avoidance of parent–offspring matings. Populations at risk of extremely high inbreeding have roughly 50 or fewer territories, mean annual growth rates of roughly 0.07 or less and immigration rates below two migrants per year (one effective migrant per year). Populations containing greater than 50 but less than 100 initial territories were not evaluated here.

For small declining populations (less than 50 initial territories), closely related pairs contributed a significant portion of mean kinship between pairs. A larger, stable population (100 initial territories) consisted mainly of moderately related pairs, as may be expected. Reproduction of closely related pairs of red-cockaded woodpeckers in North Carolina is severely compromised (Daniels & Walters, in press), but whether the fitness of moderately related pairs is reduced in proportion to their kinship coefficient remains in question. Hatching rate, for example, was reduced for closely related pairs but did not appear to be a linear function of the kinship of pairs in our study population (Daniels & Walters, in press). Further research into the genetic basis of inbreeding depression and its impact on moderately related pairs is required before the relationship between fitness and inbreeding is fully understood for this species. In the meantime, we suggest that the percentage of closely related pairs in a population may be a better measure of vulnerability to inbreeding than mean levels of inbreeding or kinship. This suggestion has no use in situations wherein kinship is unknown, but it may be important in future models or for researchers and managers of marked populations.

**Comparison of pedigree analysis with population-genetics theory**

Differences between kinship estimated through pedigree analysis and inbreeding estimated using Wright’s model suggest non-random mating in
both very small and fairly large populations of red-cockaded woodpeckers. Kinship of pairs in very small populations may be lowered by inbreeding avoidance. The level of inbreeding avoidance built into the model mimics that observed in nature: females avoid mating with fathers and sons. Such inbreeding avoidance may result in greater mating success for immigrants than for residents in these extremely small populations. Conversely, kinship of pairs in fairly large populations is higher than that expected under random mating, probably because reduced dispersal distance results in a subdivided genetic structure. Blackwell et al. (1995) found similar evidence of subdivision by comparing inbreeding calculated through pedigree analysis with that expected from Reed et al.'s (1993) estimate of effective population size for a large portion (roughly 150 groups) of the North Carolina population. Finally, fairly small populations (near 50 territories) appear to be randomly mating. However, viability of these populations is still sensitive to changes in territory dispersion (Letcher et al., 1998; J. R. Walters et al., unpublished data), suggesting that disrupted dispersal can affect demography even though mating appears to be random. Together, these results underscore the need to use a spatially explicit model to address population viability and population genetics in this species.

When used to assess the effect of immigration on inbreeding levels, both pedigree analysis and Wright’s model lead to the conclusion that inbreeding is fairly low if there are two or more migrants per year (one effective migrant or more per year). This is in close agreement with Wright’s island model of equilibrium inbreeding (Wright, 1951; Crow & Kimura, 1970).

\[ F_{eq} = \frac{1}{4N_em + 1} \]  
(8.3)

where \( N_em \) is the number of effective migrants per generation in a stable population. Four effective migrants per generation leads to an equilibrium inbreeding level of 0.06, very close to what we calculated from pedigree data after 50 years for both population sizes.

Wright’s island model is generally used to say that differentiation between two populations will be minimal if they exchange one migrant per generation in each direction (Falconer, 1989). More specifically, for ideal populations that exchange one migrant per generation, fixation of alleles is minimised while allele frequencies are allowed to diverge (Wright, 1931; Crow & Kimura, 1970; Allendorf & Phelps, 1981; Mills & Allendorf, 1996). In natural populations, more migrants may be necessary to achieve this level of connectivity (Wright, 1931; Mills & Allendorf, 1996). Recent applications of the one-migrant-per-generation concept (reviewed by Mills & Al-
lendorf, 1996) include its recommended use to eliminate inbreeding depression (Triggs et al., 1989; Gogan, 1990). Our study shows that, for red-cockaded woodpeckers, such a low rate of immigration will not reduce inbreeding. Rather, an effective immigration rate of four migrants per generation or higher is necessary to stabilise small, declining populations and keep inbreeding rates at reasonable levels.

**Implications for conservation**

Declining population sizes and rapidly increasing percentages of closely related pairs in many of our simulations suggest that small populations of red-cockaded woodpeckers are highly vulnerable to extinction from interacting genetic, demographic and environmental effects. To show this more clearly, we need to incorporate documented levels of inbreeding depression into population simulations. In a viability analysis of an extremely small, heavily managed population of red-cockaded woodpeckers, Haig et al. (1993b) found that hypothetical inbreeding depression dramatically increased the population’s probability of extinction. The model they used was individual-based but not spatially explicit.

Our analyses of inbreeding depression in this species were performed on data collected from one of the largest remaining populations of woodpeckers. It is possible that inbreeding depression may be reduced in small populations through selection against detrimental recessives, although the ability of selection to lower genetic load is under current debate (Fu et al., 1988; Hedrick, 1994; Ballou, 1997; Willis & Wiese, 1997; Lacy & Ballou, 1998). The reduction of genetic load through selection is entirely dependent on the genetic basis of inbreeding depression, which is not well understood and may vary among taxa (Hedrick, 1994; Lacy & Ballou, 1998).

Further research is required to determine the extent of inbreeding depression in the many small populations of red-cockaded woodpeckers (Daniels & Walters, in press). Although previous studies of allozyme variation (Stangel et al., 1992) and fluctuating asymmetry (Stangel & Dixon, 1995) in red-cockaded woodpeckers have failed to find strong evidence of highly inbred populations, our simulations indicate that high inbreeding is likely; therefore we feel management recommendations are justified.

Earlier research has yielded powerful management tools, such as periodic burning and intensive cavity management, that can be immensely effective in reversing the decline of red-cockaded woodpecker populations if properly used (Walters, 1991; Conner et al., in press). Prior application of the individual-based, spatially explicit model has underlined the woodpeckers’ need for tightly clustered territories (Letcher et al., 1998), and
managers can fulfill this need by appropriate placement of new cavities. Prior use of the model also indicated that very small populations can be surprisingly persistent, given a tight clustering of territories, and therefore should not be abandoned as lost causes (Letcher et al., 1998; J. R. Walters et al., unpublished data). Haig et al. (1993b) came to a similar conclusion concerning the viability of a critically endangered woodpecker population, and Stangel et al. (1992) stressed that small populations are important both as genetic reservoirs and as stepping-stones between other populations.

Thus, small populations are important and management tools are available to give small populations a reasonable chance of persisting. Our study indicates, however, that close inbreeding may threaten these populations. Specific steps to reduce inbreeding include: (1) maintenance of a stable or increasing population through prescribed burning, cavity management and clumping of territories where possible; (2) enhancing dispersal by retaining as many small populations in the region as possible and by linking disjunct inhabited areas with new cavity trees, which if in suitable habitat will become occupied (Walters et al., 1992); and (3) possibly translocating individuals to a small population with no immigration in a conscientious manner. Conscientious use of translocation will ensure that the most successful methods of moving individuals are used, that the population receiving translocated individuals is closely monitored, that the donor population is within the same geographic region (Stangel et al., 1992), and that impacts to the donor population are carefully considered (Haig et al., 1993b).


Daniels, S.J. 1997. Female dispersal and inbreeding in the red-cockaded woodpecker. M.S. thesis, Virginia Polytechnic Institute and State University, Blacksburg VA, USA.


