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Effective Population Size in Red-Cockaded Woodpeckers: Population and Model Differences

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Abstract: Loss of genetic variability in isolated populations is an important issue for conservation biology. Most studies involve only a single population of a given species and a single method of estimating rate of loss. Here we present analyses for three different Red-cockaded Woodpecker (Picoides borealis) populations from different geographic regions. We compare two different models for estimating the expected rate of loss of genetic variability, and test their sensitivity to model parameters. We found that the simpler model (Reed et al. 1988) consistently estimated a greater rate of loss of genetic variability from a population than did the Emigh and Pollak (1979) model. The ratio of effective population size (which describes the expected rate of loss of genetic variability) to breeder population size varied widely among Red-cockaded Woodpecker populations due to geographic variation in demography. For this species, estimates of effective size were extremely sensitive to survival parameters, but not to the probability of breeding or reproductive success. Sensitivity was sufficient that error in estimating survival rates in the field could easily mask true population

Tamaño poblacional efectivo en el pajaro carpintero cabeza roja: Diferencias poblacionales y de modelo.

Resumen: La pérdida de variabilidad genética en poblaciones aisladas es una cuestión importante para la biología de conservación. La mayoría de los estudios sólo involucran una única población de una especie dada y un único método de estimación de la tasa de pérdida. Presentamos análisis para tres poblaciones distintas de carpintero cabeza colorada (Picoides borealis) de diferentes regiones geográficas. Comparamos dos modelos diferentes para estimar la tasa de pérdida de variabilidad genética esperada, y testeamos su sensibilidad a los parámetros de los modelos. Encontramos que el modelo más simple (Reed et al. 1988) estimó consistentemente una tasa de pérdida de variabilidad genética más alta que aquella estimada por el modelo de Emigh y Pollack (1979). La relación entre el tamaño poblacional efectivo (que describe la tasa de pérdida de variabilidad genética esperada) y el tamaño de la población de reproductores varió ampliamente entre las poblaciones de carpintero cabeza roja debido a la variación geográfica en la demografía. Para esta especie, las estimaciones del tamaño poblacional efectivo fueron extremadamente sensibles a los parámetros de supervivencia, pero no a la probabilidad de reproducción o éxito reproductivo. La sensibilidad fue lo suficientemente importante como para que
differences in effective size. Our results indicate that accurate and precise demographic data are prerequisites to determining effective population size for this species using genetic models, and that a single estimate of rate of loss of genetic variability is not valid across populations.

Introduction

This paper addresses calculation of effective population size for Red-cockaded Woodpeckers (*Picoides borealis*), an endangered species endemic to the southeastern United States. Effective population size describes the expected rate of loss of genetic variability from a population (Crow & Kimura 1970). The U.S. Fish and Wildlife Service (1985) established an effective size of 500 as the criterion for population viability for the woodpecker based solely on genetic considerations. Population viability has become an important concept in wildlife management (see Shaffer 1981, 1987; LaCava & Hughes 1984; Gilpin & Soule 1986; Reed et al. 1986). The essence of this concept is that a population below some critical size is likely to go extinct as a result of demographic, genetic, or environmental stochasticity or catastrophe (Shaffer 1981).

Of course there are other threats to viability besides loss of genetic variability, most notably demographic stochasticity and resistance to catastrophic events (Shaffer 1981; Gilpin & Soule 1986; Ewens et al. 1987; Lande 1988; Reed 1990, 1992). Different methods for assessing population viability are complementary, not interchangeable (Gilpin & Soule 1986). Once viability based on demographic factors is calculated, the minimum population size for a given population of woodpeckers might be higher than that required to maintain genetic variability. Furthermore, regardless of population size, a catastrophe can decimate a population, as occurred with the large population of Red-cockaded Woodpeckers at the Francis Marion National Forest due to a hurricane (Hooper et al. 1990). Viability assessment should take all threats to survival into account. Our analysis thus does not address population viability per se; rather, it addresses the calculation of one component of viability, rate of loss of genetic variability.

The Red-cockaded Woodpecker inhabits pine habitats, preferring mature longleaf pine (*Pinus palustris*) savannas (U.S. Fish and Wildlife Service 1985). It is nonmigratory and disperses short distances for a bird its size (Walters et al. 1988a). It is a cooperative breeder, and thus its demography is characterized by the presence of nonbreeding adults, usually male, long generation times and relatively low variance in reproductive output among breeders (Ligon 1970; Lennartz et al. 1987; Walters et al. 1988a; Walters 1990).

Reed et al. (1988) calculated the ratio of effective to breeding population size to be 0.49 for a population of Red-cockaded Woodpeckers in the North Carolina Sandhills using a simple model based on Hill (1972); the ratio was 0.53 when corrected for non-Poisson distribution of family size (Barrowclough & Coats 1985). Heckel and Lennartz (in review) used a more complex model (EPM; Emigh & Pollak 1979) to estimate effective population size for a woodpecker population in Georgia and found the ratio of effective to breeding population size to be 0.80. They then applied the EPM to the North Carolina population with which Reed et al. (1988) worked and found a ratio of 0.75.

The difference in ratios for the North Carolina population translates into a difference of 279 in the number of breeders required for an effective population size of 500. It is unclear to what extent this difference is due to use of different data rather than to different models. Heckel and Lennartz (in review) used the same survival data as Reed et al. (1988) but combined it with reproductive data from Georgia, whereas Reed et al. used reproductive data from the Sandhills population. Both Reed et al. (1988) and Heckel and Lennartz (in review) assumed birds that disappeared had died, whereas some presumably instead dispersed from their study areas. Our objectives are (1) to calculate the effective to breeding population size ratio for the North Carolina Sandhills population using the EPM, and both survival and reproductive data from the Sandhills, (2) to correct survival estimates for dispersal from the study area and recalculate the effective to breeding population size ratio for the Sandhills population using the EPM, (3) to explore the sensitivity of the effective to breeding population size ratio to geographic variation in demography among Red-cockaded Woodpecker populations, and (4) to further explore the sensitivity of the calculated ratios to model parameters.

The Models

Reed et al. (1988) used a modified version of Hill's (1972) model for estimating effective population size, corrected for non-Poisson distribution of family size.
In an analysis of loss of heterozygosity from a simulated grizzly bear (*Ursus arctos*) population, Harris and Allendorf (1989) found that REAM adequately estimated effective population size (Appendix).

The EPM is more complex and is not formulated in terms of standard life-history parameters, although it can be rewritten in such terms (Appendix). The EPM estimates an inbreeding effective size rather than variance effective size as in Hill (1972). These two types of models typically give similar results (Kimura & Crow 1963); failure to do so with the same data implies that assumptions of one or both models are not met.

The EPM and REAM have similar assumptions: (1) random mating, (2) no difference in fertility among individuals, (3) stationary population, (4) no year-to-year variability in the number of male or female progeny, (5) no covariance between the numbers of male and female progeny, (6) a Poisson distribution of family sizes, and (7) a closed population. The fifth assumption becomes a major problem when family size is restricted, but otherwise is unimportant (Wood 1987).

The EPM has an advantage over the REAM and most other models in being better able to accommodate complicated mating systems. Its disadvantage in application to real populations is its complexity and the amount of data required for its use.

**Methods**

The primary database comes from a population of Red-cockaded Woodpeckers in the Sandhills region of south-central North Carolina. The study area includes 110,000 ha and is inhabited by over 550 adult birds. The habitat generally is second-growth longleaf pine with scattered old-growth trees, an understory of scrub oak (*Quercus* spp.), and ground cover of wiregrass (*Aristida stricta*). This study area is described in detail in Carter et al. (1983) and Walters et al. (1988a).

The total Sandhills population, about half of which is included in the study area, is one of the largest extant populations of the Red-cockaded Woodpecker (Lennartz et al. 1983). There is distinct substructure within this population. The 135 groups in the southwestern part of the population are separated from the remaining 270 groups by a region of low woodpecker density, across which there is minimal gene flow—roughly two breeding individuals in each direction per generation (Walters et al. unpublished data). Stangel et al. (1992) found genetic differentiation between the two subpopulations.

Demographic data were collected from the Sandhills population during 1980–1987. Methods of data collection are described in detail in Walters et al. (1988a). Birds were marked as nestlings with unique combinations of color bands, and their subsequent life histories were documented from annual breeding censuses in which all members of all groups were identified and their status (breeder, helper, etc.) determined. We determined the number of fledglings produced by each group as a measure of fecundity.

The parameters of the EPM are described in detail by Heckel and Lennartz (in review). They can be derived from estimates of age-specific survival and fecundity and from age-specific probabilities of achieving breeding status (Appendix). The parameters of the REAM can be derived from these same estimates. Sandhills data were sufficient to estimate age-specific parameters through age five (minimum $n = 31$). Data from older birds were combined to produce estimates that were used for all ages beyond five. In all analyses we assume an even sex ratio at fledgling, based on an observed even sex ratio in the Sandhills population (Walters 1990). For each sex, we truncated the life table at the first age beyond the last one at which 2% of the population was still living.

To produce estimates of effective size corrected for dispersal out of the study area, we assumed the rate of such dispersal to equal known rates of dispersal into the study area, as described in Walters et al. (1988a).

Measurement of demographic parameters might occur during periods of population increase or decrease. To generate a demography that might characterize the population at equilibrium, we determined the ratio of breeders to fledglings and, using the observed breeder mortality rate, adjusted transition probabilities so that the fledglings exactly replaced deceased breeders. The probabilities altered were for the transitions from fledgling to breeder and from helper (nonbreeder in the case of females) to breeder. Corresponding adjustments were made in mortality rates. We treat this as a hypothetical population that might occur in Sandhills habitat.

There appears to be geographic variation in demography in the Red-cockaded Woodpecker. Specifically, coastal populations are characterized by higher adult survival rates and lower fecundity than in inland populations such as the Sandhills one, and more southern populations differ from northern ones in the same way (DeLotelle & Epting in review; Walters et al. unpublished data). To explore how population differences in life history might affect the ratio of effective to breeding population size, we constructed parameter estimates for two additional hypothetical populations. One was based on data from a population at Camp LeJeune, located along the central coast of North Carolina. This population contains 30 groups in roughly 24,000 ha. The habitat includes longleaf pine-scrub oak forest similar to the Sandhills, but also pine flatwoods and pocosin. Demographic data were collected from the LeJeune population during 1986–1989. LeJeune data were sufficient to estimate the ratio of breeders to fledglings and breeder survival. We used very small samples ($n = 5–11$) to estimate fecundity at ages one to three, and we assumed fecundity at older ages to be constant. We estimated
fecundity above age three by the average fecundity of all birds known to be older than three (exact ages unknown; \( n = 98 \) males, 96 females). Age-specific probabilities of achieving breeding status were estimated indirectly using annual transition probabilities between status classes, for which we had fairly large samples, with the assumption that these transition probabilities are independent of age (Walters et al. 1988a). We then applied the same balancing procedure as on the Sandhills data to produce the demographic parameters used as input into the model. This is intended to represent a hypothetical stationary population characteristic of coastal North Carolina.

We employed an identical procedure to produce a hypothetical stationary Florida population, using estimates of breeder survival, helper survival, breeder fecundity, and the ratio of breeders to fledglings provided by DeLotelle and Epting (in review).

Finally, we performed a numerical sensitivity analysis using the Sandhills data, uncorrected for dispersal. By increasing and decreasing each parameter by 10%, we examined sensitivity to changes in (1) survival to age one, (2) survival beyond age one, (3) fecundity, and (4) probability of achieving breeding status. Life tables used in analyses are available from J. M. Reed.

**Results**

The EPM consistently produced a larger ratio of effective to breeding population size than the REAM. The disparity in results increased as \( N_e/N_{br} \) increased. There were substantial differences among populations in \( N_e/N_{br} \) using either model (Table 1). Variation was somewhat less when parameters were estimated indirectly using the status-class transition method (Table 1). A geographic pattern was not evident in the ratios of effective to breeding population size (Table 1).

For the Sandhills population, the observed \( l_x m_x \) schedule indicated a declining population (\( R_0 < 1 \); Caughley 1977). This is consistent with population data, although the observed rate of decline is less than that suggested by the model (Walters et al. 1988a). Adjusting for dispersal out of the study area had a dramatic effect. \( N_e/N_{br} \) increased roughly 40%, and the transformed \( l_x m_x \) schedules indicate, unrealistically, an increasing population (Table 1).

\( N_e/N_{br} \) calculated for the Sandhills using the REAM (0.42) differs from that reported by Reed et al. (1988) (0.49) because of an error in the \( l_x \) table for males in Reed et al. (1988) and use of revised parameter estimates based on additional data. The large effect of these rather small discrepancies in the data, the dramatic effect of attempting to correct for dispersal, and the general level of variation in effective to breeding population size ratios in Table 1 all suggest that results are highly sensitive to the parameter estimates used, a fact confirmed by sensitivity analysis. For the Red-cockaded Woodpecker, the models are not sensitive to changes in the probability of achieving breeding but are highly sensitive to adult survival estimates (Table 2). A 10% change in adult survival results in an average change in \( N_e/N_{br} \) of roughly 35%. Using the EPM, this leads to estimates of the number of breeders required for an effective population size of 500 as disparate as 543 and 1111. The models are equally sensitive to fecundity and first-year survival, and sensitivity to these parameters is less than sensitivity to adult survival (Table 2).

**Discussion**

Using correct and complete Sandhills data and the EPM, we obtained a ratio of effective to breeding population size intermediate to those estimated by Reed et al. (1988) and Heckel and Lennartz (in review). It appears

<table>
<thead>
<tr>
<th>Adjustment</th>
<th>Emigh-Pollak</th>
<th>Reed et al.</th>
<th>( R_0 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>None</td>
<td>0.63</td>
<td>0.42</td>
<td>0.84</td>
</tr>
<tr>
<td>Correct for Dispersal</td>
<td>0.87</td>
<td>0.61</td>
<td>1.19</td>
</tr>
<tr>
<td>+10% First Year Survival</td>
<td>0.56</td>
<td>0.38</td>
<td>0.75</td>
</tr>
<tr>
<td>-10% Adult Survival</td>
<td>0.45</td>
<td>0.30</td>
<td>0.61</td>
</tr>
<tr>
<td>+10% Adult Survival</td>
<td>0.92</td>
<td>0.60</td>
<td>1.23</td>
</tr>
<tr>
<td>-10% Breeding Probability</td>
<td>0.62</td>
<td>0.38</td>
<td>0.75</td>
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<tr>
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<td>-10% Fecundity</td>
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<td>0.38</td>
<td>0.75</td>
</tr>
<tr>
<td>+10% Fecundity</td>
<td>0.69</td>
<td>0.46</td>
<td>0.92</td>
</tr>
</tbody>
</table>

See text for an explanation of the subheadings.
that the difference in results between Reed et al. (1988) and Heckel and Lennartz (in review) is due primarily to a systematic difference between the models. One assumes that the EPM, being more complex, is more accurate, but this assertion requires corroboration. An alternative is that it is more sensitive to violations of model assumptions, and as a result is less accurate.

The REAM, when applied to the woodpeckers, appears to underestimate effective size, and therefore $N_e/N_{pr}$. This was confirmed by a pedigree analysis of parts of the Sandhills population (Blackwell et al. in review). One model assumption violated in this species is that of family sizes having a Poisson distribution; reproductive heterogeneity is less than Poisson in this species (Reed et al. 1988). It is likely that the REAM is accurate only for certain types of life tables, such as that exhibited by grizzly bears (Harris & Allendorf 1989). The large $N_e/N_{pr}$ ratios obtained indicate remarkable reproductive homogeneity in Red-cockaded Woodpeckers, a byproduct of the species' unusual social system.

Another model assumption clearly violated by using the observed Sandhills data is that of a stationary population. Our attempts to reduce the effect of this problem by "balancing" the data did not reduce the difference in performance between the models. Although application of the models to nonstationary populations is a major concern, we must look elsewhere for an explanation for the systematic difference between the models when applied to woodpecker data.

Differences in demography among Red-cockaded Woodpecker populations are substantial. For example, there are sufficient data to conclude with certainty that survival in the first year is higher in the coastal population at Camp LeJeune than in the inland population in the Sandhills, and that fecundity at all ages is lower at Camp LeJeune. Also, Heckel and Lennartz (in review) found that in the Georgia Piedmont population all males breed by age two. This is far from the case in North Carolina, where a male's probability of breeding by age two is 0.46 in the Sandhills and only 0.39 at Camp LeJeune. One might expect clines in demography to produce corresponding clines in $N_e/N_{pr}$ with inland populations characterized by lower survival and higher fecundity losing variability faster. There is little indication of such a cline in Table 1.

However, the sensitivity analysis suggests that any true differences among populations could easily be obscured by inaccuracies in estimating demographic parameters. Our analyses indicate that inaccuracies in estimating fecundity, first-year survival, or probability of breeding will cause only minor problems. Heckel and Lennartz (in review) came to a similar conclusion with regard to generation length, sex ratio, truncation of the age distribution, and fledglings produced per group. The key parameter is adult survival, inaccuracies in which produce large effects on effective size estimates. Inaccuracy in estimating adult survival will generate inaccuracy in estimating effective size not only through inclusion of an inaccurate parameter in the model, but also by increasing deviation from the stationary condition in the modeled population.

Our parameter values are based on small samples for all but the Sandhills population. An error of 10% in estimating adult survival would produce a difference in $N_e/N_{pr}$ larger than any real differences between populations are likely to be. It therefore seems pointless to estimate $N_e$ of most populations based on demographic data from those populations. The best procedure might be to use data from reference populations, possibly defined by habitat, where large data sets are available to determine geographic variation in $N_e/N_{pr}$ and then to derive estimates for individual populations based on where they lie geographically. Samples for the Georgia Piedmont and Camp LeJeune populations might be large enough in a few more years to be added to the North Carolina Sandhills as reference populations. The geographic range covered by these populations is not large, however. There is a conspicuous need for data from Florida to define the other end of the cline.

Even in a given region or population, the estimated ratio of effective to breeding population size will change depending upon population dynamics. Calculations must be restricted to periods of population stability because fewer model assumptions are likely to be violated then. There is also the problem of dispersal from the sampling area. If dispersal is restricted to within the population, it must be taken into account. Failing to do so will result in errors in estimating mortality rates, leading to large errors in calculating $N_e$. Dispersal out of the population is a different matter. There need be no correction for this mathematically because the models assume that the population is closed, and this movement represents losing genetic variability in the same way as death does. If immigration also occurs, however, its substantial effect on rate of loss of genetic variability must be considered (Allendorf 1983).

In the case of the Sandhills population, estimating dispersal from the study area as equivalent to dispersal into it resulted in an unrealistically optimistic estimate of population growth rate, and an unrealistically high estimate of $N_e/N_{pr}$. The calculation assumes that all dispersal occurs within the population, but birds are known to immigrate to the Sandhills from other small populations as far as 90 km away (Walters et al. 1988b). Migration from the Sandhills to these other populations has not been detected. It likely is more difficult for Sandhills birds to locate a cluster of 5–10 groups a long distance away than for a bird moving in the opposite direction to intercept the area used by the 400 groups in the Sandhills population. Therefore emigration is likely to be less than immigration, and the true value of $N_e/N_{pr}$ is likely somewhere between the value obtained when assuming no dispersal from the sampling area and that obtained when assuming equivalent dispersal in and out.
There seems little point in arguing about the best value of $N_e$ (Walters 1991). Our calculations suggest that a reasonable range of the ratio of effective to breeding population size for this species is 0.65–0.80, which translates into a requirement of roughly 310–390 breeding pairs for an effective population size of 500. Given the likelihood of violating model assumptions and generating inaccuracies in parameter estimates, better precision is unrealistic. The valuable information gained from these analyses is that the uncommon breeding system of the Red-cockaded Woodpecker results in an unusually high $N_e/N_{breed}$. This means that closed populations can be smaller than for many other species before loss of genetic variability becomes a problem. This might be part of the reason Stangel et al. (1992) found that even small populations of these woodpeckers retain useful amounts of genetic variability.

Finally, there is the issue of defining populations. We treat the Sandhills as one population, ignoring known substructure (Stangel et al. 1992). The relative lack of gene flow between the two parts of the population means that the rate of loss of genetic variability is greater than our calculations indicate, but less than that calculated when treating the two parts as separate populations. A viability assessment should consider gene flow from other populations in evaluating loss of variability, as is done by Blackwell et al. (in review) using a pedigree of our population.

Acknowledgments

We thank two anonymous reviewers for commenting on this paper. The research was supported by NSF grants BSR-8307090 and BSR-8717683, the North Carolina Agricultural Research Service, and the Department of Defense, Camp Lejeune Marine Base. We thank R. S. DeLolette, R. J. Epting, D. G. Heckel, and M. R. Lennartz for providing us with unpublished results. We also thank the many graduate students, undergraduates, and technicians who helped collect the data analyzed in this study.

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Appendix

The model used by Reed et al. (1988) is a modification of Hill (1972), corrected to account for non-Poisson variance in family size (Barrowclough & Coats 1985), and can be written as

$$
\frac{1}{N_e} = \left( \frac{1}{4L_{m}\bar{N}_{m}k_{m}l_{m}} + \frac{1}{4L_{f}\bar{N}_{f}k_{f}l_{f}} \right) \frac{k}{(k-1)+\frac{V_k}{k}} \quad (A1)
$$

where $L_{m}$ and $L_{f}$ = generation length (average age of breeders) of males and females respectively; $N_{m}$ and $N_{f}$ = the number of male and female breeders; $k_{m}$ and $k_{f}$ = the expected number of males born/male and females born/female; and $l_{m}$ and $l_{f}$ = the probability of surviving to the mean age of reproduction. $k$ = mean lifetime reproductive success (males/female), and $V_k$ is its variance.

The Emigh-Pollak model (1979: eq. 40) is expressed as

$$
\frac{1}{N_e} = \frac{1}{LN(1)} \left[ 1 + \sum_{i} q_{i+1}^{\max} \left( \frac{1}{l_{i+1,m}} - \frac{1}{l_{i,m}} \right) \right] + \sum_{i} q_{i+1}^{\max} \left( \frac{1}{l_{i+1,f}} - \frac{1}{l_{i,f}} \right) \quad (A2)
$$

Here $L$ is the average generation length of males and females; $P_f$ and $P_m$ = proportion of female and male newborns; $l_{i,m}$ and $l_{i,f}$ = the proportions of males and females surviving from birth to age $i$; $q_{i+1}^{\max} = \text{the probability that a newborn has a male parent of age } i + 1 \text{ or greater and a female parent of any age, and } q_{i+1}^{\max} = \text{the probability that a newborn has a female parent of age } i + 1 \text{ or greater and a male parent of any age}; N_{i}(1)$ is the effective number of newborns: $1/N_{i}(1) = 1/N_{i,m} + 1/N_{i,f}$, where $N_{i,m}$ and $N_{i,f}$ = number of newborn males and females, respectively (fledglings are considered newborns).

Equation A3 can be rewritten using standard life-history parameters:

$$
\frac{1}{N_e} = \frac{1}{L} \left( \frac{N_{0,m}}{N_{0}} \right) \left( \frac{N_{0,f}}{N_{0}} \right) \sum_{i=1}^{i_{\max}} \left[ \frac{1}{l_{i+1,m}+l_{i,m}} \left( \frac{1}{l_{i+1,m}} - \frac{1}{l_{i,m}} \right) \right] ^2 + \frac{N_{0,m}}{N_{0}} \sum_{i=1}^{i_{\max}} \left[ \frac{1}{l_{i+1,f}+l_{i,f}} \left( \frac{1}{l_{i+1,f}} - \frac{1}{l_{i,f}} \right) \right] ^2 \quad (A3)
$$

where $N_{0} = \text{number of newborns} (N_{0,f} = \text{number of newborn females}, N_{0,m} = \text{number of newborn males}), i$ and $j = \text{age}; m_{i,m}$ and $m_{i,f} = \text{age-specific reproductive success (male/female)}$; and $l_{i,m}$ and $l_{i,f} = \text{survival to age } i$ for males and females.

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