APPLICATION OF ECOLOGICAL PRINCIPLES TO THE MANAGEMENT OF ENDANGERED SPECIES: The Case of the Red-Cockaded Woodpecker

Jeffrey R. Walters

Department of Zoology, North Carolina State University, Box 7617, Raleigh, North Carolina 27695-7617

KEY WORDS: conservation, population viability, cooperative breeding, cavity, management

INTRODUCTION

A major development in the biological sciences in the 1980s was the emergence of the discipline known as conservation biology. The rise of conservation biology was triggered by growing concern about environmental problems such as tropical deforestation and the loss of biodiversity (50). Historically, conservation biology may be viewed as a union between parts of the fields of wildlife biology and ecology (50) that reflects the maturation of both.

Wildlife biology has always focused on conservation and management of natural resources. Attention was originally concentrated on those few species that were hunted (45, p. 2) and, as in all disciplines, research was mostly descriptive. Management techniques developed largely through trial and error. As the field developed, its focus broadened to include nongame species, particularly endangered species. Interest in the basic biology of the species and ecosystems of concern grew, and management increasingly was based on deductions derived from fundamental understanding of the systems involved rather than from trial and error.

Within ecology, the relevant changes have been in theory. The theory developed in the 1950s, 1960s, and early 1970s (e.g. 37) can be characterized...
as general and simple. The basic ecological principles contained within these
theories, although of fundamental importance, had limited utility in natural
resource management. Subsequently, ecological theory has become in-
creasingly precise and realistic, and increasingly able to generate accurate
predictions about the behavior of real systems. This has enabled ecologists
more effectively to address natural resource management problems.

The union of ecology and wildlife biology in conservation biology thus is a
natural one, but it is not without its difficulties. A gap between theory and
practice, the width of which varies considerably among problems, remains.
Collaboration between ecologists and wildlife biologists is inhibited by the
separation of the two fields in the infrastructures of American universities and
government agencies (50). The two disciplines have developed independently
to a large extent, and their historic and current structural separation continues
to hinder communication.

This paper illustrates both the potential and the problems characterizing the
current contribution of conservation biology to management of endangered
species, using as an example the red-cockaded woodpecker (Picoides
borealis), an endangered species endemic to the southeastern United States.
Use of artificial cavity construction illustrates the potential for deriving
management techniques from an understanding of basic biology. Attempts to
assess population viability illustrate the problems created when management
is based on theory that is not yet sufficiently mature and when managers and
researchers have difficulty communicating.

My thesis is that effective conservation of endangered species requires
insightful research that incorporates theory, and that judicious use of research
findings can result in designing successful management techniques. I choose
to illustrate this by reviewing one particular case in detail, but other examples
abound (e.g. 39). For instance Crouse et al (12) used sophisticated population
modeling techniques to show that sea turtle population numbers are much
more sensitive to mortality in the juvenile stage than at the egg or hatchling
stage. In terms of effect on populations, saving one juvenile is equivalent to
saving hundreds of hatchlings. This justifies conservation efforts to reduce
juvenile mortality by ensuring that turtle-excluding devices are installed on
shrimp boats, and it shifts emphasis away from more popular but less effec-
tive programs involving nest and hatchling protection (38).

THE BIOLOGY OF THE RED-COCKADED
WOODPECKER

The red-cockaded woodpecker has in the last 20 years become one of the most
studied avian species in the United States. Its biology has been the subject of
two symposia (57, 67), two recovery plans (58, 59), and several recent
reviews (25, 26, 36, 63). The red-cockaded woodpecker was once an abundant resident of the southeastern Piedmont and Coastal Plain, ranging from New Jersey to Texas, and inland to Kentucky, Tennessee, and Missouri (23). It is now virtually extirpated north of North Carolina and in all interior states but Arkansas. Most remaining populations are isolated, small, and fragmented (11, 24, 36, 59, 63), and only three number more than 300 breeding groups. Many populations continue to decline, some rapidly (8). Some populations are remarkably stable in their numbers (63), but none are increasing, a point to which I return.

The decline of the species is due primarily to habitat loss and alteration (25, 26, 36, 59). The species is highly adapted to pine savannahs, preferring especially longleaf pine (*Pinus palustris*). These habitats were once abundant: Longleaf pine alone once covered 25 million ha in the Southeast (40). Vast expanses of pine savannah have been lost through conversion to agriculture and forestry plantations, development, and timbering (59, 62). Virtually all the remaining habitat has been altered in ways that adversely affect the species.

**Habitat Requirements**

Red-cockaded woodpeckers are nonmigratory and territorial throughout the year. Territories are large, ranging from 50–150 ha or more in size (14, 21, 41, 59, 63). In their foraging these woodpeckers are specialists on live pine (63), feeding on invertebrates which they obtain primarily by scaling bark and pecking. Although both sexes forage on the upper trunk, only females regularly forage low on the trunk, and only males forage regularly on the twigs and limbs.

The species is just as closely tied to live pine in its nesting. It invariably excavates cavities for roosting and nesting in live pines, a highly unusual habit that may be an adaptation to a low density of snags in the fire-maintained ecosystems in which it lives (25). The pines in which red-cockaded woodpeckers nest are highly resistant to fire. Excavating in live pine poses some special problems. The cavity chamber must be excavated in the tree’s heartwood core, and cannot extend into the surrounding sapwood. Since the diameter of heartwood is largely a function of age, the birds can only excavate cavities in old trees. Cavity trees generally average 80–120 years of age (27, 59) and may be much older where many old trees are available (63). A major cause of the decline of the woodpecker species is the disappearance of trees of sufficient age for cavity excavation from much of the remaining pine savannahs, due primarily to timber harvest.

Second, the mechanics of excavating in live tissue are problematic. Heartwood is dense and difficult to work. However, the birds usually excavate in trees in which the heartwood has been softened by decay due to infestation by
red-heart fungus (*Phellinus pini*) (7). Making an entrance tunnel through the sapwood to reach the heartwood is also difficult. This appears to limit the speed with which cavities can be constructed, presumably because sap leakage into the tunnel interrupts excavation. Cavities take at least 10 months to complete, typically several years (27), and the bulk of that time is spent excavating, intermittently, through the sapwood.

A final difficulty in using cavities in live pines is that the rough surface of the trunk enables predators, especially snakes, to climb to the cavity. Red-cockaded woodpeckers maintain resin wells, places where they chip into the sapwood, around their cavities. The resulting sap flow prevents snakes from reaching the cavity by smoothing the climbing surface and interfering with the action of the ventral scales used by the snakes in climbing (46).

Remaining habitat has also been altered through exclusion of fire. Historically the interval between fires in southeastern pine savannas was only 1–5 years (26). In the absence of fire, a hardwood understory and midstory develops. There is a well-established correlation between development of this hardwood layer and abandonment of cavities by red-cockaded woodpeckers (8, 11, 24, 60). This may be related to the access to cavities provided to predators by encroaching hardwoods.

**The Social System**

Red-cockaded woodpeckers live in groups containing a breeding pair and 0–4 helpers, nearly all of which are male (63). There is no evidence that helpers participate in clutch production (63), but they assist in incubation and feeding of nestlings and fledglings (33, 35). Each member of the group has its own roost cavity. Hence a territory contains a cavity tree cluster, that is, a set of cavity trees, usually located in close proximity.

Group formation is best understood in terms of alternative life-history tactics practiced by young birds (63, 65, 66). Many fledglings disperse from their natal group during their first year to search for a breeding vacancy. This tactic is adopted by nearly all females (Figure 1) and many males (Figure 2). Although many early dispersers are breeders at age one (Figures 1 and 2), some are floaters, that is, individuals without a territory or mate (63), and some males are solitary, that is, they have a territory but no mate (Figure 2). Floaters and solitary males often become breeders in subsequent years, but their mortality rates are high (Figure 2) (63, 65). Individuals adopting this tactic may disperse long distances, although they do not always do so (Table 1).

Other individuals remain on the natal territory and act as helpers. Such individuals become breeders by inheriting breeding status on their natal territory or by dispersing at a later age to a nearby territory (Figure 2). Helpers rarely disperse long distances (Table 1) and may wait many years before
acquiring a breeding position. This tactic is adopted by many males, but very few females. Thus most helpers in this species are natal males that delay dispersal and reproduction. Once males acquire a breeding position they almost always hold it until they die (Figure 2). Breeding females, on the other hand, sometimes switch groups (Figure 1) (63, 65).

Whichever tactic individuals adopt, if they become breeders they almost always do so by replacing a deceased individual. In present populations red-cockaded woodpeckers compete for breeding vacancies in existing groups rather than form new groups. New groups might form by reoccupation of abandoned territories or creation of new territories. New territories may be created by pioneering, in which birds disperse into an area not previously occupied and construct a new cluster of cavities, or by budding, in which an existing territory and cavity tree cluster (and often the existing group) is split into two (20). In the population of over 200 groups I study in the North Carolina Sandhills, budding resulted in the formation of only 6 new groups in 8 years, and pioneering did not occur in that period (63).

Reoccupation of abandoned territories is more common, resulting in the formation of 22 new groups in 8 years in the Sandhills, for example (63). Still, in the Sandhills the rate of reoccupation of abandoned territories is only 8.7% annually (15). Once a territory is abandoned for longer than two years, it almost always stays abandoned.

That populations of red-cockaded woodpeckers are sometimes remarkably stable but seldom increase follows directly from the tendency of individuals to compete for breeding vacancies in existing groups rather than form new ones. Lack of new group formation has been a serious obstacle in recovery efforts. Research on the basic biology of the species' social structure suggests an ecological basis for the rarity of formation of new groups, and a solution to this management problem, cavity construction.
Figure 2  Annual transition probabilities for males, based on data from 775 fledglings, 354 helpers, 1033 breeders and 141 solitary males from the Sandhills of North Carolina. Only transitions involving at least 4% of all transitions for a particular class of individual are included. See Walters (63) for a complete accounting. Whether transitions involved remaining on the same territory or dispersing to another is indicated.

POPULATION DYNAMICS

The Ecology of Cooperative Breeding

The rarity with which red-cockaded woodpeckers form new groups can be related to the evolution of their cooperative breeding system. It is clear that there are several evolutionary pathways to cooperative breeding, and that no common set of ecological conditions applies to all the more than 200 species of birds characterized by this breeding system (18). Advantages inherent to group living may account for the evolution of cooperative breeding in some species, particularly those in which there are several breeders within the group, and in which per capita survival and reproductive success increases with group size (3, 53, 61). However, the most common pathway to cooperative breeding appears to be selection for delayed dispersal and reproduction, that is, retention of young within their natal group, as in red-cockaded woodpeckers.

The demographic conditions required for selection for retention of young have been described in progressively more explicit and detailed models (e.g. 17, 66, 68). These demographic models are simply an accounting of fitness,
using survival and reproductive schedules under alternative life-history tactics. Recent research provides evidence that the demographic conditions depicted in these models prevail in several species (e.g. 29, 68, 69).

What ecological factors produce the demographic conditions that favor retention of young? Emlen (17) outlined two ecological regimes under which remaining with the natal group may result in greater lifetime reproductive success than does attempting to disperse and breed early. One regime involves a harsh, unpredictable environment. In poor years, inexperienced birds reproduce poorly, so that living with the natal group is favored over independent reproduction.

The second, more common regime, traditionally termed habitat saturation because it is characterized by an apparent shortage of breeding vacancies (1, 2, 17, 52), is the one that applies to red-cockaded woodpeckers. An apparent lack of unoccupied territories has been noted in many cooperative breeders (18). The only attempt to conceptualize habitat saturation quantitatively is that of Koenig & Pitelka (28). They proposed that in species experiencing habitat saturation, reproductive success falls sharply between suitable and unsuitable habitat, and little marginal habitat exists between suitable and unsuitable habitat. Under these conditions, suitable habitat will be filled continuously.

Stacey & Ligon (54, 55) have proposed the benefits of philopatry model as an alternative to habitat saturation. According to this model, in species with unusually great variation in the quality of breeding positions, it pays individuals whose natal sites are of high quality to remain as helpers and potentially inherit breeding status, as this is an effective way to acquire a superior site. Variance in breeding positions may depend on effects of territory quality (42, 54, 55) or group size (43, 55) on fitness. If the unsuitable habitat in the Koenig & Pitelka model (28) is interpreted as incapable of supporting reproduction, then this model is distinct from the philopatry model. If unsuitable habitat is of low quality but is capable of supporting reproduction, then only high quality habitat, rather than all breeding habitat, is saturated. In this case, the two models are similar, differing primarily in the explicit role given to comparison between natal and nonnatal territories in the philopatry model (54).
The consensus is that individuals ignore vacant habitat in which they could breed successfully while competing intensely for other (higher quality) habitat. Delaying reproduction and altering dispersal behavior is viewed as an effective way of competing for high-quality breeding positions. Individuals remaining on the natal territory are supposed to have an advantage in competing for vacancies in their vicinity over those dispersing after fledging, a supposition supported by experimental evidence (70). Those adopting this tactic can be thought of as increasing their ability to compete for a restricted set of vacancies.

**Testing Theory: the Cavity Construction Experiment**

Research by my colleagues and me indicates that in the Sandhills population, fitness of males that delay dispersal and reproduction is comparable to that of males that disperse soon after fledging (66). Birds that disperse early do not have unusually low survival compared to other small landbirds, but they have an unusually low probability of acquiring a breeding position. Those that delay dispersal have a very high survival rate, both during their first year and during subsequent years spent helping. The extent to which reproductive performance improves with age among breeders is also unusually great. The average number of fledglings produced by males with both a territory and a mate increases steadily from 0.64 to 2.10 from age one to age six (66).

Thus, demography conducive to the evolution of delayed dispersal exists in this species, but this demography depends on individuals’ competing for breeding positions within existing groups rather than their forming new groups. I have proposed that the basis of this selectivity, and the intense competition for breeding positions that results, is variation in territory quality, and further, that the basis of variation in territory quality is the cavity tree cluster (63, 65). Because of the time and energy required to construct a set of cavities, the worst territories with an existing set of cavities may be sufficiently better than the best ones without cavities that it pays to compete for territories with existing cavities and ignore those without them. This may be viewed as a version of the models described above in which territory quality has a discontinuous rather than continuous distribution (55).

To test this hypothesis, my colleagues and I constructed cavities in live pines in 20 sites in our Sandhills study area, using a drilling technique (9). In each site we drilled two complete cavities, plus three additional entrance tunnels. Half of these sites were abandoned territories that contained old cavities but had not been used by red-cockaded woodpeckers for at least 3 years, and the other half were vacant sites that contained neither cavities nor birds.

Each of the experimental abandoned sites was paired with a control site that was also abandoned. We cleared hardwood midstory and understory from the
vicinity of cavity trees in both experimental and control sites. We used another set of abandoned sites in which we did no understory clearing as an additional control. We also delimited a set of vacant control sites. We cleared understory and midstory from the vicinity of trees in which we constructed cavities in vacant experimental sites, and from a set of comparable trees (in which no drilling was done) within vacant control sites. We constructed cavities from February 1988 to February 1989 and evaluated the response to the experiment in the breeding season (April–July) of 1989.

The results of the experiment were dramatic. Eighteen of 20 experimental sites were occupied by red-cockaded woodpeckers—nine abandoned sites and nine vacant sites—whereas no control sites were occupied. Although some experimental sites were used by previously existing groups of woodpeckers, the experiment resulted in a net addition of 12 groups to the population. This contrasts not only to the lack of response to controls, but the general rarity of new group formation in the population. Further details about the experiment are given elsewhere (10, 64).

A New Understanding of Population Dynamics

The results of the experiment suggest that red-cockaded woodpeckers compete intensely for some habitat while other potentially usable habitat goes unoccupied due to the absence of cavities. The population contains many nonbreeding adults (i.e. helpers), yet not all potential breeding habitat is filled. This necessitates taking an unconventional approach in modeling the population dynamics of the species.

Population dynamics are usually modeled using a life table approach in which changes in population size are a function of class- or age-specific mortality and survival parameters. Such models have proved valuable in conservation (e.g. 12, 48), but they cannot be applied to red-cockaded woodpeckers because they cannot incorporate the constraints imposed by the species’ social structure. First, population reproduction is not a simple function of adult density. Because a pool of replacement breeders (helpers) exists, variation in breeder mortality has little effect on the future number of breeders. When an epidemic resulted in the loss of 45% of the breeders and all the fledglings in a population of another cooperative breeder, the Florida scrub jay (Aphelocoma coerulescens), the number of breeders was reduced by only 27% the next breeding season and returned to the pre-epidemic level the following year (68, p. 351). Because the probability of transition from helper to breeder is a function of breeder mortality, it cannot be treated as a constant parameter in a life table analysis.

Second, the dispersal behavior of helpers introduces spatial structure into the population dynamics. One cannot assume that a given nonbreeder can fill any breeding vacancy that occurs in the population. Less conventional models
that incorporate social and spatial structure (e.g. 30, 56) are required for the red-cockaded woodpecker. One such model, which treats the population as a set of interacting groups, has been developed by L. A. Maguire and her students at Duke University (51). This and similar models could accurately predict changes in population size, the distribution of individuals among the helper, breeder, and floater classes, and population reproduction. However, they still cannot predict changes in the number of breeding groups accurately.

The number of groups in the population depends on a second process besides that which determines population size, namely that which determines distribution of cavity tree clusters and thus the number of acceptable territories. The domain of the models discussed above is the dynamics of individuals distributed among acceptable territories, not the dynamics of territory acceptability. A model of the population dynamics of red-cockaded woodpeckers must include a second level that treats territory acceptability.

Much of the observed behavior of red-cockaded woodpecker populations can readily be described in terms of population dynamics involving two levels, the first, the number of cavity tree clusters, and the second, the number of individuals distributed among those clusters. Changes in population size appear to involve primarily the first level. Territories can be lost due to hardwood encroachment on or destruction of cavities. In the absence of such losses of cavity tree clusters, populations will be extremely stable but will not grow appreciably. That is, population decline results from territory abandonment, not reductions in survival or reproduction. As populations decline, birds on occupied territories continue to do well, but fewer territories are occupied (65). Populations that have declined differ from those that have not in the proportion of territories abandoned rather than the survival and reproduction of birds on remaining territories (J. Walters, unpublished data).

The gradual nature of territory abandonment (15) can be explained in these terms. Breeders are often reluctant to abandon their territory, even if cavities are destroyed or lost to hardwood encroachment. However, nonbreeders may no longer find the territory acceptable and thus will not replace the breeders when the latter perish. A pair or a solitary male may linger on the territory for many years (63, 65), but when these individuals die, the territory is at last abandoned. It is abandoned not because replacements are unavailable, but because the territory is unacceptable.

Of course extreme variation in demography could cause some acceptable territories to be unoccupied or occupied by unpaired males. However, variation in demography appears to translate primarily into variation in group size. For example, high levels of reproduction are followed by increases in the size of the helper class and thus in group size rather than increases in the number of groups in a population (63, 65). The two levels of population dynamics are thus to a considerable degree independent.
Implications for Woodpecker Management

My interpretation of the population dynamics of red-cockaded woodpeckers has dramatic implications for their management. First, it suggests that management efforts that improve reproduction and survival have little potential to promote population recovery or to arrest decline. Such efforts would primarily affect the average group size in a population rather than the number of groups. Management should instead focus on factors that affect the number of acceptable cavity tree clusters to reduce loss of existing clusters and promote addition of new clusters.

Using this perspective, I evaluate the major techniques used in management of red-cockaded woodpeckers. These include control of hardwood understory and midstory by prescribed burning and mechanical and chemical removal, increasing the quantity and quality of foraging habitat, increasing old growth available for cavity excavation, and reducing usurpation of red-cockaded cavities by other species (11, 36, 59).

Southern flying squirrels (*Glaucous volans*) are one of the primary users of active red-cockaded woodpecker cavities (4). Flying squirrels may force individuals to roost in the open, destroy eggs and young, and even prevent a group from nesting by temporarily usurping all of a group’s cavities, but they do not destroy cavities. Thus flying squirrels have no effect on territory acceptability and do not cause territory abandonment. Controlling their interaction with red-cockaded woodpeckers may increase reproduction and survival, and thus group size, but not the number of groups in the population.

In contrast to flying squirrels, other woodpeckers that usurp cavities from red-cockaded woodpeckers destroy cavities by enlarging them. Thus these species can affect territory acceptability as well as reproduction and survival. The pileated woodpecker (*Dryocopus pileatus*) is particularly destructive. Pileated woodpeckers can enlarge all the cavities on a territory in a short period of time, thus rendering the territory unacceptable. Cavity restrictors, metal plates placed around cavity entrances, have proven effective in reducing loss of cavities to pileated woodpeckers and other species (4). Use of restrictors in areas where pileated woodpeckers and other species cause cavity loss should reduce loss of existing clusters and thus help prevent population decline.

Efforts to improve foraging habitat have the same limitations as efforts to control flying squirrels. Increased quality and quantity of foraging habitat is correlated with increased reproduction and group size (34). Foraging habitat may thus be thought of as a factor affecting quality among acceptable territories. Providing more and better foraging habitat may increase average group size but will not add groups to the population. It is likely that some amount of foraging habitat is necessary for a territory to be acceptable. The large size of territories suggests such a requirement, but there is no direct
evidence that loss of foraging habitat is a factor in current population declines. The available evidence does not support a relationship between reduction in foraging habitat and territory abandonment (8).

Our experiment suggests that control of hardwood understory and midstory alone has limited potential to convert unacceptable territories into acceptable ones and thus to promote population recovery. Presumably this is because cavities deteriorate if they are long abandoned. However, hardwood control should be effective in reducing loss of existing clusters and thus preventing population decline.

Until recently, attempts to provide additional habitat in which new cavity-tree clusters might be constructed consisted of establishing patches of old trees known as recruitment stands that the woodpeckers could colonize. That this approach was not immediately effective is consistent with the view of population dynamics presented here. One cannot expect this species to colonize habitat except at a very low rate. On the other hand, constructing cavities in recruitment stands should be an effective way to increase the number of groups in a population. This is the approach currently adopted by the US Forest Service. Using our technique and another they developed, since the fall of 1989 Forest Service personnel have been constructing cavities in abandoned territories, recruitment stands, and other vacant habitat in National Forests throughout the Southeast. Cavity construction is also beginning on other federal lands, state lands, and even private lands. The degree to which cavity construction can promote population expansion by increasing the number of acceptable territories will soon be apparent.

Cavity construction on already acceptable territories might reduce territory abandonment where cavities are lost faster than they can be replaced. In many areas, there is a scarcity of old trees in which the birds can construct replacement cavities (11). Cavity construction has been used to reduce territory abandonment on a large scale in one instance, again by the Forest Service. In September of 1989 Hurricane Hugo passed through the Francis Marion National Forest in South Carolina, devasting a population of nearly 500 groups of red-cockaded woodpeckers. About 60% of the birds perished, and 87% of the cavity trees were destroyed (22). That the number of acceptable territories was reduced even more than the number of birds created the potential for large-scale abandonment of territories among the surviving birds.

To avoid this possibility, the Forest Service constructed cavities on 222 territories (R. G. Hooper, personal communication). The birds used the cavities and even nested in them during the 1990 breeding season. Although 79 territories contained only single birds, the number of occupied territories in the 1990 breeding season was 65% of the number occupied before the storm. Thus, the number of groups was reduced by much less than the number of adults. By minimizing the loss of acceptable territories, cavity construction
will allow the population to recover much more quickly than if the number of
groups had been further reduced. Indeed, enough young were produced in
1990 to fill most of the remaining breeding vacancies on acceptable territo-
ries.

Implications for Conservation Biology

The use of artificial cavity construction in management of red-cockaded
woodpeckers illustrates the potential of conservation biology to contribute to
the management of endangered species. Where the theory is specific enough,
ecological principles can contribute to our ability to deduce effective manage-
ment principles. Application of theory in studies of basic biology has led to
insights that provide a new perspective on population dynamics and suggest a
solution to major management problems that had previously been intractable.
This new perspective would probably not have developed except from a
theory pertaining to the evolution of cooperative breeding. Further, this
perspective differs sufficiently from the conventional one that it requires a
reexamination of existing management techniques and even of the species’
recovery plan (59). Finally, this case illustrates effective communication
between researchers that enabled new research results to be quickly translated
into productive management. For this, R. E. F. Escano and R. G. Hooper of
the US Forest Service deserve much of the credit.

This case also illustrates the importance of considering the role of social
structure in population dynamics. The principle illustrated is that it often is
necessary to incorporate additional factors into general models to make them
sufficiently accurate in specific cases. Incorporating social structure into
population dynamics models may be important in a variety of contexts, for
eexample, in examining effects of habitat fragmentation on bird populations.
Social structure often affects dispersal behavior, and dispersal behavior
affects the ability of birds to colonize habitat patches. Cooperative breeders
are characterized by reduced long-distance dispersal capabilities and en-
hanced abilities to fill nearby breeding vacancies. Therefore, cooperative
breeders might be unusually good at persisting in patches large enough to
hold several neighboring groups, but unusually poor at persisting in smaller
patches that require repeated colonization.

When populations fail to behave as expected in response to management,
social structure may be a factor. The endangered Puerto Rican parrot (Amazo-
na vittata) may be an example. Although many birds live in a particular area,
there is only one breeding pair, or occasionally two (49). When a member of a
breeding pair dies, it is immediately replaced by a formerly nonbreeding bird
from the area. Releases of birds into an area may increase the population in
that area, but not the number of nesting birds. Several explanations of the low
recruitment rate of breeders have been offered (49). I offer another: Perhaps
some complex social structure exists which limits the number of breeders in an area. There is no evidence of this, but there are enough unanswered questions to impel basic research on social structure.

MINIMUM VIABLE POPULATION SIZE

Just as application of theory about the evolution of cooperative breeding to management of red-cockaded woodpeckers illustrates the potential of conservation biology, application of theory about population viability illustrates its pitfalls. In a world of fragmented habitats, the importance of establishing self-sustaining populations of rare species is obvious. To be viable, a population must be large enough to resist a number of threats, including demographic stochasticity, environmental stochasticity, loss of genetic variability, and catastrophes (47).

Conservation biologists have attempted to determine how large red-cockaded woodpecker populations must be to be viable. Unfortunately, existing theory is not sufficiently precise to enable such a determination, and this attempt has been counterproductive. Hurricane Hugo has provided a textbook example of the vulnerability of even large populations to catastrophe, arguing for the necessity of maintaining several populations. This consideration is incorporated into the species' recovery plan (59), but here the enlightened treatment of minimum viable population size in red-cockaded woodpeckers ends. A major problem is our inability to model population dynamics (see above), a prerequisite of viability analyses involving demographic and environmental stochasticity (e.g. 48, 48a). Hence, viability has been assessed solely in terms of loss of genetic variability, even though it generally is demography and environmental stochasticity rather than genetics that limits population viability (31). For this reason alone, one can have no confidence that a population size indicated by a genetic model is really sufficient to ensure long-term survival.

Further, the genetic models are terribly imprecise. These models are based on idealized populations. Although the relationship between the size of these idealized populations (effective population size) and the rate of loss of genetic variability is well known, the relationship between loss of genetic variability and population viability is not (31, 48a). The effective size necessary for viability differs among species due to differences in demographic constraints, inherent variability, and evolutionary history (32, 48a). The capability to determine what the appropriate effective size is for any particular species does not exist. This has led some to argue against the use of genetic models of population viability in conservation (13).

Additional imprecision arises in computing a population's effective size. The effective size of a population is almost always much smaller than the
Table 2  Estimates of the number of breeders required for an effective size of 500 in the Sandhills population of red-cockaded woodpeckers, using different models and different estimates of demographic parameters.

<table>
<thead>
<tr>
<th>Model</th>
<th>Demographic parameters</th>
<th>Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reed et al (44)</td>
<td>NCSU*</td>
<td>1018</td>
</tr>
<tr>
<td>USFWS (59)</td>
<td>none b</td>
<td>500</td>
</tr>
<tr>
<td>Emigh &amp; Pollak (16)</td>
<td>combined c</td>
<td>664</td>
</tr>
<tr>
<td>Emigh &amp; Pollak</td>
<td>NCSU*</td>
<td>794</td>
</tr>
<tr>
<td>Emigh &amp; Pollak</td>
<td>NCSU, dispersal correction d</td>
<td>574</td>
</tr>
<tr>
<td>Emigh &amp; Pollak</td>
<td>NCSU, +10% adult survival e</td>
<td>544</td>
</tr>
<tr>
<td>Emigh &amp; Pollak</td>
<td>NCSU, –10% adult survival f</td>
<td>1012</td>
</tr>
</tbody>
</table>

* Data collected from Sandhills population by my colleagues and I. Assumes no dispersal out of study area.

b Assumes effective size equals the number of breeders

c From Heckel and Lennartz (19). They use a combination of our data on survival and their data from another population on reproduction
d NCSU data, corrected for dispersal out of study area (see 60)
e NCSU data without dispersal correction, adding 10% to our estimates of adult survival
f NCSU data without dispersal correction, subtracting 10% from our estimates of adult survival

The actual number of breeders (5, 48a). Effective size is estimated using mathematical models that make a number of simplifying assumptions about reproduction, mating structure, and variation among individuals (e.g. 44). These assumptions are surely violated in real populations, introducing error of unknown magnitude into calculations of effective size (48a). Two models have been used to calculate the effective size of red-cockaded woodpecker populations (19, 44). These two models give very different results when applied to the same population, and even the more complex, presumably more accurate, model gives widely varying results depending on the accuracy of estimates of demographic model parameters (Table 2). Further, these models assume that populations are closed, whereas many are not. If populations receive immigrants, estimates of the rate of loss of genetic variability must be corrected for addition of genetic variability due to gene flow from other populations.

Implications for Woodpecker Management

Clearly one cannot determine precisely how large a viable red-cockaded woodpecker population must be currently, especially if genetic models provide the only criteria. Yet that is exactly what is being done. The US Fish and Wildlife Service, in its recovery plan for the species (59) and its enforcement policies, has defined a minimum viable population size based on genetic models, and uses that definition in making decisions about whether habitat
alterations jeopardize populations. The USFWS uses an effective size of 500 as its minimum standard. Originally effective size was equated to the number of breeders (59), but now various other values within the range given in Table 2 are used for the required number of breeders. I suggest that the genetic models are too imprecise to be useful in making management and policy decisions. The USFWS cannot be faulted for considering genetically based viability standards—the considerable literature on the topic essentially forces them to consider these standards. The fault lies with researchers involved in viability analysis, myself included, who have failed in communicating the limitations of these analyses to managers and policy-makers. This is an example of the premature application of ecological theory in management, resulting in an illusion of rigor that disguises the arbitrariness of individual decisions and inhibiting use of more reasonable approaches with other bases.

The red-cockaded woodpecker would be better served if the health of populations were assessed solely by criteria other than estimates of effective size. Other criteria are used by the USFWS in determining whether habitat alterations jeopardize populations, and these criteria could be given even more weight if genetically based viability assessments were excluded from consideration. Population goals are essential, but I suggest that the availability of genetically based standards inhibits the development of standards based on more reasonable approaches. Such approaches include demographic modeling and empirical studies (49). Even standards with little basis in theory, for example, deviation from maximum population density (6) may be more effective in achieving the goal of species preservation than use of genetically based viability assessments.

SUMMARY

The case of the red-cockaded woodpecker exemplifies how modern conservation biology can contribute to the management of endangered species. The value of artificial cavity construction illustrates how successful management can be deduced from ecological theory. Studies of basic biology have resulted in a new understanding of populations dynamics and a new management technique that, in combination with habitat preservation and restoration, has the potential to bring the species back from the brink of extinction.

Set against such promises are the problems involved in population viability analysis. In this case theory is not sufficiently developed, and it is best to resist the temptation to apply it. In such cases trial-and-error management, and use of criteria other than those derived from theory in decision making, are more appropriate. Improved communication between managers and researchers, based on increased understanding and appreciation of one another, is a necessity if we are to distinguish those situations in which we can use
theory from those in which we cannot. The successes promise to increase and the problems to diminish as conservation biology matures, to the betterment of society and the natural world.

ACKNOWLEDGMENTS

My research on red-cockaded woodpeckers in the Sandhills has been supported by NSF grants BSR-8307090 and BSR-8717683, and the North Carolina Agricultural Research Service. I thank my collaborators, Drs. P. D. Doerr and J. H. Carter, III for their many contributions to the woodpecker research. I also thank the many graduate and undergraduate students who have contributed to data collection and analysis. M. Hassler assisted with the tables and E. Seaman with the figures. F. James provided a helpful review of the manuscript.

Literature Cited


