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### An Application of O'Connor's Brood-Reduction Model

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Avian brood reduction has been described as an adaptive strategy that allows some offspring to survive at the expense of their nest mates (Lack 1954, 1968, Ricklefs 1965). In years when resources are limiting, the fitness of parents, surviving offspring, and even dead offspring may be enhanced by differential feeding of the young so at least some survive (O'Connor 1978). For food-limited populations, laying a large clutch, although leading to brood reduction in most years, may be advantageous during years with abundant food. Presumably, this occasional success offsets the energetic expense of producing inviable nestlings in other years. In the typical mortality pattern for brood reduction, the last-hatched chick dies of starvation soon after hatching and thus at a point when little investment has been made in this chick (Lack 1954, 1968, Ricklefs 1965, Slagsvold 1982, Scott and Martin 1986, Gibbons 1987). Brood reduction has been promoted as one explanation for the maintenance of asynchronous hatching of eggs (Lack 1954, 1968). By promoting size and competitive differences among young in a brood, hatching asynchrony may facilitate parental adjustment of brood size to the availability of food resources (Lack 1954, 1968).

O'Connor (1978) provided a model for the evolution of brood reduction based on the difference between a nestling's survival rate in a brood of  $B$  young and that of  $B - 1$  young. According to the model, a nestling's fitness is derived from its direct fitness component, based mostly on its survival probability, and its indirect fitness component gained from its

surviving siblings. If survival is brood-size dependent (i.e. decreasing with increasing brood size), a nestling gains in indirect fitness in a large brood, but its own survival (hence direct fitness) is at risk. A nestling's total fitness can be calculated using survival estimates, and the difference in survival between broods of different sizes should determine the nestling's relative fitness by brood size.

As the difference between survival rates increases, selection acts first for siblicide, then for infanticide, and lastly for suicide. If each nestling's direct fitness is enhanced in reduced brood sizes, then it might be beneficial to one (or more) of the nestlings to attack another, usually smaller, sibling (the "victim"). To offset the loss of some indirect fitness due to the death of a sibling, the "survivors" must have a sufficient gain in direct fitness.

The contribution of each nestling to its parents' direct fitness component is dependent on its survival probability. A parent's fitness can be calculated as half of the combined survival probabilities of all nestlings. If the mortality difference between different brood sizes is very large, then despite the parents' loss of some fitness with the death of one nestling, the total fitness of the surviving nestlings and the parents may be increased by the improved survival of the remaining chicks. At these higher survival differentials, it becomes beneficial for the parents to ignore or even attack a nestling if the victim's death would improve the survival of the remaining chicks substantially.

Finally, if the difference in survival probabilities between different brood sizes is even more extreme, the victim actually may benefit from its own death. By giving up its life, the victim greatly promotes its siblings' survival and thus increases its indirect fit-

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ness. In all of these cases, if some nestlings do not get a fitness advantage via brood reduction, then according to this simple model, brood reduction should not occur.

Despite many descriptive (e.g. Ricklefs 1965, Howe 1976, Schifferli 1978, Zach 1982, Murphy 1983, Richter 1984) and experimental (e.g. Slagsvold 1982, Gibbons 1987, Skagen 1987) studies of avian brood reduction, the mortality differential between brood sizes (sensu O'Connor 1978) has not been determined except in Hagan's (1986) study of Ospreys (*Pandion haliaetus*). These mortality differentials not only indicate the mechanism by which brood reduction should occur (e.g. siblicide), but whether it should occur at all (O'Connor 1978).

The costs of brood reduction and the life-history consequences of raising small versus large broods currently are receiving much attention (e.g. Forbes 1993, 1994, Mock and Forbes 1994, Slagsvold et al. 1995, Stoleson and Beissinger 1995, Amundsen and Slagsvold 1996). O'Connor's model does not, however, account for any future effects brood size might have on parents or offspring. Such long-term effects of brood size include a parent's ability to recover from the energetic expenses of rearing large broods (Askenmo 1979, Smith et al. 1987, Smith 1988, Nur 1988, White et al. 1991, Slagsvold et al. 1995) and an offspring's potential for survival and recruitment after reaching independence (Murphy 1983, Gard and Bird 1990, Tinbergen and Daan 1990, Amundsen and Slagsvold 1996).

In this paper, I present mortality differentials for Red-cockaded Woodpeckers (*Picoides borealis*) to make predictions about the existence of brood reduction and its mechanisms. Indications of brood reduction in Red-cockaded Woodpeckers include reports of brood sizes at fledging that are smaller than clutch sizes (Ligon 1970, 1971, Lennartz et al. 1987), and a mortality pattern consistent with brood reduction (LaBranche and Walters 1994). Incubation is thought to begin with the penultimate egg, and hatching typically is asynchronous (Jackson 1994). Nestling mortality is highest during the first six days after hatching; after this time, little mortality occurs until fledging (ca. 26 days; LaBranche and Walters 1994).

*Methods.*—Data are from an ongoing study of >200 groups of color-banded Red-cockaded Woodpeckers initiated in 1980 in the sandhills of south-central North Carolina. Red-cockaded Woodpeckers are cooperatively breeding residents of southern pine forests (Jackson 1971, USFWS 1985, Ligon et al. 1986, Walters 1990). They live in groups consisting of a breeding pair and up to four male helpers (Beckett 1971, Ligon 1971, Lennartz and Harlow 1979, Lennartz et al. 1987, Walters et al. 1988). In the sandhills population, clutch sizes range from one to five eggs ( $\bar{x} = 3.3$ ; Carter 1989, LaBranche and Walters 1994). Data collection procedures, which include monitor-

ing all nests, are described elsewhere (Carter et al. 1983, Walters et al. 1988, LaBranche and Walters 1994).

O'Connor's (1978) model was tested using mortality rates calculated by the Mayfield (1961, 1975) method (LaBranche 1988). Mortality rates excluded nests where all the young were lost between checks at a nest. The mortality of an entire nest (during the egg or nestling stage) can be attributed to causes other than brood reduction, including abandonment, predation, and usurpation of the cavity by other cavity users (LaBranche and Walters 1994). In addition, I used only nests found during the egg stage, and thus of known clutch size. All nestlings in a brood were assumed to be full siblings (Lennartz et al. 1987, Walters 1990). Data were separated by brood size, and average daily mortality rates were calculated for each brood size in each year. These average daily rates were used to calculate the difference ( $D$ ) in mortality rates in broods of different sizes:

$$D = \mu(B) - \mu(B - 1), \quad (1)$$

where  $\mu(B)$  is the mortality rate of a brood of size  $B$ .

To use O'Connor's model, thresholds were calculated for differences in daily mortality rates that are sufficient to produce fitness advantages to the survivor ( $S$ ), adult ( $A$ ), or victim ( $V$ ), respectively. These threshold percentages per day are ( $T$  = length of the nestling period):

$$d_s = (1/T) \ln[(B + 1)/B], \quad (2)$$

$$d_A = (1/T) \ln[B/(B - 1)], \text{ and} \quad (3)$$

$$d_v = (1/T) \ln [(B + 1)/(B - 1)]. \quad (4)$$

When the magnitude of the difference in mortality rates ( $D$ ) exceeds one of these thresholds, then selection should favor the individual(s) whose total fitness increases with the reduction in brood size. Thus, if  $D > d_s$ , the surviving nestlings accrue a fitness advantage from brood reduction, and siblicide is expected. Similarly, if  $D > d_A$ , then selection favors infanticide, and if  $D > d_v$ , selection favors suicide. Note that the surviving nestlings always benefit whether siblicide, infanticide, or suicide occurs, and the parents also benefit from nestling suicide. However, when the parents do not accrue benefits from the loss of one of their nestlings but the survivors do, then conflicting selective pressures occur.

*Results.*—In some years, daily mortality rates for broods of five were an order of magnitude higher than those for broods of two (Fig. 1), suggesting that mortality is brood-size dependent. Mortality differentials for broods of four equaled the threshold for siblicide in one year and exceeded that for infanticide in two other years (Fig. 2). In the other seven years, the mortality differentials were below the siblicide threshold (Fig. 2).

Because broods of five were very rare, mortality rates could be calculated only in four years (Fig. 1).

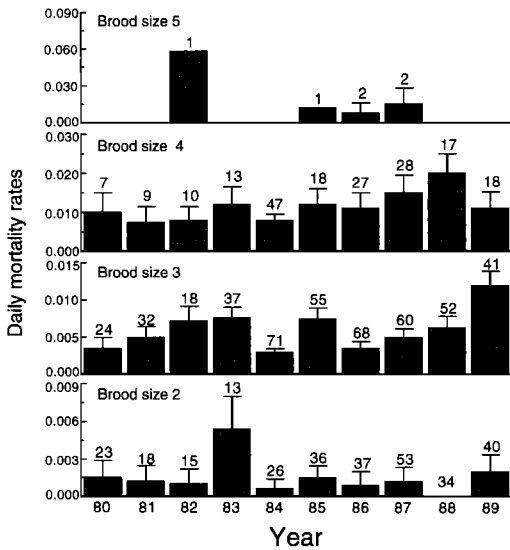


FIG. 1. Mean daily mortality rates (whiskers indicate SD) for Red-cockaded Woodpecker broods of different sizes, 1980 to 1989. Note that the scales for mortality rates differ by brood size. Sample sizes are indicated above bars.

The rate differential for broods of five exceeded the threshold for suicide in 1982 and did not exceed any threshold in 1987. In 1985 and 1986, broods of five survived better than those of four, resulting in negative differential values, although this may have been an artifact of the small number of broods of five. For other brood sizes (two and three), differences in mortality rates were below all threshold levels in all years (Fig. 2).

*Discussion.*—Although survival rates were consistently related to brood size, in only 3 of 10 years were mortality differentials large enough that O'Connor's model suggested selection for brood reduction in Red-cockaded Woodpeckers. As one might expect, selection for brood reduction occurred only in the largest broods. The model suggested that in 2 of the 10 years, the parents' fitness would be enhanced by reducing their brood from four to three nestlings, thus suggesting infanticide as the mechanism of brood reduction. In a third year, the surviving offspring could enhance their fitness by attacking or otherwise causing the death of a sibling, thus suggesting siblicide as the mechanism.

Although the patterns of early nestling mortality in six years (1980 to 1985; LaBranche and Walters 1994) are consistent with the brood-reduction hypothesis, O'Connor's model does not predict selection for brood reduction in those years. It may be that the brood-reduction hypothesis does not explain early nestling mortality in Red-cockaded Woodpeckers. Alternatively, there may be intermittent selection

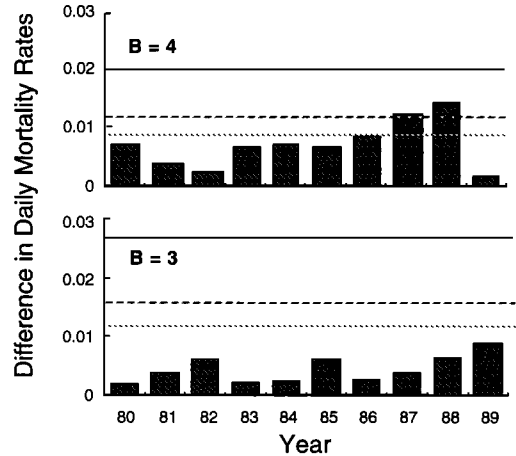


FIG. 2. Yearly differences between mortality rate for broods of size  $B$  and size  $B - 1$  (sample sizes are in Fig. 1). Threshold differentials: dotted line = siblicide; dashed line = infanticide; solid line = suicide.

for brood reduction. If the mortality differential is large enough, as it appeared to be in 1986 to 1988, then brood reduction may be favored only in some years. If this selection pressure is strong enough in any one of these years, this could promote some brood reduction in years when it is not advantageous, assuming that the proximate control of brood reduction is imprecise.

Another alternative is that the model does not allow an adequate test of the brood-reduction hypothesis. There are several drawbacks to this simple model. First, by its strictest definition, brood reduction is the loss of nestlings soon after hatching, suggesting that the model's assumption of constant mortality contradicts the typical pattern of mortality. For Red-cockaded Woodpeckers, little mortality occurs after the young are six days old. Second, the model assumes that survival of an individual after fledging is constant, or at least independent of brood size. Elsewhere, I showed that the relative (i.e. within-brood) mass of Red-cockaded Woodpecker nestlings at the time they are banded is a good predictor of a nestling's probability of surviving to its first adult year (LaBranche 1992; data for 1980 to 1986 only). Large nestlings (especially the largest in a brood) have higher probabilities of surviving through their first winter and surviving to become breeders than do their smaller nest mates. The strength of this effect varied among years. If small siblings remain at a considerable survival disadvantage after fledging, then selection also may act to reduce parental investment in these young via brood reduction. It is likely that there are many positive and negative selective forces on brood reduction, which could be evaluated by determining offspring quality (e.g. Slagsvold 1986),

offspring recruitment potential (e.g. Slagsvold et al. 1995), or reproductive values of nestlings and entire clutches (e.g. Tinbergen and Daan 1990). However, the scope of this paper is limited to selective forces predicted by the mathematical model. Additional selective factors only strengthen the idea that there is selection for brood reduction in this population.

Parental effort was not measured in this study and is not addressed by O'Connor's model. Reduced effort in current reproduction (via brood reduction) may promote parental survival and improve subsequent reproduction (Askenmo 1979, Smith et al. 1987, Smith 1988, Nur 1988, White et al. 1991, Forbes 1993, Mock and Forbes 1994, Slagsvold et al. 1995). These evolutionary tradeoffs cannot be evaluated from a model based solely on nestling mortality rates, but they are interesting nonetheless. My only estimate of the relationship between parental effort and survival is anecdotal: in 1991, four of the five double-brooded females disappeared and were presumed dead before the subsequent breeding season (LaBranche et al. 1994). Although the results reported here cannot be extended to make predictions about life-history strategies, it would be surprising if there were no effects of parental effort on future survival and reproduction. O'Connor's model only skims the surface of the multiple effects that select for or are costs of brood reduction.

O'Connor's model suggests that infanticide or siblicide are the mechanisms by which brood reduction occurs in Red-cockaded Woodpeckers. The use of cavities prevents direct observations of behaviors that would promote brood reduction, but several personal observations may shed light on siblicidal mechanisms. During nest checks, it was not unusual to observe a nestling positioned above or on top of others in the small space at the bottom of a cavity. From a nest of four-day-old young, I removed a flattened nestling that did not live beyond one day after hatching (trampling may not have caused the death but is indicative of the abilities of these nestlings to gain position advantages). Siblicide likely is promoted by competition for position and food rather than by aggression, because small nestlings have poor head and neck control. Differential feeding and direct attacks on young have been suggested as modes of infanticide (e.g. O'Connor 1978, Drummond et al. 1986, Urrutia and Drummond 1990), although the former is more common. I have no observations to support or refute either method of infanticide in Red-cockaded Woodpeckers.

This descriptive study is not a critical test of O'Connor's model. Ideally, experimental manipulations of clutch size or brood size should be employed to circumvent problems associated with differences in breeding experience, territory quality, group quality, or timing of breeding. Because experimental manipulations are inappropriate for an endangered species, I have assumed that mortality is similar for

all groups raising young regardless of possible variability in these measures. This assumption requires scrutiny because quality (parental, territorial, etc.) may be related to optimum clutch or brood size and thus to the resulting mortality rates. Red-cockaded Woodpecker nests initiated early in a breeding season have lower mortality rates than those initiated late in a season (LaBranche and Walters 1994). Also, females in their first adult year initiate nests later than do their older counterparts (LaBranche and Walters 1994). Data from this population suggest that helpers provide little incremental improvement on reproductive output and that territory quality is correlated with the presence and number of helpers (Walters et al. 1988, Walters 1990). Despite the certain relationship between quality and nestling mortality rates, my results are conservative. If different circumstances promote different optimum brood sizes, then the mortality differentials between nests of different qualities are underestimated. The mortality differentials, calculated from my descriptive data and uncorrected for quality, should not have indicated selection for brood reduction, but they did. Thus, my results are an important contribution to the understanding of selection for brood reduction, especially considering the large sample size, the long-term nature of the study, and the paucity of tests of O'Connor's model.

O'Connor's model predicts selection for brood reduction in Red-cockaded Woodpeckers for some brood sizes in some years. Because an individual's fitness cannot be assessed only by survival probabilities during the nestling period, I suggest that O'Connor's model is insufficient for detecting brood reduction in all of the years in which it is favored by selection. The low mortality late in the nestling stage, seasonal variations in mortality, the long-term effects of small nestling size, the potential for improved parental survival and future reproduction, and territory or group quality could cause smaller threshold differences than the model predicts. I suggest that selection for brood reduction occurs frequently in broods of Red-cockaded Woodpeckers.

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