ON THE LIMITED BREEDING OPPORTUNITIES HYPOTHESIS FOR AVIAN CLUTCH SIZE

Martin (1993) examined the clutch size of cavity-nesting birds that did and did not excavate nest holes to test the limited breeding opportunities hypothesis for avian clutch size. Although comparative data presented by Martin corroborated the hypothesis by showing that clutch size was more highly correlated with nest site availability than with either nest failure rates or adult survival rates, critical predictions remain untested.

The limited breeding opportunities hypothesis (Beissinger and Waltman 1991; Martin 1992) suggests that a limited availability of nest sites favors larger clutch sizes, which may hatch asynchronously, because reproductive effort should be high when residual reproductive value is low (Williams 1966; Stearns 1976). Thus, when nesting opportunities are limited through intra- or interspecific competition, females might be expected to invest heavily in reproductive effort by laying large clutches, if food supply permits, whenever the chance to nest arises. Nesting opportunities would include the availability of either nest sites for cavity-nesting species or territories for noncavity nesters (Beissinger and Waltman 1991; Martin 1992). The early onset of incubation should also be indirectly favored when breeding opportunities are limited (Beissinger and Waltman 1991), because early incubation would serve to defend the nest site and eggs against intruding pairs through occupancy; promote large clutch sizes by minimizing the energy expenditures of females during egg laying through decreased locomotor activity (Walsberg 1983; Beissinger 1987); and minimize the time that nestlings and breeders are exposed to predators during the nestling phase, when predation rates are often highest, since asynchrony reduces the amount of time before the first chick fledges (Clark and Wilson 1981; Hussell 1985; Magrath 1988).

A number of predictions of the limited breeding opportunities hypothesis for avian clutch size can be tested by making carefully controlled interspecific comparisons. The key prediction is the expected demographic trade-off between clutch size and the opportunity to breed: the proportion of individuals in a population that breed annually should be negatively related to clutch size. The probability of breeding is the most direct test of this hypothesis and is likely to be affected by (and hence will need to be controlled for) both age and body size. Martin (1993, p. 944) recognizes that this is the critical prediction when he states that "work is needed on breeding frequencies to test the hypothesis explicitly." The proportion of breeders (or, conversely, nonbreeders) is rarely given in many demographic studies and can often be difficult to measure in the field. However, as more long-term field studies are completed, better comparative data should be available to test this prediction. The density of intra- and interspecific competitors

for nesting opportunities might be used as an indirect measure of the expected proportion of breeders in the population.

If breeding opportunities are limited, they could also be reflected in a delay in the age of first breeding (see, e.g., von Haartman 1971; Eriksson 1982; Brawn 1987). Thus, a second demographic prediction of the limited breeding opportunities hypothesis is that the average age of first breeding should be positively related to clutch size. Like the proportion of breeders, the average age of first breeding will need to be controlled for body size (Western and Ssemakula 1982; Saether 1988; Gaillard et al. 1989).

Predictions of the limited breeding opportunities hypothesis can also be tested with comparative behavioral data. Interference competition among potential breeding pairs for nesting sites (see, e.g., Ingold 1989; Barba and Gil-Delgado 1990; Brawn 1990) or territories, sometimes leading to infanticide (see, e.g., Freed 1986; Johnson and Kermitt 1990; Pribil and Picman 1991; Waltman and Beissinger 1992), should be exhibited if opportunities to breed are limited. Thus, species with larger clutch sizes are predicted to defend their nest sites or territories more vigorously or frequently, and to experience more severe competition for nest sites or territories than species with smaller clutch sizes. Likewise, the likelihood of nest site or territory takeovers and the frequency of infanticide should be positively related to clutch size.

Martin (1993) tested the limited breeding opportunities hypothesis by examining the correlation between the percentage of nests in existing cavities and clutch size. This comparison gave a good demonstration of the potential for cavity limitations to select for large clutch sizes. But it is a corollary rather than a test of the hypothesis, because the percentage of nests excavated is an indirect index of nest site limitations. It does not take into consideration variation in the number and density of intra- and interspecific competitors for cavities (e.g., bats, bees, rodents, or other species of birds; Snyder et al. 1987; Barba and Gil-Delgado 1990; Brawn 1990) or the availability of natural cavities (Gutzwiller and Anderson 1988; Walankiewicz 1991). Both factors can vary among populations and may exhibit latitudinal trends (Gibbs et al. 1993). Furthermore, territorial behavior and interference competition can limit access to cavities even when cavities are available and unoccupied (see, e.g., Verner 1977; Harris 1979; Brawn and Balda 1988). The approach used by Martin would be corroborated by demonstrating that clutch size and the percentage of nests in existing cavities were negatively related to the density of potential cavities, positively related to the density of competitors for holes, and negatively related to the ratio of these two factors (cavities/competitors).

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