

ABSTRACT

PODOLSKY, ANDREI LVOVICH. Behavioral Ecology and Population Status of Wood Thrush and Ovenbird in Great Smoky Mountains National Park. (Under the direction of Theodore R. Simons and Jaime A. Collazo.)

Population declines of Neotropical migratory landbirds are attributed primarily to habitat fragmentation, higher rates of predation, and brood parasitism. These findings have stimulated many studies of avian reproductive success and comparisons of the source-sink dynamics of avian populations in fragmented and contiguous forests. Limited demographic data often impose a number of simplifying assumptions on source-sink models of forest passerines, such as assumptions about the number of possible breeding attempts, adult and juvenile survival rates, and pairing success.

In 1999-2001, I studied the relationships between food availability, predation risk, reproductive success, demography, and parental behavior of Ovenbird (*Seiurus aurocapillus*) and Wood Thrush (*Hylocichla mustelina*) populations in Great Smoky Mountains National Park. I monitored 178 Wood Thrush and 110 Ovenbird nests, ascertained the pairing status of 326 Ovenbird males, marked and identified the age of 30 reproducing Ovenbird females, and sampled parental behavior of the focal species at 50 food-supplemented nests and 62 control nests during 283 four-hour observational sessions conducted at three times of day and three standardized nestling ages.

For Ovenbirds, I estimated pairing success at 60%, daily nest survival rate at 0.95, annual survival of adult females at 0.63, of juvenile females at 0.32, annual

fecundity at 0.96 female offspring per breeding female, and a finite rate of population increase (λ) of 0.94. However, such λ -estimate is erroneous, because Ovenbird populations in the park do not appear to be rapidly declining sinks. Neither do they appear to be fast growing sources, so the most likely scenario is a population at equilibrium, or a moderate population sink. In either event, my findings suggest that this large unfragmented tract of presumed high quality forested habitat does not appear to function as a significant population source.

I developed a population viability model for the Ovenbird with varying rates of pairing success, renesting, and double brooding. Model simulations yielded λ 's close to 1 only at high rates of pairing success and renesting after nest failure, and a double brooding rate of 0.33. I propose that at the southern limits of Ovenbird distribution, double brooding may occur at higher rates, than previously thought, and may compensate for its low annual fecundity.

I developed a conceptual model linking parental care of Wood Thrushes and Ovenbirds to their reproductive success and food availability. My major findings were similar for both species. Daily nest survival rates were significantly higher in food-supplemented (treatment), than in control nests. The nestling period of food-supplemented nests was shorter than of control nests, which reduced the exposure of treatment nests to predation. Treatment nests showed much higher productivity, than control nests. Nestlings at treatment nests were heavier prior to fledging, despite the fact

that feeding rates at treatment and control nests were similar. Parental attendance was significantly higher at food-supplemented nests than at control nests.

I conclude that parental behavior, mediated by food availability, has adaptive significance in Wood Thrushes and Ovenbirds because it improves their reproductive success when food is abundant.

Food supplementation is rarely applied to ground-foraging insectivorous passerines because of the practical difficulties. I provided mealworms at feeding stations made of plastic transparencies covered with a thin layer of green moss. Only 16% of breeding pairs of Wood Thrush and Ovenbird failed to use supplemental food. Only minor amounts of mealworms were taken by non-target consumers. I conclude that my method is effective for the focal species, and its applicability to other ground-foraging insectivorous passerines should be tested in the field.

**BEHAVIORAL ECOLOGY AND POPULATION STATUS OF
WOOD THRUSH AND OVENBIRD
IN GREAT SMOKY MOUNTAINS NATIONAL PARK**

by

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This work is dedicated to my wife, Marina Podolsky, and my children, Galina and Igor, who stoically bore with me during almost seven years of my graduate education, and who were my major inspiration and support.

BIOGRAPHY

Andrei Lvovich Podolsky spent his childhood in southeastern Europe, in the state of Saratov in Russia. Not unlike North Carolina, which hosts a wide range of landscapes, from the mountains with truly northern vegetation to the coastal sand-dunes, the state of Saratov has it all: northern pine and spruce forests, southern deciduous oak stands, shrub-steppe, tall-grass prairie, semi-desert, chalk cliffs and beautiful beaches along the Volga River. Such a wide range of vegetation and climate sustains the impressive diversity of birds found there. The Volga River, a major bird migration corridor in continental Eastern Europe, contributes many Arctic and Siberian species to the state bird list. No surprise, Andrei fell in love with wild birds at the age of 5, and started to keep his bird-watching notes at the age of 6.

Ornithology, however, was not (career-wise) a very promising occupation with four ornithological positions in a state the size of Virginia. After college, he did the ‘Bird-Habitat Associations’ project for the local university. The best non-scientific result of this venture was getting married to his field assistant, Marina Lazko. Shortly after, Andrei started to work for the Saratov State Center for Environmental Education as an extracurricular teacher, and in a short while became a deputy director. He still feels nostalgic about working with kids, grades 5 to 7, his favorite age... His children, Galina and Igor, were born at that time. He organized summer and winter field ornithological camps, and a state-wide competition in field ecology for school students, grades 5 to 11.

However, Andrei decided to change his life dramatically and to open new

horizons ...as well as see new birds! He crossed the ocean and landed in New Haven, CT. His Masters' years at Yale were a wonderful time of discovery of North American education, life, culture, nature, and of course – birds!! In August of 1997, the Podolsky family of four undertook the grand tour, driving a 7,000-mile loop in three weeks across the continent, through 22 states and 8 National Parks. The result was over 200 new species on his bird list, and about 50 National Monuments, museums of natural sciences and history, art galleries, safari parks, zoos and aquariums.

In January 1999, Andrei was accepted to the PhD program at North Carolina State University, and spent three wonderful field seasons in one of the most beautiful places he has ever seen, the Great Smoky Mountains National Park. He immensely enjoyed living in North Carolina, a state with a rich history and nature. This dissertation is the culmination of his four years in North Carolina.

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My wife, Marina Podolsky, and children, Galina and Igor, have been supportive in many ways, including putting up with my crazy schedule.

My parents, Galina and Leo Podolsky, were the ones who encouraged my interest in birds and unusual – for a little Russian boy – hobby: bird watching.

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INTRODUCTION

Population declines, observed in Neotropical migratory landbirds in eastern North America, are attributed primarily to habitat fragmentation, higher rates of predation, and brood parasitism (Whitecomb et al. 1981; Robbins et al. 1989; Terborgh 1992; Askins et al. 1990; Peterjohn et al. 1995; Sauer et al. 1996; Askins 2000). These findings have stimulated many studies of avian reproductive success and comparisons of the source-sink dynamics of avian populations in fragmented and contiguous forests (Faaborg et al. 1995; Donovan et al. 1995; Manolis et al. 2000; Flaspohler et al. 2001; Murphy 2001). However, limited demographic data often imposed a number of simplifying assumptions on source-sink models of forest passerines. These included assumptions about the number of possible breeding attempts (Pease & Grzybowski 1995), the relationship between clutch size and annual fecundity (Flashpohler et al. 2001), adult and juvenile survival rates (Temple & Cary 1988; Burke & Nol 2000; Simons et al. 2000), and pairing success (Villard et al. 1993; Van Horn et al. 1995).

Another important issue to consider in relation to the population declines of Neotropical migratory birds is whether protected areas, containing large tracts of unfragmented contiguous forest, serve as refuges for these species. The southern Appalachians, including Great Smoky Mountains National Park, sustain an exclusive diversity of breeding Neotropical migrants, constituting over 80% of the breeding bird community (Terborgh 1989).

The reproductive success of birds depends largely on levels of predation and food availability (Skutch 1949; Wilcove 1985; Martin 1992, 1995). A number of studies have investigated whether breeding birds are able to buffer the detrimental effects of predation with parental care (Mangel and Clark 1986; Clutton-Brock 1991), and whether parental care depends on food availability (Simons and Martin 1990; Ward 2001).

In this dissertation I focus on: (1) how additional breeding attempts (renesting and multiple brooding) and pairing success influence population growth rates, and (2) how parental care affects nesting success under conditions of varying food availability. The focal species of my study (1999—2001), Wood Thrush (*Hylocichla mustelina*) and Ovenbird (*Seiurus aurocapillus*), are typical Neotropical migrants, whose populations have been declining steadily in the southern Appalachians (Van Horn and Donovan 1994; Roth et al. 1996).

In Chapter 1, I build a demographic model for the Ovenbird in Great Smoky Mountains National Park using empirical data on reproductive success and indirect estimates of Ovenbird survival, renesting, double brooding and pairing success. By incorporating uncertainties related to additional breeding attempts, pairing success, and bird survival, into a source-sink model for the Ovenbird, I show that the population growth rates are sensitive to assumptions about renesting, double brooding and pairing success, suggesting that these parameters should not be overlooked or ignored in population models. Model oversimplification is treacherous because of the high relative importance of adult and juvenile female survival, renesting, multiple brooding, and pairing success. To assume 100% pairing success and 100% renesting, or >80% annual

survival of adult female could result in a false source population. At the same time, assumption of a 0% multiple brooding in a “normally” single-brooded species could yield a false sink.

In Chapter 2, I build a model relating parental behavior to food availability, and show how behavioral responses can potentially buffer the risk of predation. I experimentally manipulated food availability at nests and monitored the differences in parental time budgets, nest attendance, and in nest survival at food-supplemented (treatment) and control nests. Paying tribute to Lack (1954), this study confirms that food availability does influence nest survival. However, the mechanisms are different from those proposed by Lack. Parental vigilance at nest seems to play an important role in reduction of predation risk.

Chapter 3 discusses the practical difficulties of food supplementation in experimental field studies of insectivorous birds (Boutin 1990) and gives an expanded review of the technique I developed and tested on Wood Thrushes and Ovenbirds.

Future studies aimed at empirical evaluation of demographic parameters based on the monitoring of marked birds are needed to better understand the population status of the Neotropical migratory species. Using multiple levels of food supplementation in future experimental work (Steury et al. 2002) would allow quantification of the rate of behavioral changes in parental birds.

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CHAPTER 1

IMPORTANCE OF PAIRING SUCCESS AND MULTIPLE BROODING IN SOURCE-SINK MODELS OF OVENBIRD POPULATIONS¹

¹ Andrei L. Podolsky, Theodore R. Simons, and Jaime A. Collazo. Prepared for submission to “Conservation Biology”.

Abstract. Population declines of Neotropical migratory landbirds are attributed primarily to habitat fragmentation, higher rates of predation, and brood parasitism. The fragmentation paradigm proposes that large tracts of unfragmented habitat sustain populations with higher rates of reproductive success in these species. In 1999-2001, we studied the reproductive success and demography of the Ovenbird (*Seiurus aurocapillus*) populations in Great Smoky Mountains National Park. We monitored 110 nests, ascertained the pairing status of 326 males, and marked and identified the age of 30 reproducing females. Direct and indirect evidence suggests a possibility of double brooding. We estimated pairing success at 60.1%, a daily nest survival rate of 0.95, successful brood size at 3.8 offspring, annual survival of adult females at 0.63, of juvenile females at 0.32, annual fecundity at 0.96 female offspring per breeding female. Applied to a population growth model, these values yield $\lambda = 0.94$. Ovenbird populations in the park do not appear to be declining rapidly, and the Breeding Bird Survey estimated regional population declines of 0.26-1.5% annually. Therefore, our estimate of λ is probably not correct. The most likely scenario is a population at equilibrium, or a moderate population sink. In either event, our findings suggest that this large unfragmented tract of presumed high quality forested habitat does not appear to function as a significant population source. We developed a population viability model for Ovenbirds with varying rates of pairing success, renesting, and double brooding. Model simulations yielded λ close to 1 only at high rates of pairing success and renesting after nest failure, and a double brooding rate of 0.33. We propose that at the southern limits of

its distribution, double brooding may occur in this species at higher rates than previously thought. The potential for double brooding to compensate for low annual fecundity in this species deserves further investigation.

INTRODUCTION

Population declines, observed in Neotropical migratory landbirds in eastern North America, are attributed primarily to habitat fragmentation, higher rates of predation, and brood parasitism (Whitecomb et al. 1981; Wilcove 1985; Robbins et al. 1989; Terborgh 1989, 1992; Askins et al. 1990; Hagan & Johnston, eds. 1992; James et al. 1992; Martin & Finch, eds. 1995; Peterjohn et al. 1995; King et al. 1996; Sauer et al. 1996, Donovan et al. 1997; Askins 2000). These findings have stimulated many studies of avian reproductive success and comparisons of the source-sink dynamics of avian populations in fragmented and contiguous forests (Villard et al. 1992; Faaborg et al. 1995; Manolis et al. 2000; Flaspohler et al. 2001; Murphy 2001). According to Thompson et al. (2001), 70% of studies published from 1984–1997 did not distinguish between nest success and annual reproductive output, and only 10% of the articles estimated annual fecundity. Recent studies that have measured reproductive output have shown that reneesting and multiple brooding may account for up to 40% of annual productivity in birds (Murray 1991, 1992; Martin 1995; Schroeder 1997; Farnsworth and Simons 2001).

Model building in population ecology always involves trade-offs among generality, realism, and precision (Levins 1966). Limited demographic data often impose a number of simplifying assumptions on source-sink models of forest passerines. These include assumptions about the number of possible breeding attempts (Pease & Grzybowski 1995), the relationship between clutch size and annual fecundity (Flashpohler et al. 2001), and adult and juvenile survival rates (Temple & Cary 1988;

Burke & Nol 2000; Simons et al. 2000). Pairing success is another important and often overlooked parameter. It shows considerable variation across species' ranges and habitats (Villard et al. 1993; Van Horn et al. 1995). Pairing success is poorly studied and therefore not usually included in source-sink models, despite the fact that only paired individuals participate in reproduction and contribute to the annual reproductive output.

While the fragmentation paradigm predicts that large tracts of unfragmented habitat sustain population sources for Neotropical migratory birds (Robinson et al. 1995), results of a few recent studies suggest that populations of even relatively abundant species in large tracts of old-growth forests do not always act as strong sources (Simons et al. 2000). Delibes et al. (2001a) proposed "attractive sinks" and "deceptive sources" as a possible explanation: when birds lack proper cues, associated with increased fitness, their selection of habitat can be maladaptive. Attractive sinks can occur when high risks of mortality are encountered in apparently optimal habitat (Delibes et al. 2001b).

We used the Ovenbird (*Seiurus aurocapillus*) as a model species in our study for several reasons. It is a common Neotropical migratory bird with high nesting densities in the southern Appalachians (Simons & Shriner 2000), and its populations have declined at an average annual rate of 1% over the past three decades (Robbins et al. 1989; Van Horn & Donovan 1994). The Ovenbird is considered a single-brooded species, although a few cases of multiple brooding have been reported as far north as Ontario (Zach & Falls 1976; Van Horn & Donovan 1994). Many species of temperate zone passerines are known to have multiple broods at the lower latitudes of their breeding ranges (Payevski 1985). Although there are many published studies of the reproductive success and

population status of Ovenbirds elsewhere in the breeding range (Wander 1985; Gibbs & Faaborg 1990; Donovan et al. 1995*a*, 1995*b*; King et al. 1996; Burke & Nol 1998, 2000; Porneluzi & Faaborg 1999; Flaspohler et al. 2001), few published data on the reproductive ecology of the Ovenbird are available from the southern parts of its distribution.

The objectives of our research were to assess the population status of the Ovenbird in Great Smoky Mountains National Park using field data on adult survival, nesting success, and productivity, and to evaluate the potential influence of pairing success and multiple-brooding on population growth rates.

METHODS

Study Area

Great Smoky Mountains National Park, established in 1934, is located along the North Carolina—Tennessee border. It protects the largest contiguous old-growth forest in eastern North America. Our seven study sites were located between Gatlinburg, TN (N 35°42'52", W 83°30'41"), and Waterville, NC (N 35°47'02", W 83°06'44"), within the Gatlinburg, Mount Le Conte, Jones Cove, Mount Guyote, Hartford, Waterville, Cove Creek Gap, and Lufte Knob USGS quadrangles. The sites were comprised of large contiguous tracts of mixed deciduous forest ≥ 65 years old, ranging in elevation from 400—1100 m.

Annual Female Survival, Annual Fecundity, and Source-Sink Models

Source-sink studies rarely have an opportunity to estimate bird survival directly due to time and effort constraints. We estimated annual female survival (P_A) from ratios of after-second-year to second-year birds, as proposed by Ricklefs (1997). Although this method is imperfect because it assumes a stable age distribution, it is widely exploited in field studies of songbird populations (Porneluzi & Faaborg 1999; Simons et al. 2000) as an alternative to using published estimates of survival based on banding data (Donovan et al. 1995b; Burke & Nol 2000; Flaspohler et al. 2001). Application of banding data often assumes that there is no regional variation in. Although few empirical data exist to support Ricklefs' approach, we feel that it provided the best survival estimates possible from our study sites.

Because some studies have discovered sex-related heterogeneity in the survival of Ovenbirds (Wander 1985), we did not mist-net both sexes, but instead captured females on their nests using a butterfly net. Birds were aged using the shape of the number 3 rectrix (Donovan & Stanley 1995). No study has directly measured the annual survival of juvenile Neotropical migrants (Porneluzi & Faaborg 1999) due to the fact that many first year breeders do not return to the sites where they were born. Therefore, as in most published studies, we used Ricklefs' (1973) suggestion to assume the annual survival rate of juvenile females (P_J) to be the half of estimated adult female survival rate.

We define annual fecundity (β) as the number of juvenile females produced annually per breeding female (Ricklefs 1973). The finite rate of population growth (λ) =

$= P_A + P_J \times \beta = 1$ for a population at equilibrium, and $\lambda > 1$ for a source population (Pulliam 1988). Consequently, for a source population $P_J \times \beta > 1 - P_A$, i.e. the annual mortality of adult females is smaller than the number of juvenile females that survive to breed.

Among breeding attempts, we identified the first breeding, reneating after a failed first nesting attempt, and second breeding after a successful first nesting or successful reneating. We developed two Ovenbird population models to explore how variations in rates of pairing success (p_p), reneating (p_r), and double brooding (p_d) might influence the predictions of demographic models. In these models, p_s represents an estimate of nesting success based on the Mayfield method (1967, 1975).

1. *Model ignoring pairing success* (by setting $p_p = 1$). Assumptions of this model are: independence of P_A of p_s , p_r , and p_d , equal sex ratio in fledglings, homogeneity of fledged brood size (F) among consecutive breeding attempts, only one reneating after the first nesting failure, and a second nesting attempt after the first successful nesting:

$$\begin{aligned}\lambda &= P_A + P_J \times \beta = P_A + P_J \times \frac{1}{2} [p_s \times F + (1 - p_s) \times p_s \times p_r \times F + p_s \times p_d \times F] = \\ &= P_A + P_J \times \frac{1}{2} F \times p_s \times (1 + p_r - p_s \times p_r + p_d).\end{aligned}\tag{1}$$

We propose several variations of this model:

a) *Monocyclic reproduction without reneating* ($p_r = p_d = 0$). Equation (1) is simplified to the following expression:

$$\lambda_1 = P_A + P_J \times \beta = P_A + P_J \times \frac{1}{2} F \times p_s.\tag{2}$$

b) *Monocyclic reproduction with all females reneating after failure* ($p_r = 1, p_d = 0$):

$$\begin{aligned}\lambda_2 &= P_A + P_J \times \beta = P_A + P_J \times \frac{1}{2} [p_s \times F + p_s \times F \times (1 - p_s)] = \\ &= P_A + P_J \times \frac{1}{2} F \times p_s \times (2 - p_s).\end{aligned}\quad (3)$$

c) *Monocyclic reproduction with some females re-nesting after failure* ($0 < p_r < 1$, $p_d = 0$):

$$\begin{aligned}\lambda_3 &= P_A + P_J \times \beta = P_A + P_J \times \frac{1}{2} [p_s \times F + (1 - p_s) \times p_s \times p_r \times F] = \\ &= P_A + P_J \times \frac{1}{2} F \times p_s (1 + p_r - p_s \times p_r).\end{aligned}\quad (4)$$

d) *Bicyclic reproduction with all females re-nesting after the failure of the first brood* ($p_r = 1$, $0 < p_d < 1$):

$$\begin{aligned}\lambda_4 &= P_A + P_J \times \beta = P_A + P_J \times \frac{1}{2} [p_s \times F + (1 - p_s) \times p_s \times F + p_s \times p_d \times F] = \\ &= P_A + P_J \times \frac{1}{2} F \times p_s \times (2 - p_s + p_d).\end{aligned}\quad (5)$$

e) *Bicyclic reproduction with some females re-nesting after first nest failure* ($0 < p_r < 1$, $0 < p_d < 1$). This scenario is described by the equation (1).

2. *Model incorporating pairing success.* The assumptions of this model are: closed population; pairing success rates are different from 100% ($0 < p_p < 1$); breeders always breed ($N_0 \times p_p \times \lambda^t$); non-breeding individuals never breed and their $\beta = 0$ ($N_0 \times [1 - p_p] \times P_A^t$). An average life-span of Ovenbirds is 2.7 yr and they start breeding the first spring after fledging (Van Horn & Donovan 1994). With only two breeding seasons per average bird, we feel that the above assumption does not cause any strong bias because it is likely that breeders becoming non-breeders compensate for non-breeding individuals eventually becoming breeders. The number of individual females in the population at time t (N_t) is:

$$N_t = N_0 \times \lambda^t = p_p \times N_0 \times \lambda^t + (1 - p_p) \times N_0 \times \lambda^t, \quad (6)$$

where the first term represents the reproducing part of the population, and the second term represents non-paired individuals. The influence of pairing success on the finite rate of population growth can be described as:

$$\lambda = P_A + P_J \times \beta \times p_p = P_A + P_J \times \frac{1}{2} F \times p_s \times (1 + p_r - p_s \times p_r + p_d) \times p_p. \quad (7)$$

This equation could be simplified to equations (2)—(5) with the second term multiplied by p_p , depending on the values assumed for p_r and p_d .

We explored the sensitivity of the finite rate of population increase to variations in the probability of reneating, double brooding, and adult female survival, and compared our estimates of the population status of Ovenbirds in the Great Smoky Mountains National Park with temporal trends in abundance. We also evaluated the relative importance of pairing success on source-sink dynamics by running models with different values of p_p . We then selected the best fitting scenarios and proposed possible interpretations for the population status of the Ovenbird in the park.

Pairing Success

Assuming an even sex ratio, the abundance of female Ovenbirds in a population should be equal to the number of territorial males. However, all singing males may not be successfully paired or reproductive. Estimating pairing success is important for source-sink analyses because only the actively reproducing fraction of population contributes to population growth.

We estimated p_p using singing rates. In central Missouri, Gibbs (1988), Gentry (1989), and Van Horn (1990) recorded that paired males sang ≤ 6 songs during a 5-minute sample period, whereas unpaired males had higher singing rates. Because singing rates may vary geographically, we first sampled paired males at known nests to identify their highest singing rate (the cut-off rate). We then sampled the singing rates of Ovenbirds of unknown pairing status on our study sites from mid-May to late June (when transit individuals were not likely to occur) and used our cut-off rate to distinguish between paired and unpaired males. We estimated pairing success as the proportion of paired males to all males.

Additional Breeding Attempts

The only way to precisely measure the frequency of renesting and multiple brooding is to continuously observe marked individuals. However, it is extremely difficult to apply this method to migratory songbirds, because it is rarely possible to capture every reproducing female in a population, and many marked birds disperse before nesting or between consecutive nesting attempts (Payevski 1985).

We captured and marked female Ovenbirds on their nests, but our samples were not sufficient to estimate rates of renesting and double brooding (we observed three instances of double-brooding and one instance of renesting next to a failed nest). For this reason, we used an indirect approach, based on the timing of reproduction, duration of a successful breeding, and the length of the breeding season (Pease & Grzybowski 1995; Farnsworth 1998). Although this is a correlative approach, it is often the only practical

way to estimate rates of renesting and multiple brooding for most passerines. We observed three distinct clusters of nest initiation in our populations, and used this pattern to estimate p_r and p_d for the purpose of population modeling.

Because the chronology of reproduction may vary annually due to weather, we used the average (over 3 years) time between the earliest nest initiation and the latest fledging as a measure of the breeding season length (T_s). We estimated the duration of a single breeding attempt as the average number of days from nest initiation until fledging (T_b). For a given renesting interval (T_i), birds can potentially undertake $T_s / (T_b + T_i)$ successful reproductions per season. We assumed, however, that only p_r females would renest after the first breeding failed, and that only p_d females would undertake double brooding.

Female Ovenbirds arrive on breeding grounds within an average of 7 days, and nest initiation takes place over a similar time span (Van Horn & Donovan 1994). Assuming a conservative estimate of nesting synchrony, we considered nests initiated within 20 days from the earliest start, and within 7 days from the average start, the first breeding attempt. To investigate the influence of model parameters on population growth rates, we classified nests started after 20 days and before $(T_b + T_i)$ days as renesting attempts. All later nests were classified as second broods. Assuming the independence of nests in our study and constant nest searching effort, and using empirical values of nesting success (p_s), we estimated the rates of renesting and double brooding as follows:

$$p_r = \text{number of renesting attempts} / \text{number of first broods that failed} =$$

$$= \text{number of renesting attempts} / (\text{number of first broods} - \text{number of first broods} \times p_s);$$

p_d = number of second broods /total number of discovered nests.

Daily Nest Survival, Nesting Success, and Productivity Estimates

We searched study sites for nests from the third week of April until end of July following the guidelines of Martin & Geupel (1993). Once located, nests were monitored every three days during nest building, egg-laying, and incubation. Nests were monitored every other day from just prior to hatching until day 6 of the nestling stage. Monitoring then continued on a daily basis until nests were no longer active. Nests were checked with care to prevent attracting predators or premature fledging. Nests found empty before the expected fledging date (day 7), were considered predated. Nests were only considered successful if signs of successful fledging (flattened nest edge, feces in and next to the nest, dandruff-like flakes from unfolded feathers, and fledgling activity in the vicinity of nests) were observed.

We estimated nesting success using the Mayfield method (1961, 1975). We calculated daily survival rates (d_{sr}), stage-specific survival rates (ssr) for both egg and nestling stages, and nesting success rates (p_s), using our original data for stage-specific lengths:

$d_{sr} = 1 - \text{number of failed nests} / \text{total number of exposure-days summed across all nests},$

$$ssr = d_{sr}^n,$$

$$p_s = d_{sr}^n,$$

where n is duration (days) of a specific stage from our data. We restricted our analysis to nests in which eggs or nestlings were present. Estimates of reproductive success were based on a minimum of 20 nests as recommended by Hensler & Nichols (1981). Standard errors of daily survival rates and test-statistics (z) for evaluating the difference in daily survival rates among years, sites, and consecutive breeding attempts were calculated following Johnson (1979). Approximate confidence intervals for p_s were estimated as the range of values between high and low estimates of nest survival:

$$p_s (\text{high}) = (dsr + SE)^n,$$

$$p_s (\text{low}) = (dsr - SE)^n.$$

We avoided using the χ^2 -statistics for comparing daily survival rates for the reasons discussed in Johnson (1979). We did, however, use χ^2 tests for evaluating the differences in nesting success (expressed as ratios of predated to total nests) among years, consecutive nesting attempts, and study sites (Donovan et al. 1995b; Porneluzi & Faaborg 1999; Burke & Nol 2000).

We calculated average clutch size, hatched brood size and fledged brood size (F), and compared these among years, study sites and consecutive breeding attempts, using Analysis of Variance (ANOVA: General Linear Model; MINITAB® Software for Windows 1998).

RESULTS

Chronology of Reproduction

From 1999-2001, we monitored 110 Ovenbird nests in the Great Smoky Mountains National Park. On average, the earliest nest was initiated on 14 April, and produced fledglings on 15 May. Average date of the late nest initiation was on 20 June, with fledging on 18 July. Therefore, the observed time span of Ovenbird reproduction in the park, $T_s = 96$ days. We observed only minor annual variations in the timing of reproduction. Ovenbirds started their nests on average 2 d earlier in 2001, and 2 d later in 2000, than in 1999.

For nests, initiated in April and early May, average $T_b = 31$ d. Later nesting attempts were one day shorter (Table 1). Information on renesting intervals is very scarce (Van Horn & Donovan 1994). We observed renesting intervals of 2–6 days at four nests. Assuming a conservative estimate of $T_i = 7$ d, 37–38 d were required to successfully fledge a brood. Thus, the estimated duration of the breeding season on our study sites would allow for two successful nesting attempts ($96 / 38 = 2.5$). We used 62 nests classified as first nesting attempts to estimate p_r and p_d . These nests were initiated between 14 April–3 May (27 April ± 0.5 d SE) and fledged on 15 May–2 June (27 May ± 0.5 d SE). Nests, initiated on 14 May ± 1.3 d SE and fledged on 14 June ± 1.3 d SE, were classified as renesting attempts after the failure of the first brood ($n = 28$). We assumed that 20 nests, initiated on 5 June ± 1.4 d SE and fledged on 4 July ± 1.2 d SE, were second nests of successful first broods (Fig. 1).

Nesting Success and Productivity

Successful nests produced 3.79 ± 0.19 SE fledglings (Table 1). There was no significant site effect on clutch size, hatched brood size, or fledged brood size. Although clutch size underwent annual variations, and both clutch and hatched brood sizes declined over the breeding season, the size of successful broods remained constant over years and within seasons (Table 2). As a result, productivity was constant from April through July.

We did not observe cowbird parasitism at any nest. Of 62 failed nests, 10 nests were abandoned by the parents (5 before egg-laying, and 5 during egg-laying and incubation), 29 were predated during incubation, and 23 were predated during the nestling period. We found no evidence of predation on breeding females. Nest predation rates, expressed as proportions of failed nests to the total number of nests, did not vary among years, study sites, and consecutive nesting attempts (Table 3). The daily survival rate of 0.95 did not vary significantly between the incubation and nestling stages ($z = 0.70$, $P = 0.48$). Overall nesting success, p_s , was estimated as 0.31. Stage-specific survival was higher for nestling (0.63), than for the incubation (0.50) period (Table 4).

Survival Rates

Nineteen of the 30 breeding females captured were after second-year birds which produced annual adult female survival estimates, $P_A = 0.63 \pm 0.09$ SE (Table 1), and annual juvenile female survival estimate, $P_J = 0.32 \pm 0.04$ SE (Table 5).

Additional Nesting Attempts, Annual Fecundity, and Pairing Success

From our data, $p_r = 28 / (62 - 62 \times 0.31) = 0.66$, and $p_d = 20 / 110 = 0.18$. We used mean, low, and high estimates of F , P_A , P_J , and p_s for calculating of annual fecundity, $\beta = 0.96$ female offspring per female (0.80—1.15). Corresponding values of equilibrium fecundity (i.e. fecundity maintaining zero population growth) were 1.16 (1.67—0.77) (Table 5).

We sampled the singing rates of males at 72 active nests on two occasions. The average rate was 4.5 ± 0.14 SE, range 1-9 songs / 5 min. We assumed that the maximum rather than average rate of singing was indicative of the pairing status of males. Thus, we assumed that birds singing ≤ 9 songs / 5 min were paired males. We sampled on additional 326 males of unknown pairing status on our study sites. Their average singing rate was 8.0 ± 0.25 SE, range 1-23 songs / 5 min. Males with singing rate exceeding 9 songs / 5 min comprised 39.9% of birds, so we estimated pairing success, p_p , at $0.601 \pm \pm 0.03$ SE (Table 1). Singing rates did not vary between years or among study sites (Table 2).

Models of Population Growth

We used the range of values of p_r (from 0 to 1) and p_d (from 0 to 0.33), and p_p (from 0.6 to 1) to model Ovenbird population dynamics in the park. Models of monocyclic reproduction with no reneating (1a) or reneating rate of 0.66 (1c) resulted in the lowest estimates of λ (0.8—0.9). Our empirical estimate of productivity, and indirect

estimates of the probabilities of adult and juvenile female survival, and of the probability of double brooding (0.18) yield $\lambda = 0.98$ only if reneesting is considered the typical pattern (model 1d). Our indirect estimate of p_r (0.66) in the double brooding model (1e) suggests a strong population sink ($\lambda = 0.94$), similar to the monocyclic reproduction with 100% reneesting (model 1b) (Table 5). Source populations are achieved only if $p_r > 0.9$ and $p_d > 0.33$ (Fig. 2 & Table 6).

The incorporation of pairing success (model 2) produces striking changes in population growth rates. Using our empirical value of $p_p = 0.6$, even $p_r = 1$ and $p_d = 0.33$ produce very strong sink populations (Fig. 2) that decline 37% in three years and 66% in seven years (Table 6). Positive population growth occurs only under the highly unlikely conditions of $p_p = 1$, $p_r = 1$, and $p_d = 0.33$ (Table 6). Even with $p_p = 0.9$, total reneesting, and 33% double brooding, λ barely exceeds 0.95 (Fig. 2).

DISCUSSION

Population Trends

Breeding Bird Survey data for the southern Appalachian region suggest annual declines in Ovenbird populations, possibly exceeding 1.5% (Van Horn & Donovan 1994). Although we did not conduct quantitative surveys of abundance at our sites during this study, we observed no evidence of large population changes during the three years of our research. Similarly, population monitoring conducted in the park since 1996

provides no indication of such changes (Simons & Shriner 2000). Given these findings, we did not expect our sites to be supporting strong population sources of Ovenbirds, but we surprised when all but one of our models implied that they are strong population sinks with $\lambda = 0.82\text{--}0.95$ (Table 5).

Survival and Nesting Success

Our estimates of adult female survival (0.633) agree with recent published data from the unfragmented landscapes in other regions which ranges from 0.60 (Flaspohler et al. 2001) to 0.623 (Donovan et al. 1995b; Burke & Nol 2000) and 0.628 (Porneluzi & Faaborg 1999). Daily nest survival rates (0.953 ± 0.006 SE) and productivity (1.90 female offspring per breeding female) were derived from large samples, and they are within the published range for contiguous forested habitats. Reported values of Ovenbird's *dsr* and productivity in WI, MN, and MO range from 0.947—0.985 and from 1.47—2.15, correspondingly (Donovan et al. 1995b; Porneluzi & Faaborg 1999; Flaspohler et al. 2001).

Productivity was constant within a season ($P = 0.33$) and across our study sites ($P = 0.98$) and years ($P = 0.98$), despite the fact that clutch size varied over the course of our work from 4.2 to 4.8 eggs ($P = 0.005$), and decreased over the May to July breeding season from 4.8 to 3.8 eggs ($P = 0.000$).

Nesting success of 0.31 is on the low end of published estimates for unfragmented landscapes: 0.26 (Porneluzi & Faaborg 1999), 0.380-0.421 (Donovan et al. 1995b), and

0.685 (Flaspohler et al. 2001). A similar finding was reported for Wood Thrush (Simons et al. 2000). Higher rates of nest predation on protected areas, the “paradox of predation” (Suarez et al. 1993), may reflect the diversity and abundance of predators sustained by complex topography and structurally diverse forest vegetation in Great Smoky Mountains National Park. It is possible that the park is acting as an attractive sink (*sensu* Delibes et al. 2001a) for dispersing Ovenbirds. If Ovenbirds use predominantly visual cues for choosing breeding habitat, then large and diverse old-growth forest would attract them as a locality that could potentially favor their reproductive success. However, if high predation rates result in relatively low reproductive success, the selection of these habitats would be maladaptive.

Model Results: The Importance of Female Survival, Renesting, Double Brooding, and Pairing Success

Studies of the source-sink dynamics are often prompted by concerns about negative population trends. Estimates of population trajectories are usually based on assumptions about survival rates and empirical measures of fecundity. Most models ignore the potential influence of pairing success and rates of renesting and double brooding. Our estimates of adult and juvenile female survival, and annual fecundity produce strong population sinks with $\lambda = 0.82$ (Table 5) implying 45% population decline over three years and 75% population decline over seven years (Table 6). Such substantial population declines would have been impossible to overlook over the course of our study.

Given our strict monitoring protocol, the criteria used to assess nest fates, and large sample sizes, we feel our estimates of nesting success and productivity are accurate. Alternatively, constant high immigration rates on our study sites might be sustaining our populations in spite low nesting success. However, the park and adjacent National forests are surrounded by fragmented landscapes, and it seems highly unlikely that these habitats are serving as population sources. Therefore, we believe that other factors affecting annual fecundity must be considered. These factors include adult and juvenile female survival, the probability of renesting after failure of the first brood, the frequency of double brooding, and pairing success.

Female Survival

Although our adult survival rate estimate (0.633) was based on a small sample of females, it was very similar to published estimates. Given our fecundity estimates and assuming total pairing success, a minimum adult survival rate of 0.773 would be necessary for population stability. While it is possible that the conventional wisdom about passerine survival is wrong, such high rates for a Neotropical migratory species exposed to the risks of long-distance migration would be very surprising and are not supported by published empirical evidence for Ovenbirds. Similarly, there is no empirical evidence to suggest that juvenile female survival may be higher than half of the adult survival. Nevertheless, better survival estimates are clearly needed.

Figure 3 shows how λ values change with varying probabilities of female survival and pairing success given our empirical and indirect estimates of other model parameters.

The most realistic scenario of $\lambda = 0.97$ occurs with a pairing success is 0.8 and adult female survival slightly exceeds 0.7 (Fig. 3).

Renesting

Models that ignored renesting, i.e. assumed $p_r = 0$, produced strong population sinks (model a in Tables 5 & 6). However, our observations suggest that assuming $p_r = 1$ (models b and d) is not justified either. On five occasions, when breeding pairs, spatially isolated from other pairs, lost their nestlings to predators, we did not observe any evidence of renesting, in spite of intensive searching. Passerines re-nest more readily if nests fail early in the nesting period (Payevski 1985). Because predation was responsible for essentially all nest failures in our study, renesting rates should largely depend on predation rates during incubation. We observed only one clear case of renesting, when Ovenbirds started building another nest 7 m from their original nest two days after it was predated. Our indirect estimate of renesting, $p_r = 0.66$, may be low because even renesting rates of 90% were not enough to achieve $\lambda = 1$ with the assumptions of our base model (Table 6).

Double Brooding

Similarly, we could not reliably estimate the frequency of multiple brooding in our populations using direct observations of marked birds. We observed two females feeding their recently fledged young and carrying nesting material, presumably for a

second nest. The second nest was not found in either case, but the bird's behavior suggests that double brooding does occur in this species. Because our populations occur at the southern edge of the species' breeding range, double brooding may be more common than it is for the North. However, direct observations of marked birds are necessary for accurate estimates of p_d . Our indirect estimate of 0.18 did not produce $\lambda > 0.98$ even at renesting rates (p_r) = 1 and pairing success (p_p) = 1 (models 1d and 1e, Table 5). All monocyclic models ($p_d = 0$) produce strong population sinks, which as discussed above, we do not believe to be the case. Our models suggest that double brooding rates as high as 0.33—0.40 may be needed to sustain populations when predation rates are high (Table 6).

Pairing Success

Pairing success is another factor influencing the reproductive capacity of a population. We do not believe that all of the territorial males in our study population were paired because we regularly observed territorial males singing in locations where we were unable to find evidence of breeding. Our empirical estimate of pairing success (p_p) = 0.601 is probably low because detecting probabilities are a function of singing rates (Farnsworth et al. 2002). Thus, there is a lower probability of detecting a bird with singing rate 1-2 / 5 min than a bird singing 10 or more times during the same time interval. Therefore, because paired males sing less frequently, we were likely to underestimate their proportion in the local populations. Higher values of pairing success

(75-100%) were reported for Ovenbirds in other large unfragmented areas (Villard et al. 1993; Van Horn et al. 1995; Burke & Nol 1998).

Because the Ovenbird is a common species in the park, and it is known that high breeding densities may result in lower pairing success due to the abundance of non-territorial floaters (Bayne & Hobson 2001), 0.85—0.95 pairing success may be a more realistic estimate for our populations. Assuming adult female survival rates of 0.63 and our measured rates of nesting success, a 90% pairing success, and a 90% renesting rate, a double brooding rate of over 40% would be necessary for population stability (Fig. 2).

CONCLUSIONS

Because Ovenbirds populations in the Great Smoky Mountains National Park do not appear to be declining or growing rapidly, we think that it is most likely that our populations are near equilibrium or declining slightly ($\lambda = 0.98$ —1.00). In either event, our findings suggest that this large unfragmented tract of high quality habitat is not functioning as a significant population source for this common species, and may in fact be acting as an attractive sink. Source-sink models of Wood Thrush populations in this area produced similar results (Simons et al. 2000).

Parameterization of our demographic model did not yield estimates of λ close to 1, unless pairing success and renesting rates exceeded 0.9 and at least one-third of breeding females produced two broods (Fig. 2). We hypothesize that because our

populations live at the southern limit of species breeding distribution, double brooding may occur at much higher rates than previously assumed. Renesting and double brooding may buffer our populations, partially compensating for high levels of nest predation that we measured. Understanding the significance of these parameters on population growth rates awaits more intensive studies of marked individuals. Nevertheless we feel that it is impossible to adequately evaluate the status of songbird populations unless population models incorporate estimates of pairing success and the probability of multiple nesting attempts.

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Table 1. Reproductive parameters of Ovenbird populations and annual survival of adult females in Great Smoky Mountains National Park, 1999–2001.

<i>Parameter</i>	<i>Mean</i>	<i>SE</i>	<i>Sample size</i>	<i>Range of variation</i>	<i>Low estimate</i>	<i>High estimate</i>
Pairing success	0.601	0.027	326	0.516 – 0.818	0.574	0.628
Clutch size	4.49	0.073	89	3 – 6	4.42	4.57
Hatched brood size	4.12	0.121	64	1 – 6	4.00	4.25
Fledged brood size	3.79	0.193	43	1 – 6	3.60	3.98
Construction ^a , days						
First nest	7.1	0.09	11	7 – 8	7.0	7.2
Additional nest	5.8	0.20	5	5 – 6	5.6	6.0
Egg-laying, days	2.49	0.073	89	1 – 4	2.42	2.57
Incubation, days	13.21	0.188	21	11 – 14.5	13.03	13.40
Egg stage, days	15.64	0.196	21	14 – 17	15.45	15.84
Nestling stage, days	8.65	0.173	36	7 – 11	8.48	8.83
Nesting period (1 st egg to fledging) ^b , days	24.44	0.327	9	23 – 26	24.12	24.77
T_b ^c , days						
First nesting	31.39	–	–	–	–	–
Additional nesting	30.09	–	–	–	–	–
Adult female survival	0.633	0.088	30	–	0.545	0.72

Table 1 (continued)

^a *Estimated from our observational data (4-6 d nest construction and 1-2 d pause before egg-laying).*

^b *For successful nests found before egg-laying. Summing up egg and nestling stages, we would obtain very similar result (24.30 d).*

^c *Average number of days from nest initiation until fledging, calculated by summing up construction, egg, and nestling stages.*

Table 2. Comparison of reproductive parameters of Ovenbird populations in Great Smoky Mountains National Park, 1999-2001.

<i>Parameter</i>	<i>Comparisons (ANOVA: general liner model)</i>								
	<i>among years</i>			<i>among sites</i>			<i>among broods^a</i>		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Pairing success	2.96	1	0.086	1.96	6	0.076	—	—	—
Clutch size	5.62	2	0.005	0.43	6	0.860	20.06	2	0.000
Hatched brood size	0.83	2	0.440	0.59	5	0.707	7.47	2	0.001
Fledged brood size	0.02	2	0.983	1.25	5	0.305	1.14	2	0.330

^a Among the first brood, renesting after the first brood failure, and second brood.

Table 3. Comparisons of nest predation rates in Ovenbird populations among years, consecutive reproductive attempts, and study sites.

<i>Scale of comparison</i>	<i>Number of nests</i>		<i>Predation</i>			
	<i>Depredated</i>	<i>Total</i>	<i>rates^a, %</i>	χ^2	df	<i>P</i>
<i>Years:</i>						
1999	22	33	66.7			
2000	34	45	75.6			
2001	27	44	61.4	0.397	2	0.820
<i>Broods:</i>						
First	33	62	53.2			
Re-nesting	18	28	64.3			
Second	11	20	55.0	0.265	2	0.876
<i>Field sites:</i>						
Albright	7	9	77.8			
Big Creek	9	11	81.8			
Cosby	25	43	58.1			
Roaring Fork	37	51	72.5			
Other sites	5	8	62.5	0.742	4	0.946

^aPredation rates are expressed as the proportions of depredated nests to all nests.

Table 4. Reproductive success of Ovenbirds in Great Smoky Mountains National Park, 1999-2001.

<i>Stage of nest development</i>	<i>Exposure- days</i>	<i>Nests failed</i>	<i>Daily survival (SE)</i>	<i>Stage-specific and overall nest survival</i>		
				<i>mean</i>	<i>low estimate</i>	<i>high estimate</i>
Eggs	780.5	34	0.956 (0.007)	0.501 ^a	0.442	0.561
Nestlings	437.5	23	0.947 (0.011)	0.627 ^b	0.568	0.690
Contents ^c	1218	57	0.953 (0.006)	0.310 ^d	0.266	0.362

^a *Probability of successful hatching.*

^b *Probability of successful fledging of hatched nests.*

^c *Eggs and nestlings combined.*

^d *Neting success: p_s = probability of nest survival from the first egg until fledging.*

Table 5. Estimates of annual fecundity (β) and finite rates of increase of Ovenbird populations (λ) in Great Smoky Mountains National Park, 1999-2001.

<i>Estimates^a</i>	P_A	P_J	F	p_s	β^b	<i>Equilibrium fecundity^c</i>	<i>Estimates of λ, given by models 1a—1e^d</i>				
							a	b	c	d	e
Mean	0.633	0.317	3.79	0.310	0.96	1.16	0.82	0.95	0.90	0.98	0.94
Low	0.545	0.273	3.60	0.266	0.80	1.67	0.68	0.77	0.74	0.80	0.76
High	0.721	0.361	3.98	0.362	1.15	0.77	0.98	1.15	1.09	1.19	1.14

^a P_A is an adult female survival, P_J is a juvenile female survival, F is a successful brood size, p_s is nesting success.

^b β is annual fecundity (number of female offspring produced annually per breeding female in a population) calculated from equation (1).

^c Annual fecundity corresponding to $\lambda = 1$.

^d Estimates of population growth rates (λ) given by the following models assuming $p_p = 1$: (a) $p_r = p_d = 0$; (b) $p_r = 1$, $p_d = 0$; (c) $0 < p_r < 1$, $p_d = 0$; (d) $p_d = 0.182$; $p_r = 1$; (e) $p_r = 0.655$, $p_d = 0.182$ (our indirect estimates), where p_p is pairing success, p_r is renesting rate, and p_d is probability of double brooding.

Table 6. Projected persistence of Ovenbird populations under different parameter values ^a.

<i>t</i>	p_r^b	p_d^c	<i>Model</i> ^d	$p_p^e = 0.6$	$p_p = 0.7$	$p_p = 0.8$	$p_p = 0.9$	$p_p = 1$
3	0	0	1a/2a	0.41	0.44	0.48	0.51	0.55
7	0	0	1a/2a	0.13	0.15	0.18	0.21	0.25
3	1	0	1b/2b	0.56	0.62	0.69	0.77	0.85
7	1	0	1b/2b	0.25	0.33	0.42	0.54	0.68
3	0.66	0	1c/2c	0.50	0.56	0.61	0.67	0.74
7	0.66	0	1c/2c	0.20	0.25	0.32	0.40	0.49
3	0.8	0	1c/2c	0.52	0.58	0.64	0.71	0.78
7	0.8	0	1c/2c	0.22	0.28	0.36	0.45	0.56
3	0.9	0	1c/2c	0.54	0.60	0.67	0.74	0.82
7	0.9	0	1c/2c	0.24	0.30	0.39	0.49	0.62
3	1	0.18	1d/2d	0.60	0.67	0.76	0.85	0.94
7	1	0.18	1d/2d	0.30	0.40	0.52	0.68	0.87
3	1	0.33	1d/2d	0.63	0.72	0.81	0.92	1.03
7	1	0.33	1d/2d	0.34	0.46	0.62	0.81	1.06
3	0.66	0.18	1e/2e	0.54	0.61	0.67	0.75	0.82
7	0.66	0.18	1e/2e	0.24	0.31	0.40	0.50	0.64
3	0.66	0.33	1e/2e	0.58	0.65	0.73	0.81	0.90

Table 6 (continued)

t	p_r^b	p_d^c	Model ^d	$p_p^e = 0.6$	$p_p = 0.7$	$p_p = 0.8$	$p_p = 0.9$	$p_p = 1$
7	0.66	0.33	1e/2e	0.28	0.36	0.47	0.61	0.78
3	0.8	0.18	1e/2e	0.57	0.63	0.71	0.79	0.87
7	0.8	0.18	1e/2e	0.26	0.34	0.45	0.57	0.73
3	0.8	0.33	1e/2e	0.60	0.68	0.76	0.85	0.95
7	0.8	0.33	1e/2e	0.30	0.40	0.53	0.69	0.89
3	0.9	0.33	1e/2e	0.62	0.70	0.79	0.88	0.99
7	0.9	0.33	1e/2e	0.32	0.43	0.57	0.75	0.97

^a Table entries are the proportions of initial population size at time t (years) calculated from equations(6) and (7) using empirical values of $P_A = 0.633, P_J = 0.317, F = 3.79$, and $p_s = 0.31$.

^b Renesting rate: 0.66 is our indirect estimate.

^c Rate of double brooding: 0.18 is our indirect estimate.

^d Model 1: $p_p = 1$, model 2: $0 < p_p < 1$. (a) $p_r = 0, p_d = 0$; (b) $p_r = 1, p_d = 0$; (c) $0 < p_r < 1, p_d = 0$; (d) $p_r = 1, 0 < p_d < 1$; (e) $0 < p_r < 1, 0 < p_d < 1$.

^e Pairing success: 0.6 is our indirect estimate.

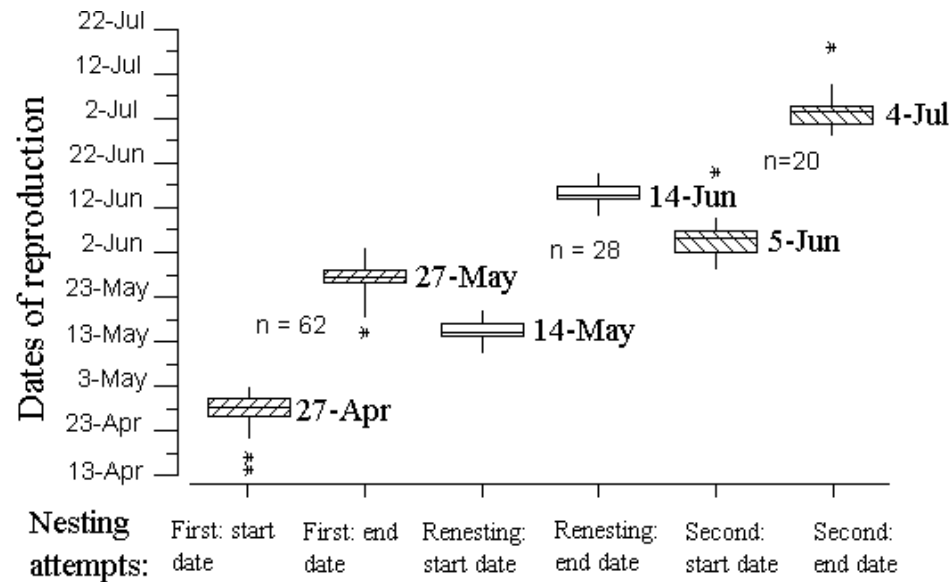


Figure 1. Chronology and duration of Ovenbird reproduction in Great Smoky Mountains National Park, 1999—2001.

Numbers at boxplots are average dates of nest initiation and fledging for the first nesting attempt, renesting after the failure of the first brood, and second nesting attempt after successful first brood. Sample sizes are indicated between the boxplots representing initiation and fledging dates of nesting attempts.

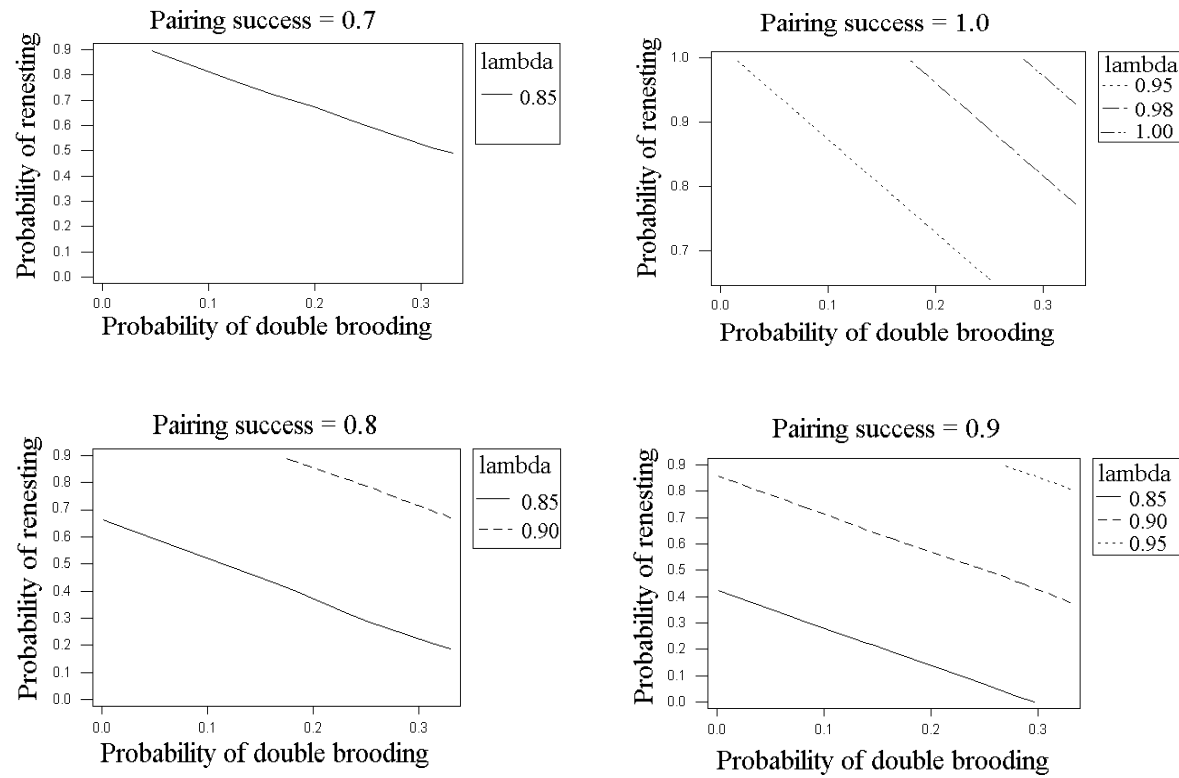


Figure 2. Sensitivity of λ to the varying probabilities of reneating, double brooding, and pairing success under empirical values of annual fecundity (0.96) and adult survival (0.633) (Ovenbird data, 1999—2001).

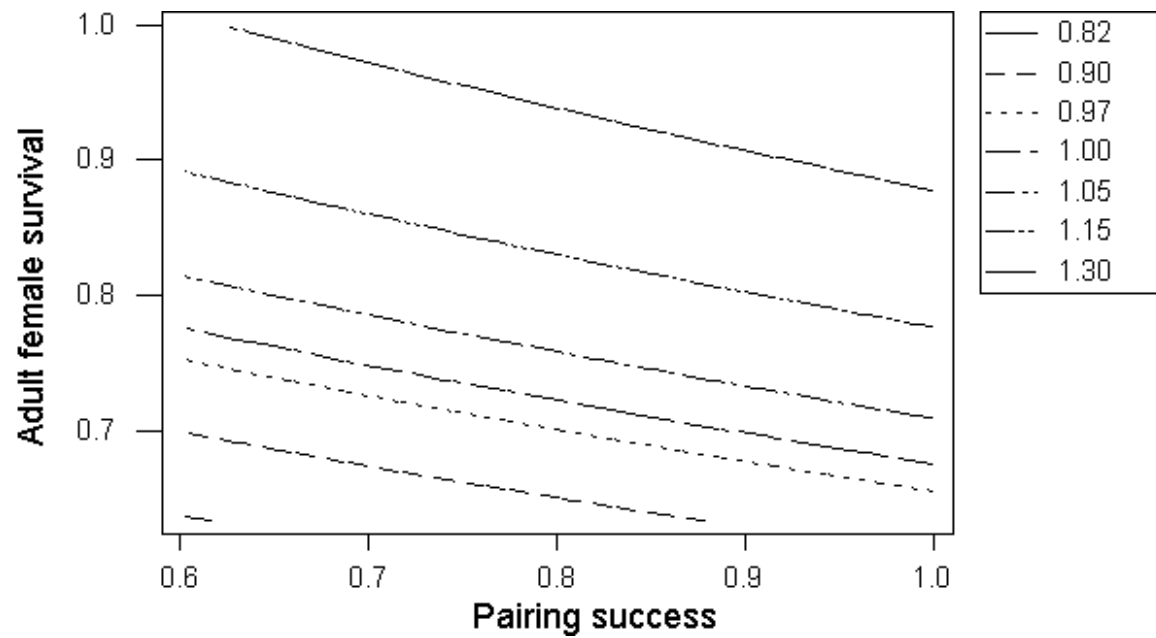


Figure 3. Sensitivity of λ to the varying probabilities of female survival and pairing success under indirect and empirical estimates of other model parameters (Ovenbird data, 1999-2001).

CHAPTER 2

AN EXPERIMENTAL STUDY OF AVIAN PARENTAL CARE UNDER VARYING FOOD AVAILABILITY¹

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Abstract. We developed a conceptual model of the constraints on breeding forest songbirds during the nestling period, when parental behavior can be expected to vary in response to changes in food availability and predation risk. This model predicts reproductive consequences linked to the behavior of parental birds. From 1999-2001, we monitored 178 Wood Thrush (WOTH) and 110 Ovenbird (OVEN) nests to estimate their reproductive success, productivity, and nest predation rates in the southern Appalachians. We designed a field experiment with food supplementation (treatment) at 28 WOTH and 22 OVEN nests. Treatment and control nests (37 WOTH and 25 OVEN) were sampled for parental behavior during 283 four-hour observational sessions at three times of day and three standardized chick ages. Our major findings were similar for both species. Daily nest survival rates were significantly higher in treatment than in control nests. The nestling period of food-supplemented nests was shorter than of control nests, which reduced the exposure of treatment nests to predation. Treatment nests showed much higher productivity (number of fledglings per hatched nest) than control nests. Nestlings at treatment nests were heavier prior to fledging, despite the fact that feeding rates at treatment and control nests were similar. Parental attendance was significantly higher at food-supplemented nests than at control nests. We conclude that parental behavior, mediated by food availability, has adaptive significance in these species. When food is abundant, parental vigilance at the nest increases, predation rates decrease, and reproductive success increases.

INTRODUCTION

The time budgets of breeding songbirds reflect trade-offs between finding food, avoiding predators, and other aspects of reproduction (Mangel and Clark 1986, Clutton-Brock 1991, Clutton-Brock and Godfray 1991). Martin (1992) has argued that these trade-offs are largely explained by the interaction of a nest predation and food limitation as primary constraints on songbird reproduction. The nestling period is the most energetically demanding part of the reproductive cycle because parents must feed and maintain themselves and their young, protect themselves and their offspring from predators (including additional exposure to predation risk caused by feeding trips to the nest), and defend territorial resources from competitors (Linden and Moller 1989). Lack (1947, 1948) proposed that food is the major factor limiting bird reproduction. In contrast, Skutch (1949) insisted on the exclusive role of predation, proposing that higher levels of activity at the nest increase the risk of predation. He hypothesized that high rates of nest predation would select for smaller clutches because larger broods would require higher levels of parental activity.

Martin (1987, 1988, 1992, 1995) incorporated food limitation and nest predation into a model of avian reproductive strategies. At the species level, he found that higher rates of predation were associated with shorter nestling periods and higher rates of multiple brooding, and that variations in adult survival and fecundity were associated with variations in predation rates among nest sites, rather than food availability.

Martin's (1992) model predicted trade-offs between the time allocated to foraging (searching for and consuming food away from the nest) and guarding (perching and preening in the immediate vicinity of the nest, and active defense against predators). He proposed that the reproductive strategies of birds reflect complementary sets of parental behaviors (foraging, perching, parental care) and traits (clutch size, nestling growth rate, juvenile and adult mortality) affecting lifetime reproductive success. Martin's conceptual model yields four major predictions. First, because predation is a major source of nest loss, reproductive strategies that minimize the risk of predation should be favored by natural selection (Martin 1988, 1991). Second, during the nestling period, foraging demands compete with the demands of nest defense (Orians and Pearson 1979, Högstedt 1980). Third, food abundance influences the time spent foraging near the nest vs. more distant sites (Robinson 1988). Fourth, higher food availability results in better nestling survival, higher rates of multiple brooding, higher productivity, and lower nest predation rates (as a consequence of higher growth rates of nestlings and shorter nestling period).

These predictions are rarely tested at the intraspecific level. A comprehensive study of the relationships between food availability, nest predation rates, life-history traits, and parental behavior, conducted on Cactus Wren (*Campylorhynchus brunneicapillus* Lafresnaye) (Simons 1988, Simons and Martin 1990), showed that food supplementation increased the amount of parental vigilance at nests, the frequency of anti-predator defense, rates of nestling growth, nestling survival, and the frequency of multiple brooding. Experimental studies of House Wrens (*Troglodytes aedon* Vieill.) and Seychelles Warblers (*Acrocephalus sechellensis* Oustalet) confirmed that higher

predation risk favored more intensive vigilance and reduced rates of food delivery to nestlings (Martindale 1982, Komdeur and Kats-Romke 1999). Ward (2001) experimentally manipulated nestling starvation risk and adult predation risk in the American Robin (*Turdus migratorius* L.) and found that parents with well-fed young were more likely to attack potential predators. However, studies of Song Sparrows (*Melospiza melodia* Wilson) and Black-billed Magpies (*Pica pica* L.) did not find a link between nest predation rates and food availability (Högstedt 1981, Arcese and Smith 1988).

The effectiveness of predator deterrence varies across bird species (Greig-Smith 1980, Arcese and Smith 1988, Weatherhead 1989). Perching near the nest to guard young may allow parents to respond to approaching predators by active or passive defense. Passive defense includes acoustic cues to quiet the young, and other behaviors to distract predators (East 1981). Both behaviors can reduce nest predation rates (Greig-Smith 1980, Knight and Temple 1988). Active defense improved the nesting success of African *Ploceinae* and Red-winged Blackbirds (*Agelaius phoeniceus* L.) (Collias and Collias 1971, Weatherhead 1990).

We developed a conceptual model that links the behavior of breeding forest songbirds during the nestling stage to variations in food availability and shows how their behavioral decisions minimize predation risk (Fig. 1). The model predicts that higher food availability: (1) allows adult birds to devote less time to foraging and more time to active nest defense and vigilance, (2) increases feeding rates and the volume of food delivered per feeding visit, (3) increases nestling growth rates, and (4) shortens the

nestling period and the cumulative risk of nest predation. The model assumes that parents can search for food for themselves and their young at the same time, and that their self-maintenance and vigilance can be largely accomplished simultaneously. We chose the Ovenbird (*Seiurus aurocapillus* L.) and the Wood Thrush (*Hylocichla mustelina* Gm.), to test the predictions of our model. These species are ground foraging Neotropical migrants that are relatively abundant on our study sites, but differ in their strategies of nest placement and nest concealment (Van Horn and Donovan 1994, Roth et al. 1996). The Wood Thrush (WOTH) builds conspicuous cup-shaped nests low in the trees and shrubs (mostly eastern hemlocks (*Tsuga canadensis*), whereas Ovenbird (OVEN) is a ground nester. Both parents build the nest in WOTH, only females in OVEN. In WOTH and OVEN, incubation is accomplished solely by females, while feeding the young is conducted by both parents. Common nest predators observed on our study sites were black rat snakes (*Elaphe obsoleta*), American Crows (*Corvus brachyrhynchos*), Blue Jays (*Cyanocitta cristata*), black bears (*Ursus americanus*), raccoons (*Procyon lotor*), gray foxes (*Urocyon cinereoargenteus*), red squirrels (*Tamiasciurus hudsonicus*), southern flying squirrels (*Glaucomys volans*), forest mice (*Peromyscus sp.*), and voles (*Microtus sp.*) (Farnsworth and Simons 2000, *pers. observ.*).

The goals of our experiment were to evaluate the relationship between food availability and nesting success in the two species, and to determine whether parental behavior is affected by food availability. For both species, we studied whether (and how) food availability affected the time-activity budgets of parental birds, predation-induced juvenile mortality, and productivity.

METHODS

Study area and design

We established seven study sites in the northeastern part of Great Smoky Mountains National Park between Gatlinburg, TN (N 35°42'52", W 83°30'41"), and Waterville, NC (N 35°47'02", W 83°06'44"), at elevations of 500 to 1000 m. The complex topography and consequent broad gradients of temperature and moisture on these sites support a diverse mixed deciduous forest (MacKenzie 1991). From 1999-2001, we studied the effects of food supplementation at 178 WOTH and 110 OVEN nests (Fig. 2). Only hatched nests were included in the experiment. All food-supplemented nests (treatments) were sampled for parental behavior. Of non-food-supplemented nests (controls), some were sampled for bird behavior (behavioral controls) and others not (unwatched controls) because some nests were predated too early in the nesting period to be watched or were not suitable for observation. All treatments and behavioral controls were randomly assigned. For all comparisons, one-tailed statistical tests were used to test the directional predictions of our hypotheses (Fig. 1).

Nesting success and productivity estimates

We searched for nests from the third week of April until the end of July, using the guidelines of Martin & Geupel (1993). Once located, nests were monitored every three days at the stage of nest building, egg-laying, and incubation. We monitored nests every other day from just prior to hatching until day 6 of the nestling stage in OVEN and day 8

in WOTH (counting the hatching day as a day 0), and checked nests daily until they were no longer active. This protocol allowed us to estimate the chronology of reproduction and nest fates accurately. Nests found empty before the expected fledging date were considered predated. Of nests that were empty near the expected fledging date, only those which had signs of fledging (flattened nest edge, feces in and around the nest, abundant flakes of unfolded feather sheaths, and fledgling activity in the vicinity of nests), were considered successful.

We estimated reproductive success for samples of 20 or more nests (Hensler & Nichols 1981) using the Mayfield's (1961, 1975) protocol of calculating the daily survival rate (*dsr*) as

$$dsr = 1 - \frac{\text{number of failed nests}}{\text{number of exposure - days}} \quad (1)$$

and nest survival rate as

$$nsr = dsr \quad (2)$$

where t is a time interval from the first egg to fledging. Standard errors of *dsm*'s and test-statistics (z) for evaluating the difference in survival probabilities among controls and treatments were calculated following Johnson (1979). We also calculated high and low values for nest survival rates:

$$nsr_{\text{high}} = (dsr + SE)^t, \quad (3)$$

$$nsr_{\text{low}} = (dsr - SE)^t \quad (4)$$

We estimated the incubation period using all available nests. The duration of the nestling stage was estimated separately for treatment and control nests and compared using two-sample *t*-tests. Consequently, *t*-statistics were calculated separately for treatment and control nests. We calculated the average number of fledglings per hatched nest for control and treatment nests and compared these using a two-sample *t*-test. To account for random variation in fledged brood sizes between the two groups of nests, we compared the number of fledglings per successful brood at treatment and control nests using two-sample *t*-test.

Food supplementation

Experimental studies involving food supplementation are rare in insectivorous songbirds because it is difficult to get wild birds to eat novel foods, and to contain live insects and prevent them from being eaten by ants, mammalian predators, or other birds. For this reason, the relationships between parental feeding rates of insectivorous birds, the amount of food brought on a single visit to a nest, nestling growth rates, and food availability are most often studied using correlational (expensive and laborious techniques of videotaping nests and sampling natural abundance of arthropods) rather than experimental approaches (e.g. Buehler et al. 2002). In this study, feeding stations were established on the ground, 3—6 m from OVEN nests and 6—12 m from the WOTH nests. We placed live mealworms on thin 21.6 x 27.9 cm plastic sheets, completely covered with green moss. This method kept the mealworms from drying out, prevented them from burrowing into the leaf litter, and reduced losses to ants and other predators.

We could also tell if mammalian or large avian predators visited the station, because these predators always moved pieces of moss away from the plastic sheets. We provided live food at treatment nests daily during approximately 70% of the nestling period, 8 d for WOTH and 6 d for OVEN. Taking into consideration that nestling growth rates are highest during the first two-thirds of the nestling period (Roth et al. 1996, Van Horn and Donovan 1994), we started food supplementation on day 1 in OVEN and day 2 in WOTH.

The relationship between total daily energy expenditure (*TDE*, kcal) and passerine weight (*W*, kg) is described by the expression:

$$TDE = 317.7 * W^{0.7052} \quad (5)$$

(King 1974). Using available estimates of adult and nestling weights, and average brood sizes (Roth et al. 1996, Van Horn and Donovan 1994), an energetic value of 2 kcal/g for mealworms, and an utilization efficiency of 0.85 (Karasow 1990), we delivered 40 g of mealworms to WOTH and 25 g of mealworms to OVEN daily. These amounts accounted for 60-95% of the per-family (parents and their brood) energy requirements, depending on nestling age on the day of delivery.

Assessment of nestling fitness

To reduce disturbance at the nest and to prevent premature fledging, we weighed accessible nestlings two days before their average fledging date (day 5 in OVEN and day 8 in WOTH). We subsequently used these weights as indices of nestling fitness, and compared treatments and behavioral controls using a two-sample *t*-test.

Measuring behavioral responses of birds: experimental design

Using a 2 x 3 x 3 factorial design, we sampled the behavior of treatment and behavioral control parental birds every 15 sec during three 4-hr observational sessions, at three times of day (6:30-10:30 am, 10:30 am -2:30 pm, 2:30-6:30 pm), and three standardized chick ages (day 2, 4, 6 in OVEN, or day 3, 5, 8 in WOTH). Observational sessions were assigned to maintain the equal representation of each time of day and chick age for behavioral controls and treatments of each species. Nests were watched by observers sitting on the ground and using 8-12x binoculars and a 40x scope. Observers sat 6—20 m from OVEN nests and 7—25 m from WOTH nests to ensure the normal behavior of birds. We did not conduct behavioral observations during adverse weather. Twenty behavioral types, representing several broad behavioral categories were sampled. These included vigilance (brooding, resting, preening on the nest or at nest site), feeding (searching for food and feeding in the visible vicinity of nest, feeding trips to nestlings), vocalizing (singing, calls of nestlings), active nest defense (chasing and attacking potential predators), passive nest defense (displacement behavior, warning calls), and absence from the nest site. Frequencies of occurrence of different forms of behavior were standardized to hourly rates prior to data analysis. Initially, frequencies of performing the twenty behavioral types by behavioral controls and treatments were compared using Analysis of Variance (ANOVA: General Linear Model; MINITAB® Software for Windows 1998), including three primary terms (manipulation, time of day, age of nestlings) and three secondary terms (interactions). We accepted the significance

of behavioral differences only if we obtained (a) $P \leq 0.05$ for manipulation and $P \geq 0.05$ for all other model terms (time of day, nestling age, interactions), or (b) $P \leq 0.05$ for manipulation and age or time, and $P \geq 0.05$ for the relevant interaction terms. We then compared major behavioral categories (vigilance, feeding, active nest defense) and several important minor behavioral types (displacement behavior, vocalizations of young in the nest, warning calls of adults to their nestlings, resting and preening close to the nest, brooding and resting on the nest) at control and treatment nests using two-sample t -test.

RESULTS

Nesting success, productivity, and nestling fitness

We monitored 288 nests (both species combined) over three breeding seasons, from 1999-2001. Of these, 187 nests hatched and were divided into 50 food-supplemented and 137 control nests, including 62 behavioral controls and 75 unwatched controls (Fig. 2). At 10 randomly assigned treatment nest (2 OVEN nests and 8 WOTH nests), birds did not find feeding stations. Feeding stations were removed and nests were watched as behavioral controls. Predation was the only cause of failure for nests containing eggs or chicks. No nests were lost to weather or abandonment by both parents. We observed 6 cases of predation on feeding or incubating females, 4 WOTH and 2 OVEN. In each case, males abandoned their nests after the female died. All other nest losses (96.4% in each species) were the result of predation of eggs or nestlings.

Although fledged brood size did not vary between control and treatment nests, the number of fledglings per hatched nest was considerably greater in food-supplemented nests due to better brood survival (Table 1). The productivity of treatment nests was 50.7% higher for WOTH and 94.2% higher for OVEN than control nests. Treatment nestlings were heavier than control nestlings by 4.4% for WOTH and 5.4% for OVEN. The duration of the nestling stage at food-supplemented nests was shortened by 0.5 d (5.6%) for OVEN and 1 d (8.1%) for WOTH (Table 1), and daily survival rates were higher by 5.4% at treatment nests for both species (Table 2). Overall nesting success at food-supplemented nests was 60% higher for OVEN and 52% higher for WOTH than at control nests (Table 2).

Changes in parental behavior during the nestling stage

Feeding rates at food-supplemented and control nests were similar (Table 3). In both species, the proportion of time allocated to brooding, resting, and preening on the nest, vocalizations associated with passive anti-predator defense, and the occurrence of displacement behavior did not vary with food availability. Treatment OVEN chased and attacked potential predators somewhat more frequently ($P = 0.02$) than control birds (Table 3). Treatment OVEN spent 62% more time and treatment WOTH spent 200% more time resting and preening in the vicinity of their nests compared to control birds. Parents at food-supplemented nests spent much more time searching for food in the vicinity of their nests compared to parents of control nests (Table 3). Overall time allocations to vigilance on or close to the nest were by 17% higher for WOTH and 30.5%

higher for OVEN at food-supplemented nests compared to control nests. We did not find statistically significant interactions between nestling age (day 2, 4, 6 in OVEN, or day 3, 5, 8 in WOTH) and/or time of day (“morning”, “day”, “evening”) and manipulation (control or treatment), except for the proportion of time spent by WOTH on feeding in the vicinity of nests, where we found a significant interaction with nestling age ($F = 3.15$, $df = 2$, $P = 0.046$), and a significant interaction between manipulation and nestling age ($F = 3.21$, $df = 2$, $P = 0.044$).

DISCUSSION

Nestling growth rates and juvenile survival

As hypothesized, food supplemented nestlings of both species grew faster and reached greater fledging weights (Table 2). Similar results for nestling growth rates were reported for the Cactus Wren (Simons 1988, Simons and Martin 1990) and the Goshawk (*Accipiter gentilis* L.) (Dewey and Kennedy 2001). Our predictions of a shorter nestling period and subsequent smaller cumulative risk of predation at food-supplemented nests was also supported (Table 1). We also hypothesized (Fig. 1) that higher feeding rates would result in higher nestling growth rates. In the Cactus Wren (Simons and Martin 1990), visitation rates tended to be lower when food was more abundant, because the amount of food delivered per trip increased. In our study, feeding rates were similar between behavioral control and treatment nests of both species. It is possible that birds

were bringing more food items per feeding trip, but we do not have empirical evidence supporting this because it was impossible to quantify prey items at most nests.

Daily nest survival rates were similar to those reported from other studies (Donovan et al. 1995; Farnsworth and Simons 1999). Surprisingly, they were very similar in WOTH and OVEN, despite the fact that OVEN nests are much less conspicuous. Productivity was higher at food-supplemented nests of both species due to better nest survival. In contrast, productivity at treatment Cactus Wren nests increased due to more frequent multiple brooding (Simons 1988). The number of fledglings per hatched nest (as an index of productivity) almost doubled for OVEN treatment nests and increased by half for treatment nests of WOTH compared to control nests. However, fledged brood sizes did not differ among control and treatment nests of both species (Table 1), i.e. there was no random variation in fledged brood sizes of control and treatment nests. Therefore, food availability, rather than random variation, accounted for differences in productivity of control and treatment nests of both species.

Food availability and nest survival: mediating role of parental behavior

To date, very few field experimental studies (Simons and Martin 1990, this study) have obtained evidence of higher rates of nest vigilance or nest survival under conditions of higher food availability. The mechanisms, linking bird behavior to more effective anti-predator defense are not well understood. Simons (1988) showed that adult birds at food-supplemented nests were more likely to attack a simulated predator. We sampled bird behavior on a finer scale (20 behavioral types), and our results tell a different story.

Although we did not find significant differences among the time allocated to most fine scale behaviors (e. g. brooding, resting on the nest edge, resting within the nest site, warning vocalization of parents, vocalizations of young in nest, etc.), we did find differences in several broad categories of behavior that seem to be tied to food availability (Table 3). For example, although brooding on the nest, or resting and preening on the nest or in the vicinity of the nest were not different between treatment and behavioral control nests, nest vigilance defined as a combination of the above behaviors, was significantly higher at treatment nests.

Experimentally created conditions of high food abundance at the nest site produced a range of behavioral responses among individuals of both species. Some birds continued searching for food away from their nests while others chose to forage almost exclusively in the immediate vicinity of their nests. We conclude that the effects of food availability are manifest at the population (rather than individual) level, according to the proportion of birds that alter their behavior.

Many studies (Högstedt 1981, Arcese and Smith 1988) have shown physiological responses, e.g. bigger clutches when food availability increases. Our findings indicate that birds respond to variations in food availability during the nestling stage by changing their behavior. When food is abundant, birds devote more time to nest vigilance, and nest survival rates increase.

Possible biases

Contrary to the predictions of our model, we did not find strong evidence of more frequent active anti-predator defense (chasing or attacking predators) at treatment nests. Anti-predator defense is a relatively rare behavior, and because we only observed nests for 7.1% of the total nestling period of OVEN and 5.6% of the total nestling period of WOTH, we may have underestimated the occurrence of such attacks. We did observe both WOTH and OVEN successfully chasing away stronger and bigger predators (even black bears) on several occasions, but overall it appears that passive anti-predator defense (vigilance) plays a more important role in nest survival for these species.

It is also possible that treatment nests were more likely to be found by predators because daily food deliveries caused additional disturbance or because predators were attracted to the food we provided. We did in fact observe predators at feeding stations on several occasions. In spite of this possible bias, the predation rates of treatment nests were lower than those of control nests. Therefore, we concluded that treatment nests survived better due to higher rates of parental vigilance.

CONCLUSIONS

Our study revealed a link between food availability, parental behavior, and nesting success in two species of forest songbirds. While most of our hypotheses were confirmed, some (more food items per feeding trip, higher occurrence of active anti-

predator defense and displacement behavior at food-supplemented nests) were not supported, perhaps due to insufficient data. One hypothesis (higher feeding rates at food-supplemented nests) proved to be wrong. We feel that feeding rates were similar among control and treatment nests because birds at treatment nests chose to restrict their movements to the immediate vicinity of their nests to avoid attracting predators. We conclude that behavioral responses to food abundance vary individually, and therefore they are meaningful at the population level. We consider that both active and passive anti-predator defense are important to nesting success, and propose that passive mechanisms maybe more important for nestling survival than previously thought. In WOTH and OVEN, parents respond to differences in food availability by altering their time and activity budgets. When food is abundant, nestlings grow faster and fledge sooner, and adult birds devote more time to vigilance at the nest. These adaptations presumably contribute to higher fitness.

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**Table 1. Reproductive parameters and productivity estimates of Wood Thrush and Ovenbird populations
in Great Smoky Mountains National Park, 1999-2001.**

	OVEN			WOTH		
	Treatment	Control (*) or behavioral control (**)		Treatment	Control (*) or behavioral control (**)	
Egg stage, days \pm SE (<i>n</i>)	15.64 \pm 0.20 (21)			14.66 \pm 0.19 (32)		
Nestling stage, days \pm SE (<i>n</i>)	8.20 \pm 0.14 (15)	8.69 \pm 0.25 (13)*		11.35 \pm 0.32 (20)	12.35 \pm 0.31* (21)	
2-sample <i>t</i> -test ^a : T, df (<i>P</i>)	1.70	19	(0.05)	-2.22	38	(0.02)
Contents ^b , days	23.84	24.33*		26.01	27.01*	
Fledged brood size:						
- per hatched nest \pm SE (<i>n</i>)	2.68 \pm 0.45 (22)	1.38 \pm 0.22 (47)*		2.11 \pm 0.31 (28)	1.40 \pm 0.23 (45)*	
2-sample <i>t</i> -test ^c : T, df (<i>P</i>)	-2.59	31	(0.01)	-1.84	55	(0.04)
- per successful nest \pm SE (<i>n</i>)	3.69 \pm 0.37 (16)	3.92 \pm 0.31 (13)*		2.88 \pm 0.27 (17)	2.83 \pm 0.20 (23)*	
2-sample <i>t</i> -test ^c : T, df (<i>P</i>)	0.49	26	(0.68)	0.17	30	(0.43)

Table 1 (continued).

	OVEN			WOTH		
	Treatment	Control (*) or behavioral control (**)		Treatment	Control (*) or behavioral control (**)	
Standardized chick weight ^e , g ± SE (n)	12.64 ± 0.23 (38)	11.99 ± 0.21 (62)**		31.18 ± 0.39 (20)	29.88 ± 0.46** (29)	
2-sample <i>t</i> -test ^c : T, df (<i>P</i>)	-2.08	86	(0.02)	-2.14	46	(0.02)

^a Testing $\mu_{\text{control}} = \mu_{\text{treatment}}$ VS. $\mu_{\text{control}} > \mu_{\text{treatment}}$.

^b Cumulative duration of the egg-stage and nestling stage.

^c Testing $\mu_{\text{control}} = \mu_{\text{treatment}}$ VS. $\mu_{\text{control}} < \mu_{\text{treatment}}$.

^d Testing for differences between fledged brood sizes of control and treatment nests (general linear model).

^e Taken on day 5 of OVEN nestling development and day 8 of WOTH nestling development.

Table 2. Reproductive success of Wood Thrush and Ovenbird in Great Smoky Mountains National Park, 1999-2001.

	OVEN		WOTH	
	Treatment	Control	Treatment	Control
Exposure-days	390.5	604	554.5	1370.0
Number of failed nests	5	19	9	42
Daily survival rates \pm SE	0.987 ± 0.006	0.968 ± 0.007	0.984 ± 0.005	0.969 ± 0.005
<i>z</i> -test of comparison of <i>dsr</i> 's ^a , <i>z</i> (<i>P</i>)	-2.05 (0.02)		-2.03(0.02)	
Nest survival rates ^b :				
mean	0.735	0.459	0.653	0.431
high	0.850	0.547	0.745	0.496
low	0.636	0.385	0.572	0.375

^a Calculated as in Johnson (1979). Testing $dsr_{\text{control}} = dsr_{\text{treatment}}$ vs. $dsr_{\text{control}} < dsr_{\text{treatment}}$.

^b Mean is calculated as *dsr* taken to the power of cumulative duration of the egg stage and nestling stage, high and low values are calculated as $dsr \pm \text{SE}$ taken to the same power.

Table 3. Behavioral responses to food supplementation in Wood Thrushes and Ovenbirds, 1999-2001^a.

	OVEN		WOTH	
	Treatment	Behavioral control	Treatment	Behavioral control
Feeding rates ^b	2.23 ± 0.24 (53)	2.29 ± 0.16 (65)	3.34 ± 0.25 (76)	3.60 ± 0.23 (89)
2-sample <i>t</i> -test ^c : T, df (<i>P</i>)	0.23 95	(0.41)	0.79 158	(0.22)
Birds on/at nest, %time ^d	37.7 ± 4.52 (50)	30.9 ± 3.73 (61)	71.7 ± 2.62 (73)	66.9 ± 3.18 (70)
2-sample <i>t</i> -test ^e : T, df (<i>P</i>)	-1.15 100	(0.13)	-1.16 134	(0.12)
Birds close to nest, %time ^f	16.6 ± 2.38 (50)	10.2 ± 2.09 (61)	3.57 ± 0.90 (73)	1.28 ± 0.32 (70)
2-sample <i>t</i> -test ^e : T, df (<i>P</i>)	-2.02 103	(0.02)	-2.40 89	(0.01)
Feeding close to nest, %time ^g	2.94 ± 0.18 (50)	0.18 ± 0.05 (61)	2.41 ± 0.75 (73)	0.06 ± 0.02 (70)
2-sample <i>t</i> -test ^e : T, df (<i>P</i>)	-4.85 49	(0.00)	-3.11 72	(0.00)
Vigilance, %time ^h	64.1 ± 3.48 (53)	49.1 ± 3.30 (65)	81.6 ± 1.56 (76)	69.8 ± 2.36 (89)
2-sample <i>t</i> -test ^e : T, df (<i>P</i>)	-3.12 113	(0.00)	-4.18 148	(0.00)

Table 3 (continued) ^a.

	OVEN		WOTH	
	Treatment	Behavioral control	Treatment	Behavioral control
Warning calls of adults, %time ⁱ	4.40 ± 1.52 (50)	4.88 ± 1.09 (61)	0.67 ± 0.22 (73)	0.56 ± 0.19 (89)
2-sample <i>t</i> -test ^e : T, df (<i>P</i>)	0.23 92 (0.59)		-0.38 139 (0.35)	
Vocalizations of young in nest, %time	0.62 ± 0.31 (50)	0.52 ± 0.33 (61)	0.01 ± 0.01 (73)	0.05 ± 0.04 (70)
2-sample <i>t</i> -test ^c : T, df (<i>P</i>)	- 0.20 108 (0.58)		1.20 72 (0.12)	
Chasing/attacking a predator, %time	0.06 ± 0.02 (50)	0.01 ± 0.01 (61)	0.03 ± 0.03 (73)	0.01 ± 0.01 (70)
2-sample <i>t</i> -test ^e : T, df (<i>P</i>)	2.10 72 (0.02)		0.83 76 (0.21)	
Displacement behavior, %time ^j	2.16 ± 0.83 (50)	1.86 ± 0.65 (61)	0.22 ± 0.22 (73)	0.003 ± 0.003 (70)
2-sample <i>t</i> -test ^e : T, df (<i>P</i>)	-0.29 97 (0.39)		0.99 69 (0.16)	

^a Mean ± standard error (sample size).

Table 3 (continued) .

^b Per-hour nest visitation rate; n is a number of observational sessions.

^c Testing $\mu_{\text{control}} = \mu_{\text{treatment}}$ VS. $\mu_{\text{control}} > \mu_{\text{treatment}}$.

^d Parental birds brooding on nest and resting/preening on the nest edge.

^e Testing $\mu_{\text{control}} = \mu_{\text{treatment}}$ VS. $\mu_{\text{control}} < \mu_{\text{treatment}}$.

^f Parental birds resting or preening in the visible vicinity of nest.

^g Parental birds feeding in the visible vicinity of nest.

^h Parental birds on the nest or in the vicinity of nest.

ⁱ Parental birds giving alarms calls or calls to quiet their young in the nest.

^j “Broken-wing display”, etc.

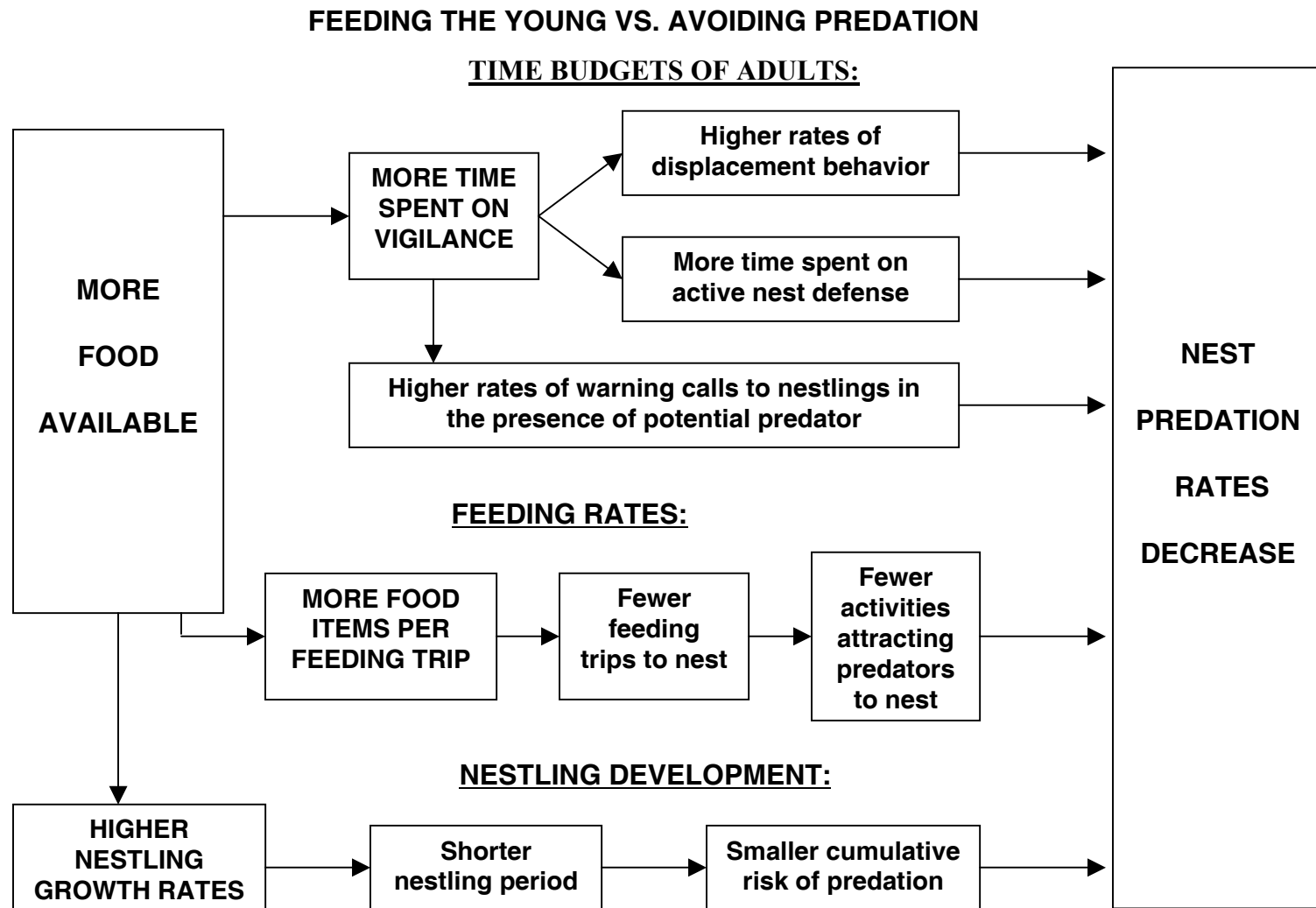


Figure 1. Conceptual model of how behavioral responses of parental birds mediate food availability and nest predation rates.

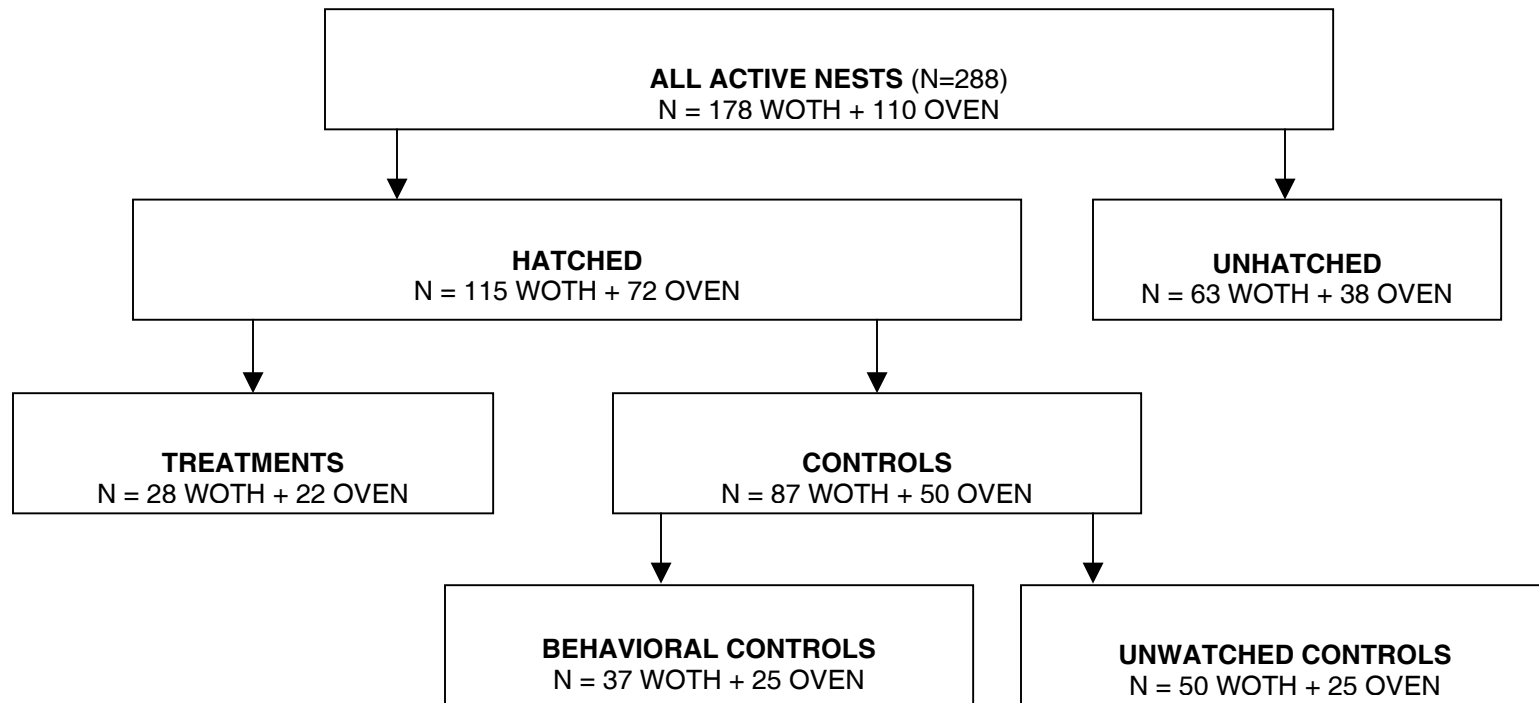


Figure 2. Categories and sample sizes of nests used in this research.

WOTH – Wood Thrush. *OVEN* – Ovenbird. *Unhatched* – nests lost prior to nestlings. *Treatments* – treatment nests, i.e. hatched nests that were food-supplemented. All of them were sampled for behavioral responses of parental birds. *Controls* – control nests, i.e. all hatched nests without supplemental food provisioning. *Behavioral controls*– control nests that were sampled for behavioral responses of parental birds. *Unwatched controls* – control nests not involved in behavioral observations.

CHAPTER 3

METHOD OF FOOD SUPPLEMENTATION FOR GROUND-FORAGING INSECTIVOROUS SONGBIRDS ¹

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Abstract. Food supplementation can be an important experimental technique in studies of avian reproductive ecology, energetics, and parental care. We developed a method of food supplementation suitable for ground-foraging insectivorous passerines and tested it on Ovenbird (*Seiurus aurocapillus*) and Wood Thrush (*Hylocichla mustelina*). We provided mealworms at the feeding stations made of plastic transparencies, covered with a thin layer of green moss. Feeding stations were placed on the ground, or on logs or boulders in the vicinity of nests. Direct and indirect evidence suggested that 92% of breeding pairs of Ovenbird and 79% of breeding Wood Thrushes used supplemental food. Non-target consumers were observed eating at approximately one-third of the nests of each species. However, diurnal non-target consumers were only detected on single occasions, and nocturnal consumers fed on small amounts of mealworms left after daytime feeding experiments. This method proved very effective for Ovenbird and Wood Thrush, and it may be applicable to other ground-foraging insectivorous passerines.

INTRODUCTION

Food supplementation can be useful in experimental studies of avian physiology, reproductive ecology, and behavior. Passerines are subject to food supplementation experiments much more often than other bird taxa (Boutin 1990). Food supplementation was used to test Lack's (1954) hypotheses about food and population regulation in wintering birds (Brittingham and Temple 1988; Nakamura 2000), and to investigate how food availability prior to the breeding season affects the timing of reproduction (Davies and Lundberg 1984; Kallander and Karlsson 1993). Field experiments with food supplementation tested reproductive stress hypothesis (Moreno 1989; Cavitt and Thompson 1997; Slagsvold and Johansen 1998) and food-related clutch size (Nilsson 1992), studied the patterns of songbird territorial behavior (Franzblau and Collins 1980; Starin and Mumme 1988; Askenmo et al. 1994; Thomas 1999) and influence of food availability on fitness-related traits (Styrsky et al. 2000). Other studies investigated the influence of food availability on bird survival (Armstrong and Perrott 2000) and reproductive success (Simons and Martin 1990; Nakamura 1995), variable mating systems (Davies and Lundberg 1984), and allocation of time to different behaviors (Davies and Lundberg 1985; Simons and Martin 1990; Garcia et al. 1993; Cucco and Malacarne 1997; Tieleman and Williams 2002).

The total number of food supplementation studies reported is surprisingly small. Only 57 experimental studies of birds in natural environment, involving food supplementation, were published in peer-reviewed periodicals prior to 1989 (Boutin

1990), and even fewer since then. Of these 57, only 4 (involving 3 species) provisioned arthropod food to insectivorous passerines. We have documented 13 other studies published since 1989, using exclusively arthropods as a supplemental food (Table 1). There are several practical difficulties surrounding these types of studies, especially for ground-foraging insectivores. Supplying arthropod food to open-nesting songbird species is difficult for several reasons. First, it is not easy to make birds (especially, those nesting openly above the ground) to find and take supplemented arthropod food. Second, it is difficult to keep arthropods alive for sufficiently long time and to prevent them from escaping from the feeding stations into the leaf litter or soil. Finally, it is important to protect supplemental food from non-target consumers and to be able to identify their impact without continuous direct observations.

Studies used different techniques to prevent non-target consumers from eating at the feeding stations. Simons and Martin (1990) used a double plastic bowl and filled the outer bowl with water to keep ants away from food. A tunnel-shaped roof on the top of a bowl with mealworms (Askenmo et al. 1994; Cavitt and Thompson 1997), wire mesh cages around feeders (Thomas 1999), and cans, placed horizontally and opened on one end (Strain and Mumme 1988), have been used to keep larger birds away from supplemental food. However, in the studies using the wire-mesh protection, small songbirds did have access to the food. Thomas (1999) placed wire cages 10 cm above the ground to keep small rodents and shrews away from feeders.

Only 6 species of ground-foraging insectivorous passerines were previously reported in food-supplementation studies (Table 1). However, ground-foraging

insectivorous birds, such as Ovenbird (*Seiurus aurocapillus*) and Wood Thrush (*Hylocichla mustelina*), may constitute a substantial part of forest songbird communities in the eastern United States and can have high local densities (Van Horn and Donovan 1994; Roth et al. 1996). These two species were repeatedly used in studies of songbird ecology and population dynamics (Donovan et al. 1995; Porneluzi and Faaborg 1999; Burke and Nol 1998, 2000; Simons et al. 2000; Bayne and Hobson 2001; Flaspohler et al. 2001). Taking into account the importance of Ovenbird and Wood Thrush as model species for ecological research, our goal was to develop an inexpensive, simple, and effective method of food supplementation for them.

METHODS

Field work was conducted in 1999-2001 in Great Smoky Mountains National Park, on seven study sites between Gatlinburg, Tennessee, and Waterville, North Carolina, at elevations of 500 to 1000 m. We have found 178 active Wood Thrush nests and 110 active Ovenbird nests. In 1999, we attempted several different techniques of food supplementation (reviewed above), but none worked well for Wood Thrushes and Ovenbirds. We used mealworms (larvae of the beetle *Tenebrio monitor*) as supplemental food. Birds ate mealworms placed on the edge of their nests readily, but they were afraid of alien objects, such as small wicker baskets, plastic bowls (especially double bowls filled with water), cans, and other types of food containers placed near their nests. In addition, containers were ineffective because they did not protect mealworms against

desiccation, and they made mealworms easily visible for non-target consumers. Both Wood Thrushes and Ovenbirds were observed taking mealworms placed on the ground in the vicinity of their nests. However, most mealworms hid in the leaf litter before birds were able to spot them. Consequently, the amount of supplemental food provided could not be controlled.

We concluded that, using mealworms as a supplemental food, we would need to provide mealworms in a natural setting but constrained so that they would not crawl away or dig to the leaf litter. Plastic transparencies covered with a thin layer of green moss proved to be a successful solution. We placed them in dry and warm location (e.g. sunlit patch) and provided wet and naturally looking cover, so that the focal birds would not be afraid of such feeding stations, and mealworms would avoid to escape laterally, but would rather be able to hide under this cover, becoming invisible for non-target consumers but still easily accessible for ground-foraging songbirds.

We were setting out feeding stations at each nest. If focal birds did not visit the feeding stations during the next 48 hrs, they stations were removed, and birds were considered experimental controls for the rest of the study. Wood Thrush feeding stations were placed 6-12 m from the base of the nest tree. Ovenbird feeding stations were set out 3-6 m from the nest. Placing the food closer to the nest would increase nest predation risk by non-target consumers of supplemental food. We made small trails of mealworms from the feeding stations to the nest to facilitate discovery of supplemental food by focal birds. For Ovenbird, we spread a line of mealworms linearly from feeding station to the

nest edge. For Wood Thrush, the trail led from the feeding station toward the nest tree, or to some conspicuous log or boulder adjacent to it.

In 2000—2001, we used our method of food supplementation to study the relationships between food availability and reproductive success of Ovenbirds and Wood Thrushes. Each treatment and control nest was subject to three observational sessions: on days 2, 4, and 6 for the Ovenbird, and on days 3, 5, and 8 for the Wood Thrush. We checked feeding stations every morning for disturbance and the presence of mealworms. Food was placed on the stations immediately before the four-hour observational sessions at the nests. On non-observational days, mealworms were delivered early in the morning.

We provided commercially raised mealworms (small for young nestlings, medium for older nestlings) at treatment nests daily during approximately 70% of the nestling period, days 2—8 for Wood Thrush and days 1—6 for Ovenbird. The amounts were determined by the relationship between total daily energy expenditure (*TDE*, kcal) and passerine weight (*W*, kg) described by the expression:

$$TDE = 317.7 * W^{0.7052}$$

(King 1974). We used published adult and nestling weights and average brood sizes (Van Horn and Donovan 1994; Roth et al. 1996), an energetic value of 2 kcal/g for mealworms, and a utilization efficiency of 0.85 (Karasow 1990) to estimate daily food delivery for both species. These amounts (40 g for Wood Thrush and 25 g for Ovenbird) provided 60—95% of energy requirements of the parents and their brood (depending on the brood size and nestling age).

RESULTS

We attempted food supplementation at 24 Ovenbird nests and 38 Wood Thrush nests. All but two of the Ovenbird pairs (92.7%) and all but 8 of the Wood Thrush pairs (79%) fed readily on mealworms (Table 2). Overall, 12.9% of focal birds failed to use supplemental food on our feeding stations, and another 3.2% only used it occasionally (Table 2).

Non-target consumers were directly observed, or their activities were deduced from the appearance of feeding stations, at approximately one-third of the stations (Table 2). We observed ants taking mealworms at two treatment nests of each focal species. However, we found that relocating the feeding stations was sufficient to remedy the losses to ants at each of those nests. We observed Wood Thrush feeding at Ovenbird feeding stations on two occasions, and Wood Thrush feeding stations were visited by Ovenbirds on four occasions and by an American Robin (*Turdus migratorius*) on one occasion. Chipmunks were seen taking mealworms at three Wood Thrush nests but they were never noticed at Ovenbird' nests. Nocturnal predators, apparently raccoons, opossum, and skunks, at mealworms at 16.7% Ovenbird feeding stations and 10.5% of the Wood Thrush feeding stations (Table 2).

DISCUSSION

We were able to provide supplemental food at Wood Thrush and Ovenbird nests by placing mealworms on moss-covered plastic sheets near active nests. Bending the sheets into a shallow depression prevented the mealworms from escaping laterally, and although the moss cover provided good protection for mealworms, they could still be detected by focal birds. Although Wood Thrush and Ovenbirds did not disturb the moss cover, while feeding, it was obvious when chipmunk or bigger predators visited the stations because the moss was often pushed off the slippery surface of the plastic sheet. Plastic has the added benefit of being light and easy to carry in the field, and it does not rot from moisture.

Non-target consumers did not significantly affect our food supplementation experiments. Diurnal consumers were observed on single occasions at 14 of 62 food-supplemented nests. The effects of nocturnal consumers was limited because birds were usually able to consume 70—100% of mealworms within four hours of when they were provided. No feeding stations were visited by non-target consumers (with the exception of ants) earlier than the fourth day of food supplementation, and on most occasions, non-target consumers were not detected until the sixth or seventh day of food supplementation.

Our method worked especially well for Ovenbirds, perhaps because we were able to place feeding stations close to their nests. Approximately one-fifth of breeding Wood Thrush pairs failed to use the food we provided. However, higher success may not be

possible because it is difficult to provide food directly to Wood Thrush nests. Our method of food supplementation may be useful in other experimental studies of ground-foraging insectivorous passerines.

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Table 1. Review of experimental field studies that food-supplemented insectivorous passerines exclusively with live arthropods.

	Cavity-nesting species, foraging predominantly above ground		Open-nesting species, foraging above ground	Ground-foraging species	All insectivorous
	Food placed in nest boxes	Food placed on/by nest boxes	Feeder above ground	Feeder on the ground	species
Number of studies:					
all studies	3	4	3	7	17
during the breeding season	3	4	2	5	14
published prior to 1989	0	1	1	2	4
using only mealworms	3	4	2	5	14
Number of focal species	3 ^a	3 ^b	3 ^c	6 ^d	14
Non-target consumers					
observed: ^e					
yes	0	3	1	2	6
no	3	0	0	2	5
unknown	0	1	2	3	6

Table 1 (continued)

	Cavity-nesting species, foraging predominantly above ground		Open-nesting species, foraging above ground	Ground-foraging species	All insectivorous
	Food placed in nest boxes	Food placed on/by nest boxes	Feeder above ground	Feeder on the ground	species
Non-target consumers: ^f					
ants	0	0	1	0	1
Woodpeckers	0	1	1	0	2
<i>Corvidae</i>	0	0	1	1	2
Thrashers	0	0	1	0	1
small songbirds	0	0	0	1	1
unknown	0	2	0	0	2

^a Mountain Bluebird (Garcia et al. 1993), Pied Flycatcher (Slagsvold and Johansen 1998), House Wren (Styrsky et al. 2000).

^b European starling (Crossner 1977; Kallander and Karlsson 1993), Marsh Tit (Nilsson 1992), House Wren (Cavitt and Thompson 1997).

^c Carolina Wren (Strain and Mumme 1988), Cactus Wren (Simons and Martin 1990), Alpine Accentor (Nakamura 1995).

^d Rufous-sided Towhee (Franzblau and Collins 1980; Wasserman 1983), Northern Wheatear (Moreno 1989), Rock Pipit (Askenmo et al. 1994), Black Redstart (Cucco and Malacarne 1997), European Robin (Thomas 1999), Hoopoe-lark (Tieleman and Williams 2002).

^e Number of studies that observed or did not observe non-target consumers on focal species' feeding stations, or did not investigate the issue.

^f Number of studies that detected different species or groups of non-target consumers of supplemental food.

Table 2. Effectiveness of proposed technique of food supplementation: use of feeding stations by the focal species (Ovenbird and Wood Thrush) and other consumers.

	Ovenbird		Wood Thrush		Focal species combined	
	N	%	N	%	N	%
Attempted food supplementation ^a	24	100.0	38	100.0	62	100.0
Partial failure to take mealworms ^b	2	8.3	0	0.0	2	3.2
Complete failure to take mealworms ^c	0	0.0	8	21.0	8	12.9
Non-target consumers ^d	8	33.3	14	36.8	22	35.5
Ants	2	8.3	2	5.3	4	6.5
Chipmunks	0	0.0	3	7.9	3	4.8
Unknown nocturnal consumers ^e	4	16.7	4	10.5	8	12.9
American Robin	0	0.0	1	2.6	1	1.6
Another focal species ^f	2	8.3	4	10.5	6	9.7

Table 2 (continued)

^a Number of food-supplemented breeding pairs.

^b Birds were not observed to take mealworms consistently or in significant amounts.

^c Birds did not take mealworms.

^d Feeding stations were never disturbed/visited by non-target consumers earlier than on the 4th day of food supplementation.

On most occasions, non-target consumers were detected on the 6th—7th day of food supplementation.

^e Probably, large nocturnal mammals (raccoons, skunks, etc.). Feeding stations disturbed during the night.

^f Wood Thrushes taking food from Ovenbird's feeding stations, and Ovenbirds feeding on Wood Thrush's feeding stations.