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ASSESSING THE CONSEQUENCES OF BROOD PARASITISM AND NEST PREDATION ON SEASONAL FECUNDITY IN PASSERINE BIRDS

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ABSTRACT.—Brood parasites and nest predators reduce the seasonal fecundity and, hence, the population growth rates of their victims. However, most field studies do not measure directly how parasites and predators decrease seasonal fecundity, but instead measure the impact of these organisms on individual nesting attempts. Because a female may renest after losing a nest to predation, abandoning a parasitized nest, or successfully fledging a brood, knowing how brood parasites and nest predators reduce the number of offspring fledged from individual nesting attempts is not equivalent to knowing their impact on seasonal fecundity. We address this problem by developing a mathematical model that: estimates several parameters describing the natural history of this system, including the brood-parasitism rate, nest-predation rate, and probability of nest abandonment in response to a parasitism event; and extrapolates to seasonal fecundity from these parameters and others describing the length of the breeding season, the timing of events in the nesting cycle, and the productivity of parasitized and unparasitized nests. We also show how different researchers using different observational methodologies to study exactly the same population likely would arrive at noticeably different conclusions regarding the intensity of brood parasitism, and we provide mathematical formulas for comparing among several of these measures of parasitism. Our procedures extend Mayfield's method for calculating nest-success rates from nest-history data in that we simultaneously estimate parameters describing nest predation and brood parasitism, predict seasonal fecundity from these parameters, and provide confidence intervals on all parameter estimates. The model should make the design and interpretation of logistically difficult empirical studies more efficient. It also can be specialized to species affected by nest predators but not brood parasites. We use the model to analyze Prairie Warbler (*Dendroica discolor*) and Black-capped Vireo (*Vireo atricapillus*) nesting data. We estimate the model's parameters for these species and use the resulting estimates to predict seasonal fecundity. For both species, the predicted seasonal fecundity closely matches the value measured directly. *Received 30 November 1993, accepted 15 February 1994.*

BROOD PARASITES AND NEST PREDATORS cause many passerine nests to fail before any young are fledged (Ricklefs 1969). In addition, when a parasitized nest is not immediately abandoned, the number of host young that can be fledged is often greatly reduced. As Rothstein (1990) summarized, about 80 bird species are interspecific brood parasites, including cowbirds (Emberizidae, Icterinae), cuckoos (Cuculidae, Cuculinae and Neomorphinae), the Cuckoo-finch (*Anomalospiza imberbis*), whydahs (Ploceidae, Viduinae), honeyguides (Indicatoridae), and the Black-headed Duck (*Heteronetta atricapillus*; Friedmann 1929, 1955, Weller 1959, Payne 1977, Wyllie 1981). Nest predation is known from all passerines studied in any detail, and includes predation by small mammals, birds, snakes and ants.

Most nest predators are omnivores, and some brood parasites, such as cowbirds (*Molothrus* spp.), are host generalists (Friedmann et al. 1977, Friedmann and Kiff 1985, Wiley 1985). Consequently, the abundances of cowbirds and most nest predators are believed to be insensitive to the abundances of some of the species they affect. This can lead to the extirpation or near extirpation of some of their prey and host species. For example, the presence of foxes explains the absence of certain passerine species from chaparral habitat islands with apparently suitable vegetation (Soulé et al. 1988). Cowbirds have dramatically impacted populations of some hosts (e.g. Kirkland's Warblers [*Dendroica kirklandii*], Mayfield 1965; Yellow-shouldered Blackbirds [*Agelaius xanthomus*], Post and Wiley 1976, Wiley 1985).

Although there is a large empirical literature on brood parasitism and nest predation in birds (e.g. Ricklefs 1969, Payne 1977, Rothstein 1990), few studies directly measure how brood parasitism and nest predation affect seasonal fecundity (but see, for example, Nolan 1978, Smith 1981). Because directly measuring seasonal fecundity requires tracking a group of females through the entire breeding season, many field workers have instead adopted the surrogate goal of quantifying how nest predators and brood parasites reduce the number of offspring fledged from individual nesting attempts. However, females may renest after nest failures, and the number of such renesting attempts depends on the frequency of nest predation, the probability of nest abandonment in response to parasitism, and the length of the breeding season, among other variables. For example, females subjected to higher predation rates may renest more frequently, and could even produce the same number of young in a breeding season as females less subject to nest predators. Thus, extrapolating from data on individual nesting attempts to inferences about seasonal fecundity remains a problem.

An additional difficulty is the wide variation in the protocols (and their implementation) that different researchers use in collecting data on how brood parasites and nest predators affect reproductive success. For example, because host females abandon some parasitized nests, these nests will have different life expectancies than unparasitized nests subject only to nest predation (Nolan 1978). Procedures that do not account for this difference will produce different estimates of parasitism than those that do. As recognized by Ricklefs (1973) and Mayfield (1975), such differences, together with a failure to derive standardized parameter estimates from the raw data, confound interpretation of these data, making it difficult to compare results among studies. Differences between studies due to differences in sampling protocol cannot be separated from the actual biological differences among the species or geographic localities being compared. Mayfield's (1975) technique for standardizing disparate measures of nest failure is currently in wide use. However, there is no comparable method for overcoming the biases in estimating levels of brood parasitism that are similar to those encountered in measuring nest failure, or for producing from a single data set standard measures of nest predation and brood parasitism. Also, no general method is available for extrapolating to seasonal fecundity from such parameters.

In this paper we develop a mathematical model that allows seasonal fecundity to be calculated from parameters describing how brood parasitism and nest predation affect individual nesting attempts. We describe the critical model parameters and our methods for estimating them, and for computing seasonal fecundity from them. We also derive mathematical formulas that convert among different measures of brood parasitism used or approximated by field workers. We then apply the model to nesting data from the Prairie Warbler (*Dendroica discolor*) and the Black-capped Vireo (*Vireo atricapillus*), both of which are parasitized by Brown-headed Cowbirds (*Molothrus ater*). Empirical estimates of parameters describing the effect of nest predators and Brown-headed Cowbirds on nesting attempts made by the warbler and vireo are derived with their confidence intervals. We show that the seasonal fecundity predicted by the model using these parameter estimates closely matches that measured directly. Lastly, the discussion describes how one could prospectively test this model, use it to help design field studies on passerine breeding biology, and assist in endangered-species management.

THE MODEL

The mathematical model central to this paper predicts seasonal fecundity from the natural-history parameters described in Table 1. The primary complication in undertaking this calculation is properly accounting for renesting attempts. Our mathematical model is effectively a bookkeeping method for tracking the number of females at different stages of the breeding season and nesting cycle (Fig. 1).

Breeding season and nesting cycle.—The breeding season is the total period of breeding activity. It encompasses all the calendar dates during which a female can initiate nesting attempts (Fig. 1). For North Temperate migratory passerines, the breeding season is generally one to several months of the spring and summer.

The nesting cycle describes the sequential events that occur during a single successful nesting attempt, starting with nest building, and continuing through parental care of fledged young (Fig. 1). Brood parasitism and nest predation occur only during certain time windows

TABLE 1. Model parameters.

	A simple model
p	Brood-parasitism rate (per day)
d	Nest-predation rate (per day)
a	Probability host nest abandoned when parasitized (dimensionless)
t_e	Beginning of both windows of susceptibility[a]
t_i	End of window of susceptibility to brood parasitism[a]
t_f	End of window of susceptibility to nest predation[a]
t_r	Time when successful females renest after terminating parental care[a]
s_s	Time in breeding season the last nesting cycle initiated[b]
f_u	Number of host young fledged from successful unparasitized nests
f_p	Number of host young fledged from successful parasitized nests
F	Seasonal fecundity
	More complex models
$C(s)$	Cohort parasitism fraction (dimensionless)
Y	Seasonal parasitism fraction (dimensionless)
$S(s)$	Snapshot parasitism fraction (dimensionless)
p_u	Rate unparasitized nests become parasitized (per day)
p_p	Rate parasitized nests become parasitized again (per day)
d_u	Rate unparasitized nests are lost to nest predation (per day)
d_p	Rate parasitized nests are lost to nest predation (per day)
a_u	Probability unparasitized nest abandoned when parasitized (dimensionless)
a_p	Probability parasitized nest abandoned when parasitized again (dimensionless)
t_p	Time when non-renesting parent terminates parental care[a]
f_i	Number of host young fledged from successful nest containing *i* parasite eggs
$g(s)$	Probability of renesting at day *s* of breeding season (dimensionless)
$f(s)$	Rate previously unreproductive females enter breeding pool on day *s* of breeding season (per day)

[a] Measured in days from start of nesting cycle.

[b] Measured in days from start of breeding season.

of the nesting cycle. As discussed further below, the window of susceptibility to brood parasitism for many species extends from approximately one day before host egg laying commences to one day after it ceases, while the window of susceptibility to nest predators extends from approximately egg laying to fledging.

Seasonal fecundity, nest productivity, and renesting.—Seasonal fecundity is defined here as the number of young fledged per female during an entire breeding season and so is, in general, summed over multiple nesting attempts. Nest productivity is the number of offspring fledged from a single successful nest, where we define a successful nest as one that fledges at least one

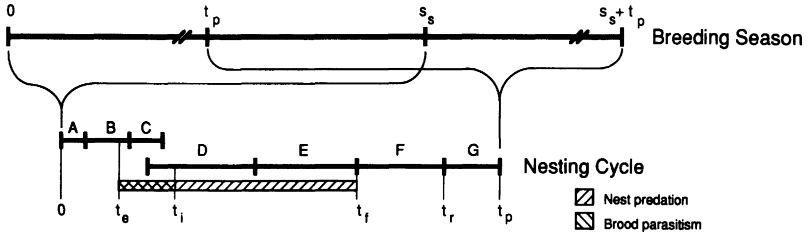

Fig. 1. Breeding season and nesting cycle. For many passerines, multiple nesting cycles are possible within a single breeding season, and more than one of these may be successful. Successful nesting attempts can begin on any day of the breeding season between 0 and s_s, and can terminate on any day between t_p and $s_s + t_p$. A single nesting cycle contains periods of: (A) inactivity before nest building; (B) nest building; (C) egg laying; (D) incubation; (E) nestling care; (F) parental care of fledglings before female renests; (G) continued parental care by non-renesting parent; (t_e to t_i) window of susceptibility to brood parasitism; and (t_e to t_f) window of susceptibility to nest predation. See Table 1 for definitions of variables.

young, be it host or parasite. In general, parasitized nests produce fewer host offspring than unparasitized nests.

Because females may renest after a nest failure or successfully fledging a brood, a single female potentially can initiate multiple nesting cycles during a single breeding season (Fig. 1). One or more of these nesting attempts may be successful. In computing seasonal fecundity, it is necessary to determine the number of days of the breeding season a female loses to each unsuccessful nesting attempt, as this determines the total number of nesting attempts possible.

We define nest predation to include all events, other than nest abandonment in response to a brood-parasitism event, which result in loss of an entire clutch or brood. This definition assigns to nest predation abiotic catastrophes, such as hailstorms, which terminate nesting attempts. By contrast, females that lose individual eggs or young, like parasitized females who do not abandon their nest, will attempt to continue their current nesting cycle, but may only fledge a reduced number of offspring. These two types of mortality have radically different population-dynamic consequences. When an entire brood is lost to predation or abandonment, the female can renest immediately, whereas with partial brood loss (or entire brood loss in some cases when female does not abandon parasitized nest), the female forgoes the opportunity to renest immediately (with the potential of raising complete brood). The model accounts for loss of individual eggs or young by incorporating these losses into nest productivity.

We recommend relegating all deaths of young after fledging to juvenile mortality. This convention is reasonable inasmuch as most nestling mortality arises from loss of entire clutchs or broods, while most mortality after fledging consists of mortality of individual juveniles. Nolan (1978) estimated, for example, that 95% of the mortality before fledging in Prairie Warblers affects all eggs or young in a nest. However, our model is flexible about setting the end of the window of susceptibility to nest predation, and can set it to times after fledging.

Fundamental equations.—In order to develop an intuitive understanding of how the following equations predict seasonal fecundity at a given level of brood parasitism and nest predation, it is useful to consider a verbal argument based on a discrete analog of the continuous-time equations given below. Our goal is to compute, for each day of the breeding season, the fraction of females that are at a given day of the nesting cycle. We start at the first day of the breeding season, and then advance through it one day at a time. For each day we compute the fraction of females that succumb to nest predation or brood parasitism. Of those parasitized, we account for the fraction that abandon their nest immediately, and the fraction that continue the nesting cycle with a parasitized nest, which, if successful, will have reduced nest productivity for most host species. We also account for females that fledge young, for females that restart the nesting cycle after a nest failure or after successfully fledging a brood, and for females that initiate breeding for the first time in the breeding season. This bookkeeping is needed to account properly for the average number of days of the breeding season lost when a nest failure occurs. We also determine the number of young fledging on each day of the breeding season, and the fraction of these nests that are parasitized and unparasitized. We then compute seasonal fecundity from this information.

Keeping the goal of accounting for all these factors in mind, we define the fraction of all females that are unparasitized on calendar date s of the breeding season, and that are between days t_1 and t_2 of the nesting cycle as

$$\int_{t_1}^{t_2} u(t, s)\, dt. \tag{1}$$

The fraction of all host females that are parasitized with n parasite eggs on calendar date s of the breeding season, and that are between days t_1 and t_2 of the nesting cycle is

$$\int_{t_1}^{t_2} p_n(t, s)\, dt. \tag{2}$$

The fraction of all females that on the calendar date s of the breeding season are either initiating a nesting attempt, nesting, or caring for fledglings is

$$\int_{0}^{t_r} [u(t, s) + p_1(t, s) + p_2(t, s) + \ldots]\, dt \leq 1. \tag{3}$$

This fraction may be less than one because fewer than 100% of the adult females actually may be breeding during some parts of the breeding season. Not all females start their first nest on the same calendar date, nor do all females terminate breeding activity on the same date at the end of the breeding season.

The next equations describe what happens as time advances, and females move through the nesting cycle and breeding season while being subjected to nest predation and brood parasitism. These equations are formally analogous to those describing the dynamics of age-structured populations (Von Foerster 1959, Metz and Diekmann 1986, Metz et al. 1988).

$$\frac{\partial u(t,s)}{\partial t} + \frac{\partial u(t,s)}{\partial s} = -d_u(t,s)u(t,s) - \rho_u(t,s)u(t,s), \tag{4}$$

$$\begin{aligned}\frac{\partial p_1(t,s)}{\partial t} + \frac{\partial p_1(t,s)}{\partial s} &= -d_p(t,s)p_1(t,s) - \rho_p(t,s)p_1(t,s)\\ &\quad + \rho_u(t,s)[1 - a_u(t,s)]u(t,s),\end{aligned} \tag{5a}$$

$$\begin{aligned}\frac{\partial p_n(t,s)}{\partial t} + \frac{\partial p_n(t,s)}{\partial s} &= -d_p(t,s)p_n(t,s) - \rho_p(t,s)p_n(t,s)\\ &\quad + \rho_p(t,s)[1 - a_p(t,s)]p_{n-1}(t,s),\\ &\quad \text{for } n \geq 2,\end{aligned} \tag{5b}$$

where n is the number of parasite eggs or young in the host nest. Because Equation 5b holds for all $n \geq 2$, it actually represents a series of equations, one equation for $n = 2$, one for $n = 3$, and so forth.

A single female may initiate a nesting cycle for any one of four separate reasons, including initiating breeding at the beginning of the breeding season, successfully fledging a brood, suffering nest predation, or abandoning a nest in response to brood parasitism. These four causes are accounted for, respectively, by the four terms on the right-hand side of the boundary condition,

$$\begin{aligned}u(0,s) &= f(s) + g(s)[u(t_r,s) + p(t_r,s)]\\ &\quad + g(s)\cdot\int_0^{t_r} d_u(x,s)u(x,s)\\ &\qquad + d_p(x,s)p(x,s)\,dx\\ &\quad + g(s)\cdot\int_0^{t_r} a_u(x,s)\rho_u(x,s)u(x,s)\\ &\qquad + a_p(x,s)\rho_p(x,s)p(x,s)\,dx,\end{aligned} \tag{6}$$

where

$$p(t,s) = p_1(t,s) + p_2(t,s) + \ldots, \tag{7}$$

and where Table 1 defines $f(s)$ and $g(s)$.

The left-hand sides of Equations 4, 5a and 5b state in mathematical symbols that, after one day has passed, all females that avoid nest predation and brood parasitism will be on the next calendar date of the breeding season and will have advanced one day in the nesting cycle. The first terms on the right-hand sides of Equations 4, 5a and 5b account for nests that nest predators destroy, thereby causing the affected female to restart the nesting cycle (third term on the right-hand side of Equation 6). The second terms on the right-hand sides of Equations 4, 5a and 5b account for brood parasitism. However, unlike nest predation, some parasitized females do not immediately abandon their nest. These unabandoned nests are accounted for by the third term on the right-hand sides of Equations 5a and 5b, and the abandoned nests by the fourth term on the right-hand side of Equation 6.

The model in Equations 1 to 7 is very general. It allows the brood-parasitism and nest-predation rates and the probability of nest abandonment after a parasitism event to vary according to the day of nesting cycle and/or breeding season, and for parasitized and unparasitized nests to have different values of these parameters. Furthermore, the model permits different females to start and end the breeding season on different dates, and allows the number of host offspring fledged from a nest to vary with the number of parasite eggs or young the nest contains.

Seasonal fecundity, F, is the number of offspring produced per adult female in a complete breeding season. Equations 1 to 7 implicitly determine the rate at which females successfully fledge broods, and also the fraction of these broods that come from unparasitized and parasitized nests. Equation 8 accumulates this information across the entire breeding season, and uses it together with information on the productivity of parasitized and unparasitized nests to estimate seasonal fecundity:

$$F = f_u \int_{t_f}^{\infty} u(t_f,s)\,ds + \sum_{n=1}^{\infty} f_n \int_{t_f}^{\infty} p_n(t_f,s)\,ds. \tag{8}$$

The first term on the right-hand side of Equation 8 is the productivity of unparasitized nests,

f_u, times the average number of successful unparasitized nests produced per female in an entire breeding season. The second term quantifies the average number of host offspring fledged from successful parasitized nests with n parasite eggs.

Constant parameters, an important special case of the model.—As a practical matter, there are rarely, if ever, sufficient empirical data to use the model in Equations 1 to 8 in its most general form. For example, even Nolan's (1978) outstanding Prairie Warbler data set is inadequate for estimating all of the parameters and functions of our general model. However, the simple version of the model that we develop next has sufficient complexity to account for the vast majority of the available data, yet is not so complicated as to contain parameters and functions that cannot be estimated empirically.

The simple (or constant-parameter) version of our model assumes that brood parasitism and nest predation occur only during certain parts of the nesting cycle (see Fig. 1), and that the rates of brood parasitism and nest predation are constants. Thus, the initial brood-parasitism event (i.e. laying of the parasite egg) only occurs between times t_e and t_i of the nesting cycle; during this window, unparasitized nests are parasitized at an instantaneous brood-parasitism rate of ρ_u, while already parasitized nests are superparasitized at rate ρ_p. A ρ_u of 0.02 per day corresponds to roughly 2% of the susceptible unparasitized nests being parasitized each day. The probability that an initially unparasitized nest is abandoned after being parasitized for the first time is a_u; the analogous abandonment probability for already parasitized nests receiving additional parasite eggs is a_p. Similarly, the simple version of our model assumes that nest predation occurs only between times t_e and t_f of the nesting cycle; during this window, unparasitized nests are depredated at rate d_u, while parasitized nests are depredated at rate d_p. This is because nest predation generally occurs over a much longer period than brood parasitism, $t_f > t_i$. With these assumptions, the model consists of Equations 4, 6, 7 and 8, together with

$$\frac{\partial p(t, s)}{\partial t} + \frac{\partial p(t, s)}{\partial s} = -d_p(t, s)p(t, s) - \rho_p(t, s)a_p(t, s)p(t, s) + \rho_u(t, s)[1 - a_u(t, s)]u(t, s). \qquad (9)$$

Moreover, when the simple model holds, the nest-predation rate is a constant within the window of susceptibility and zero outside this window. The brood-parasitism rate behaves similarly. Mathematically, $\rho_u(t, s)$ equals ρ_u for t within the window of susceptibility to parasitism, and zero otherwise; $\rho_p(t, s)$ equals ρ_p for t within the window of susceptibility to parasitism, and zero otherwise; $d_u(t, s)$ equals d_u for t within the window of susceptibility to nest predation, and zero otherwise; $d_p(t, s)$ equals d_p for t within the window of susceptibility to nest predation, and zero otherwise. Because the abandonment probability is a constant, $a_u(t, s) = a_u$ and $a_p(t, s) = a_p$. In the simple model, all females begin the breeding season on the same calendar date; thus, $f(s) = \delta(s)$, where the Dirac delta function, $\delta(s)$, mathematically describes the pulse of females that start the nesting cycle on the first day of the breeding season. Because the simple model also assumes that the breeding season is exactly the same length for all females, we have $g(s) = 1$ for $s \leq s_s$ and 0 for $s > s_s$.

We shall also assume in the simple version of our model that the number of offspring fledged from successful unparasitized nests is f_u, and that all successful parasitized nests have the same productivity, f_p, regardless of the number of parasite eggs in them. In addition, we assume that females successfully fledging a brood can renest at day t_r of the nesting cycle and that s_s is the number of days of the year in which a female can initiate a successful nesting attempt. Thus, in our model calculations, the last young fledge no later than $s_s + t_f$ days from the start of the breeding season.

Under these assumptions, the equation for seasonal fecundity simplifies to

$$F = f_u \int_{t_f}^{s_s+t_f} u(t_f, s)\, ds + f_p \int_{t_f}^{s_s+t_f} p(t_f, s)\, ds. \qquad (10)$$

When there is no empirical evidence to the contrary, it is convenient to further specialize the simple model by assuming that the brood-parasitism and nest-predation rates and the abandonment probabilities do not differ between unparasitized and parasitized nests: $\rho_u = \rho_p = \rho$; $d_u = d_p = d$; and $a_u = a_p = a$.

Lack of support for the more complex model given by Equations 4 to 8 can occur either because there are insufficient data available to test it or because, even though data are available, the simple model adequately describes them. Both reasons apply to our analysis of the Prairie Warbler and Black-capped Vireo nesting data below.

MODEL ANALYSIS

We have written computer programs that: (1) estimate the nest-predation rate, brood-parasitism rate, and abandonment probability from data on individual host nesting attempts; (2) compute seasonal fecundity, given input parameter values; and (3) determine the cohort, seasonal, and snapshot parasitism fractions (see below for definitions) corresponding to particular values of the model parameters. These programs perform many of the analyses we now describe.

Methods for estimating model parameters.—The nesting-cycle (t_e, t_i, t_f and t_r), breeding-season (s_s), and nest-productivity (f_u and f_p) parameters can be readily estimated by direct observation or obtained from the literature. By contrast, the nest-predation and brood-parasitism parameters (d, ρ and a) must be estimated from data on serial observations of nests.

In the course of estimating these parameters, it is sometimes necessary to deal with some observations in ways that deviate from some details of a species' biology. The central question in this regard is whether these modifications significantly alter the accuracy of our seasonal fecundity predictions. Our general method of answering this question is a sensitivity analysis in which we change various (we suspect minor) assumptions of the analysis, and quantify the effect of these changes on predicted seasonal fecundity (see below).

Nesting-cycle, breeding-season, and nest-productivity parameters.—The parameter t_e is the day of the nesting cycle when a clutch first becomes susceptible to brood parasitism. It can be estimated by directly counting the number of days from when a female either stops caring for her fledglings or suffers a nest failure to the beginning of the window of susceptibility to brood parasitism. Because cowbirds sometimes lay their eggs in host nests on the day before host egg laying begins, in the absence of other information it is useful to assume that t_e is this day. For many passerines, the period from which t_e is estimated consists of three to eight days total, including one or two days when the adults are searching for a new nest site, plus two to six days to complete a nest once it has been started. An inactive day sometimes occurs between the completion of a nest and the first day of egg laying. Our definition of t_e accounts for the time it takes a female to build her second and subsequent nests. As discussed below, we account for the sometimes protracted time it takes to build the first nest of the breeding season in our procedure for determining the calendar date for the start of the breeding season (Nolan 1978, Scott et al. 1987).

The parameter t_i is the last day of the nesting cycle when a host nest is susceptible to parasitism. To estimate it for species parasitized by cowbirds, observe that most cowbird eggs are laid on or before the final day of host egg laying, although a few are laid during the beginning of incubation (and in rare cases even later). We suggest, in the absence of more specific empirical data, that t_i be set as the day after the last day of egg laying. It is possible to look at these definitions of t_i and t_e from a different perspective; the number of days a host nest is susceptible to brood parasitism (i.e. $t_i - t_e$) can be estimated as the number of eggs in a normal clutch (assuming one egg is laid per day), plus two days (to account for parasite eggs laid on day before and day after egg laying).

In assessing a brood parasite's impact on seasonal fecundity, the parasitism events that matter most are those that reduce host nest productivity or cause the host to abandon a nest. For cowbirds, a significant portion of the parasitism events outside the window of susceptibility to parasitism we have defined probably do not impact the host. Parasite eggs laid prior to our window of susceptibility to brood parasitism are sometimes buried in the nest lining and consequently die, while parasite eggs laid after our window of susceptibility may not be incubated long enough to hatch. If they do hatch, they will not enjoy a developmental head-start over the host young. Our window of susceptibility to brood parasitism encompasses 89% of the cowbird egg-laying events Nolan (1978) observed.

Reasonable alternative approaches to estimating t_e and t_i are possible. Because brood parasites often have a shorter incubation time than their hosts, one alternative is to set t_i so that a parasite egg laid on day t_i of the nesting cycle will hatch on the same day that the host eggs hatch. Additionally, when the brood parasite removes or damages host eggs after laying its egg (and this occurs commonly during incubation), the window of susceptibility to parasitism in our procedure may need to be extended beyond the day after the last day of host egg laying.

The parameter t_f is the day of the nesting cycle after which a predation event typically does not result in the loss of an entire brood. Most field investigators will set it as the day of fledging, although our model can accommodate other times. One can estimate the day of fledging as the sum of the number of days spent searching for a nest site, the nest-building period, the number of days in the inactive period before egg laying, the egg-laying period, the incubation period, and the period of nestling care. However, there are some subtleties in this calculation. Because incubation generally starts at the beginning of the day on which the last or penultimate egg is laid, a day or two of the incubation period generally overlaps with the egg-laying period; this must be accounted for in determining t_f (Fig. 1). Additionally, when young fledge on different days, we recommend defining t_f as the day the first young fledges, because nest-predation events after this time typically will not result in loss of the entire brood. Incubation times and times from hatching to fledging are available for many species (e.g. Ehrlich et al. 1988) if they cannot be obtained by direct measurement.

The parameter t_r is the day of the nesting cycle on which a female can initiate a subsequent nesting attempt after successfully fledging her most recent brood. Because females fledging young have several behavioral options, some of which involve moving off their mate's territory, and because of the difficulty of detecting renesting females no longer attending their fledged young, t_r is more difficult to measure empirically than are t_e, t_i or t_f. When a researcher can follow individual females for a substantial period of time, one may estimate t_r from knowledge of the number of calendar days between identical points in two successive nesting cycles, provided the first was successful and there were no nest failures between them (see Appendix 2 for an extension of this idea). For example, this may be the number of days between when two successive broods were fledged. The number of days a renesting female cares for fledglings of her most recent brood (i.e. $t_r - t_f$) exhibits substantial variation among individuals (Nolan 1978, Scott et al. 1987, Grzybowski pers. obs.), and the data from which t_r is estimated sometimes may include unsuccessful nesting attempts. In the absence of species-specific data, we suggest 10 to 15 days as a reasonable estimate of the $t_r - t_f$ interval in multiple-brooded small passerines.

The length of the breeding season, s_s, is the most difficult parameter to estimate. The most direct way to estimate s_s would be to measure the average number of calendar days that females invest in breeding. However, much variation occurs among females. Because of the difficulties in tracking the breeding activities of individual females across an entire breeding season, data of this type are infrequently available for a large sample of females. For example, a female that is not observed to renest late in the season may have actually renested on her old territory but gone undetected, or may have moved to a new territory, perhaps even off of the study site, and renested there undetected.

An alternative approach is to estimate s_s as the time between when one-half the females have begun breeding and when only one-half of the females would initiate a new nesting attempt if given the opportunity (as after fledging a brood or suffering a nest failure). This does not require tracking individual females across a breeding season. Our constant-parameter model uses this approach.

We have identified three ways to estimate the calendar date of the start of the breeding season. First, one can plot the dates of fledging for observed nestings, and then, using a known t_f, back-calculate from the first peak in number of fledgings to the date of nest initiation. A potential complication is that the nest-construction period may be protracted for the first nesting attempt (Nolan 1978, Scott et al. 1987). We accommodate this by making an appropriate correction in the calendar date of the start of the breeding season. If the first nest takes six days to build, but subsequent renestings take only four days, then the calendar date for day 0 of the breeding season should be chosen as t_f days prior to the initial peak of fledgings (rather than $t_f + [6 - 4]$ days prior). Second, one can determine the average date eggs are first laid, and then use t_e to calculate the desired date (again noting above correction for potential increased time to build first nest). Third, for many migrants, most females arrive within a two- to four-week period (e.g. Nice 1937, Nolan 1978), and one-half of this window (or 7 to 14 days) can be added to the date of the earliest nesting starts to obtain the desired date.

Determining the calendar date at which females will no longer renest if given the opportunity is also difficult. Nolan (1978) identified four ways in which this date can be determined, and applied these methods to Prairie Warblers. One of Nolan's methods is to use the timing of the molt in females (useful only for species that molt on breeding ground), data that Pyles et al. (1986) compiled for many North American passerines. For widespread species, one must account for geographic variation in the timing of this molt.

The parameters f_p and f_u can be estimated as the average nest productivity of parasitized and unparasitized nests, respectively. This will need to be directly estimated or determined from the literature. Although our general model allows nest productivity to vary depending on the number of parasite eggs in the host nest, when such detailed data are unavailable, an average across all successful parasitized nestings often should provide a reasonable estimate of f_p. Recall that, by definition, a successful nest fledged at least one host or parasite offspring. Of course, this approach may produce an estimate of f_p that varies with the number of parasite eggs laid per host nest. Hence, an estimate of f_p specific to the population being studied should be used.

Brood-parasitism and nest-predation parameters.—These parameters generally will be estimated from a sample of nests, each revisited one or more times after being found, with known time intervals between all pairs of visits. For each visit, the researcher records (or infers; see below) both the day in the nesting cycle of the visit and the status of the nest (i.e. unparasitized, parasitized with one parasite egg or young, parasitized with two parasite eggs or young, . . . , abandoned after one parasitism event, abandonded after two parasitism events, . . . , or depredated).

If the time interval between visits is very short (e.g. one day or less), one can simultaneously estimate the brood-parasitism and nest-predation rates using a straightforward extension of Mayfield's (1975) method. To determine the nest-predation rate, one divides the number of nest-predation events observed by the time interval for which these nests were observed at risk for nest predation. Because a nest cannot suffer a second predation event after it has been depredated, and because the nest-predation events do not occur at the very ends of the time intervals between nest observations, the nest-predation at-risk period computed using the above procedure is slightly too long. This bias can be corrected using the formula

$$f = 1 - \exp(-d\Delta t),$$

where f is the fraction of a sample of nests lost to nest predation over a sampling interval of length Δt. Rearranging, this produces

$$d = -(1/\Delta t)\log_e(1 - f). \qquad (11)$$

An analogous procedure estimates the brood-parasitism rate. However, in this case, we do not recommend using the correction given by Equation 11. A nest that is parasitized but not abandoned remains susceptible to additional parasitism events and, even when abandonment does happen, it may not occur simultaneously with the parasitism event.

If the time interval between sequential visits is longer (e.g. four days or more), matters become considerably more complicated. One cannot compute the at-risk periods in the above manner because one does not know exactly when the nest-status changes occurred. For example, once a nest has been destroyed by a nest predator, that nest should no longer contribute to the at-risk period for computing the brood-parasitism and nest-predation rates. In addition, if a nest is parasitized between two visits, the researcher will either have to estimate when this occurred, or assume that the nest-predation rates on unparasitized and parasitized nests are equal. These are but two examples of the general type of problems that arise from data with longer intervals between revisits. Although one could imagine various ad-hoc procedures for dealing with these difficulties (such as assuming that nest-status changes occurred at midpoint of interval), a systematic solution is to use a maximum-likelihood method to estimate the parameters of interest (e.g. Johnson 1979, Stuart and Ord 1987). Appendix 1 explains our maximum-likelihood approach. It numerically determines which values of ρ_u, ρ_p, d_u, d_p, a_u and a_p produce a data set best matching the actual empirical observations from nests that were monitored.

Calculating seasonal fecundity.—We wrote a computer program that numerically integrates the partial differential equations given by Equations 1 to 7. It accomplishes this by making these equations discrete, and then iterating them. We used this simple method of numerical integration because all our simulations were of piecewise linear partial differential equations, which we expect to be stable under a variety of numerical-integration techniques. All calculations reported here used a step size of 0.05 days in both the nesting cycle and breeding season dimensions.

Although this computer program allows model parameters to vary across the nesting cycle and breeding season, even Nolan's (1978) extensive Prairie Warbler data were not sufficiently complete to determine how all of our model's parameters varied across the nesting cycle and breeding season. Because few studies will contain the detail of Nolan's, most of the time it will suffice to use the program in a simpler mode in which the output is seasonal fecundity, and the input consists of the parameters of the simplified model (t_e, t_i, t_f, t_r, s_s, f_u, f_p, ρ_u, ρ_p, a_u, a_p, d_u and d_p). The latter six parameters can be reduced to ρ, a and d.

Several measures of brood parasitism.—Field biologists often use significantly different protocols to gather data on brood parasitism. Such differences in sampling methodologies could cause two biologists studying the same population to arrive at quantitatively different measures of the intensity of brood parasitism. Moreover, these differences are typically large enough to be of concern.

Brood parasitism frequently is measured as the proportion of a sample of nests (or females) that suffer parasitism. Importantly, the amount of parasitism observed depends on exactly what group of nests or females one is observing. For example, one could determine the proportion of all nests in an entire breeding season that are parasitized, or the proportion of a sample of nests in a large plot that are parasitized on, say, 1 June. If the researcher is measuring the parasitism over a time interval, the amount of parasitism observed will depend on the length of the time interval chosen (e.g. one day vs. one month) and the protocol for sampling.

We have identified four measures of the intensity of brood parasitism—the instantaneous parasitism rate, and what we designate as the cohort, seasonal, and snapshot parasitism fractions. A rate indicates the probability of parasitism per unit time (e.g. per day), while a fraction is dimensionless because it indicates the proportion of some sample that is parasitized. Although our measures of brood parasitism do not include all variation seen in the literature, we believe that they do account for much of it.

Our model uses the instantaneous brood-parasitism rate (ρ_u and ρ_p) to quantify the intensity of brood parasitism. This is the rate at which parasite eggs are laid in host nests during the window of susceptibility to parasitism, and it has units of inverse days. One can readily compute these rates from data obtained by visiting a sample of nests daily during the window of susceptibility to parasitism, and (using our maximum-likelihood approach) one can extract this rate from data obtained by visiting nests less frequently. However, when nests are revisited infrequently or not at all, the reported measure of parasitism is likely to be closer to the snapshot parasitism fraction (see below).

The cohort parasitism fraction, $C(s)$, concerns a sample of nests followed from the start to the end of the window of susceptibility to parasitism. (We define "cohort" as simply any group of females. By contrast, a group of females of the same age is an "age cohort," although the adjective "age" is dropped by many authors.) This measure of parasitism intensity indicates the proportion of these nests that are parasitized at least once. When a sample of nests (or females) is monitored from nest building through at least the start of incubation, the proportion parasitized produces an empirical estimate of the cohort parasitism fraction. One can use the model to predict the value of the cohort parasitism fraction that would be observed for given values of model parameters by using the equation,

$$C(s) = \int_{t_e}^{t_i} \rho_u \frac{u(t, s+t)}{u(0, s)} \, dt. \tag{12}$$

The denominator of this ratio is proportional to the relative abundance of females who have just initiated the nesting cycle on day s of the breeding season. The numerator, $u(t, s + t)$, is proportional to the abundance of females that are t days into the nesting cycle. The ratio itself is the probability that a female who initiated a nesting cycle at day s of the breeding season will not have suffered a nest failure before day $s + t$ of the breeding season. To account for all possible days in which a nest could be lost to brood parasitism, we multiply this probability by the brood-parasitism rate, and integrate. Effectively, this equation sums the fraction of the initial cohort lost to brood parasitism during each day of the window of susceptibility to parasitism.

The seasonal parasitism fraction, Y, is the proportion of all nesting attempts in an entire breeding season that are parasitized. It arises when a researcher follows all nests (or a random sample of these nests) of a species on a study plot for an entire breeding season. It is our impression that this is the quantity many investigators implicitly assume is of interest, though few sampling regimes in use provide an adequate estimate. In terms of our model parameters, it is

$$Y = \frac{\int_0^{s_s} \int_{t_e}^{t_i} \rho_u u(t, s + t)\, dt\, ds}{\int_0^{s_s} u(0, s)\, ds}. \qquad (13)$$

When parameter values vary across the breeding season, the cohort parasitism fraction will change, depending on which day (or period) of the breeding season the cohort of females initiate their nesting cycles. Equation 13 for the seasonal parasitism fraction can be thought of as a weighted average, across the breeding season, of all possible cohort parasitism fractions. When the instantaneous parasitism rate and other model parameters do not change during the breeding season (as in the simple version of our model), the seasonal parasitism fraction and the cohort parasitism fraction are equal.

The snapshot parasitism fraction, $S(s)$, is the proportion of all active nests in the population on a given day that contain brood parasite eggs or young. It is the obvious way to report the data from a single intensive survey of a site, in which the proportion of all active nests that are parasitized is recorded. It is different from the measures above in that its sample includes nests found at all stages of the nesting cycle, rather than only those initially discovered before t_e. In terms of our model parameters,

$$S(s) = \frac{\int_{t_e}^{t_f} p(t, s)\, dt}{\int_{t_e}^{t_f} p(t, s)\, dt + \int_{t_e}^{t_f} u(t, s)\, dt}. \qquad (14)$$

The numerator is the fraction of females that are parasitized on day s of the breeding season, while the denominator is the fraction of females that have an active nest on day s of the breeding season, whether parasitized or unparasitized. In part for the reasons given when presenting Equation 3, the denominator of Equation 14 generally is not equal to one.

Parasitized nests generally will have shorter average life expectancies than unparasitized nests because of abandonment (Mayfield 1965, Nolan 1978) and because they sometimes suffer higher nest-predation rates (Finch 1983). Consequently, in any given empirical situation, the snapshot parasitism fraction generally will be less than the cohort or seasonal parasitism fraction. Restated, the proportion of all active nests in a population containing a parasite's egg or young (i.e. the snapshot parasitism fraction) is a biased estimate of the probability that a given nesting attempt will be parasitized (i.e. the seasonal parasitism fraction). Many studies in which nests are located opportunistically produce an estimate of parasitism approximating the snapshot parasitism fraction, except that the nests are found over a longer period than one day and, once discovered, may be revisited (e.g. Wiens 1963, Finch 1983, Wolf 1987). As an example of the potential empirical magnitude of this bias, Nolan (1978) estimated that the median life expectancies of parasitized and unparasitized Prairie Warbler nests are 4.2 and 9.8 days, respectively.

Many empirical studies do not use a protocol that exactly produces any one of these four measures of parasitism, but instead may approximate one of them or combine features of two or more of them. The most complete sampling would include detailed information of every nesting attempt (from their beginnings) during the entire breeding season for a representative group of females. At the other extreme are samples of single observations for a set of active nests at a specific point (or snapshot) in time. Few sampling schemes achieve either extreme. Differences in sampling protocol among existing studies affecting the parasitism estimates reported include: variation in whether previously found nests are revisited systematically; the time interval between successive visits; the stages of the nesting cycle at which the nests were discovered and subsequently monitored; and the fraction of the breeding season encompassed by the study. Moreover, the collection of data on nesting events frequently suffers from some level of biased sampling caused by spatial and temporal variation in intensity and distribution of effort, haphazard opportunities for

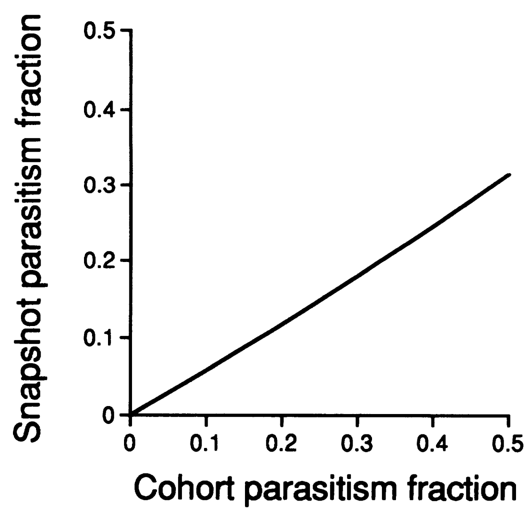

Fig. 2. Relation of cohort and snapshot parasitism fractions, showing they are not equivalent, and obtained using Equations 12 and 14 with $t_e = 4$ days, $t_i = 10$ days, $t_f = 30$ days, $t_r = 40$ days, $s_s = 60$ days, $f_u = 3.5$, $f_p = 1.0$, $a = 0.40$, $d = 0.05$ per day, ρ between 0.0 and 0.14 per day, and with approximation that $\partial u / \partial s = \partial p / \partial s = 0$ (which allowed us to derive closed-form equilibrium solutions of u and p). These parameters are representative for passerines in general, but do not correspond to any particular species.

locating nests, and differences in the skills and experience of field biologists.

To demonstrate the differences between these measures of parasitism, we wrote a computer program that takes as input the values of the instantaneous brood-parasitism rate (ρ) and other model parameters, and whose output is the snapshot parasitism fraction, and cohort parasitism fraction (the latter is equal to seasonal parasitism fraction in the constant-parameter situation; see above). Figure 2 compares the cohort and snapshot parasitism fractions for a specific set of parameter values, demonstrating that they are not equivalent. Figure 3 makes the same point in a somewhat different way; this figure shows that two numerically identical values of parasitism obtained using different sampling methodologies will correspond to different values of seasonal fecundity.

ANALYSIS OF PRAIRIE WARBLER AND BLACK-CAPPED VIREO DATA

Parameter estimates.—We reanalyzed Nolan's (1978) Prairie Warbler data, and we analyzed some of Graber's (1961) and J.A.G.'s Black-capped Vireo data. Nolan (1978) summarized data from females he followed daily over the course of the breeding seasons between 1952 and 1965. The Black-capped Vireo data are from observations made mostly in 1985 and 1986 in Kerr County, Texas, and encompass entire breeding seasons, although with limited sampling beyond 20 June. The primary goal of this monitoring was to determine the number of young fledged (i.e. seasonal fecundity) by a group of females, rather than to test the present model per se. Monitoring of nests and territories was done at time intervals of 1 to 46 days ($\bar{x} = 4.6$ ± SD of 5.0 days, $n = 365$).

Table 2 gives our estimates of the parameters that describe the timing of events in the Prairie Warbler and Black-capped Vireo nesting cycle and breeding season, and the productivity of

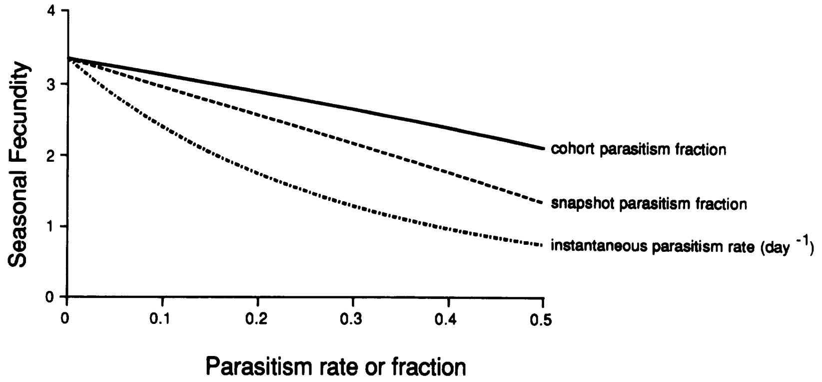

Fig. 3. Seasonal fecundity as function of three empirical measures of intensity of brood parasitism. Parameter values and methods of computation used are same as in Figure 2, except ρ is between 0 and 0.29 (snapshot), or 0 and 0.14 (cohort).

TABLE 2. Empirical estimates of Prairie Warbler and Black-capped Vireo nesting-cycle, breeding-season, and nest-productivity parameters.

Parameter	Prairie Warbler[a]	Black-capped Vireo[b]
t_c (days)	4.5	6
t_i (days)	10.5	12
t_f (days)	29.5	35
t_r (days)	38	46.5
s_s (days)	50	68
f_u	3.36	3.4
f_p	0.91	0.2[c]

[a] Nolan (1978); see Appendix 2 for details.

[b] Graber (1961), Graber (field notes), Grzybowski (field notes); see Appendix 2 for details.

[c] Black-capped Vireo nests that fledge a cowbird invariably fledge no vireos. However, our empirical sample contained a parasitized vireo nest in which the cowbird egg did not hatch, and from which vireos were fledged. This nest is properly assigned to the sample of nests from which f_p is estimated, making our estimate of it nonzero.

their successful parasitized and unparasitized nests. These estimates were obtained using the procedures we discussed in the preceding section on parameter estimation. Nolan (1978) presented a detailed discussion of the relevant Prairie Warbler data. The parameter values for Black-capped Vireos were established from observations by Graber (1961, and her field notes), or from those made in subsequent years by J.A.G. in Kerr County, Texas. See Appendix 2 for further discussion.

Table 3 gives our estimates of the Prairie Warbler and Black-capped Vireo brood-parasitism and nest-predation parameters. Because Nolan revisited the nests in his study daily, we were able to use the simple (nonmaximum-likelihood) method of estimating the Prairie Warbler brood-parasitism and nest-predation parameters (see Appendix 2). For Black-capped Vireos, we used our maximum-likelihood approach. The analyses for both species assumed that the parasitism and predation parameters were the same for unparasitized and parasitized nests, although our justification for this assumption was different in the two species. Nolan (1978), although he had large sample sizes, did not find this type of heterogeneity in his data. The Black-capped Vireo data set was too small to have enough statistical power to determine if this type of heterogeneity was present; for example, it contained only 6 unparasitized nests of 37 nests with at least one egg or hatchling.

Ambiguities in data.—As we prepared the Black-capped Vireo nest-history data for input into the computer program that estimated the parasitism and predation parameters, it became clear that there were some ambiguities in determining how the status of certain nests changed between visits. For some cases, a question arose as to whether to classify nest failures as being due to nest predation or to abandonment after brood parasitism. For example, a nest with unknown contents being incubated by an adult and later found abandoned with a vireo and cowbird egg may have been disrupted by a parasitism event that occurred after the initial observation, or may already have contained an accepted cowbird egg on the first visit and been abandoned between visits as a consequence of a nest-predation event. These situations would be scored differently (unparasitized becomes abandoned after parasitism vs. parasitized becomes lost to nest predation). As a second example, consider the case where a nest is discovered by a researcher during nest building and is abandoned after being completed, but in which no egg or young were seen. Was the nest abandoned without any vireo or cowbird egg being laid; was a vireo egg laid and removed by a cowbird as a prelude to parasitizing the nest; was the nest depredated with vireo eggs present; was it depredated with a cowbird egg present; or was it parasitized, abandoned and then depredated between visits?

Some ambiguity is also present in the nest-predation statistic itself. Some predation may be observer induced, and some may be caused by cowbirds. The latter may occur when cowbirds disrupt nests that they do not parasitize,

TABLE 3. Empirical estimates of Prairie Warbler and Black-capped Vireo brood-parasitism and nest-predation parameters (with 95% confidence intervals).

Species	Brood-parasitism rate (per day; p)	Abandonment probability (dimensionless; a)	Nest-predation rate (per day; d)
Prairie Warbler	0.049 (0.039–0.059)	0.46 (0.36–0.56)	0.057 (0.049–0.065)
Black-capped Vireo	0.32 (0.19–0.49)	0.43 (0.20–0.73)	0.035 (0.016–0.063)

such as occurs when they remove eggs or young from a host nest outside the window of susceptibility to parasitism (Graber 1961, Tate 1967, Nolan 1978). Similarly, the probability of abandonment after parasitism undoubtedly includes not only nest abandonment caused by the visit in which the parasite laid its egg, but also abandonment induced when the parasite removed host eggs prior to and after the parasite egg was laid.

The exact day of the nesting cycle on which a particular event occurred also is sometimes uncertain. If so, it must be inferred or approximated. For example, if the second visit to a nest occurred on the day of hatching, one can easily determine how far into incubation the nest was when first visited seven days previously. However, if one knew only that the first and second visits occurred during incubation and were separated by three days, there would be uncertainty as to exactly which days of the nesting cycle had been observed. In some cases, this ambiguity may be inconsequential (as when entire interval of observations is known to lie within incubation, but no further information is available), while in other cases it may be necessary to determine the earliest and latest conceivable days of the nesting cycle to which a visit may be assigned, and then assign it an intermediate value (as when the last day of the window of susceptibility to parasitism cannot be determined exactly).

Importantly, ambiguities such as those discussed in the previous three paragraphs are likely present in any data set involving sequential visits to the same nests (Mayfield 1975), even for visitation intervals of one day. We suspect that these ambiguities are currently dealt with differently by different investigators. Yet, these details are seldom disclosed in published papers (Woolfenden and Rohwer 1969) or explicitly recognized as a source of uncertainty in the data.

For each nest in the present analysis, we carefully documented our assumptions, reasoning, and rules for: (1) determining the day of the nesting cycle on which a particular visit occurred; (2) determining the nest fate (i.e. whether on last visit, nest was active, lost to nest predation, abandoned in response to cowbird parasitism, or successful in fledging young); and (3) interpreting ambiguous situations regarding nest status. Where several alternative interpretations of the data are equally likely, we advocate obtaining a bound on the estimated parameter values by separately analyzing the data under each possible interpretation. We do this for Black-capped Vireo data in Table 4, where we estimate model parameters and obtain predicted values of seasonal fecundity by first interpreting all ambiguous cases of nest loss as being due to abandonment after a brood-parasitism event, and then interpreting them all as being due to nest predation.

Predicted seasonal fecundity.—Table 4 presents the predicted values of seasonal fecundity for the Prairie Warbler and Black-capped Vireo. The 95% confidence intervals shown account for sampling variation in the brood-parasitism and nest-predation parameters (ρ, a and d).

These confidence intervals do not account for uncertainty in our estimates of the nesting-cycle, breeding-season, or nest-productivity parameters. Because these parameters were not estimated in ways that lent themselves to quantitative measures of uncertainty (i.e. confidence intervals), we instead qualitatively assessed the likely amount of uncertainty in them, and then determined a predicted value of seasonal fecundity under the highest and lowest reasonable values of each parameter. Table 4 gives the results of this sensitivity analysis.

To investigate how well our constant-parameter model approximates a more detailed model with temporally varying parameter values, we numerically simulated the general model of Equations 3 to 7 using Nolan's data showing how four of our model parameters vary during the nesting cycle and/or breeding season (see Appendix 2). The predicted seasonal fecundity allowing for variable-parameter values was identical to that computed using constant-parameter values (both were 2.2). The Black-capped Vireo data set was too small to quantify how any model parameters vary during the nesting cycle and/or breeding season. Although we suspect that our constant-parameter model will prove adequate for many Neotropical passerines, the assumption of constant parameters may need further refinement for species with longer breeding seasons.

Seasonal fecundity measured directly.—Table 4 shows that, for both the Prairie Warbler and Black-capped Vireo, the values for seasonal fecundity obtained by direct empirical observation closely match those predicted using our model. However, many of the same individuals contributed to both estimates of seasonal fecundity (Nolan 1978, Appendix 2). This causes these two estimates to be correlated, and creates

TABLE 4. Seasonal fecundity observed empirically and predicted from model (with 95% confidence intervals) for Prairie Warblers and Black-capped Vireos, followed by analysis of sensitivity of seasonal fecundity to assumptions made in its prediction. Analyses use parameter estimates in Tables 2 and 3 unless indicated otherwise.

	Prairie Warbler	Black-capped Vireo
Seasonal fecundity		
Empirical observation	2.2 (1.9–2.5)	0.9 or 1.0 (0.5–1.5)[a]
Predicted from model	2.2 (1.8–2.6)	1.0 (0.4–1.9)
Sensitivity analysis		
Ambiguous nest failure interpreted to		
Favor abandonment after parasitism[b]	—	1.0
Favor nest predation[c]	—	0.9
Window of susceptibility to brood parasitism (t_i to t_e)		
1 day shorter[d]	2.2	1.0
1 day longer[e]	2.2	1.0
End of parental care by female (t_r)		
5 days later	2.1	0.9
5 days earlier	2.3	1.0
Breeding season (s_s)		
10 days shorter	1.8	0.8
10 days longer	2.5	1.1

[a] Estimate of 1.0 assumes that two nests last observed on days 29 and 32 of nesting cycle fledged the young they contained when last observed; estimate of 0.9 assumes these young did not fledge. The 95% confidence interval assumes these young fledged.

[b] Uses same parameter estimates as predicted from model for Black-capped Vireos (see Table 3).

[c] Assumes that two nest failures in our empirical sample with ambiguous cause were due to nest predation rather than abandonment after cowbird parasitism; this implies $p = 0.28$ per day, $a = 0.34$, and $d = 0.044$ per day.

[d] Prairie Warbler: $p = 0.053$ per day and $t_i = 9.5$ days. Black-capped Vireo: $p = 0.36$ per day, $a = 0.40$, $d = 0.038$ per day, and $t_i = 11$ days.

[e] Prairie Warbler: $p = 0.040$ per day and $t_e = 3.5$ days. Black-capped Vireo: $p = 0.27$ per day, $a = 0.42$, $d = 0.034$ per day, and $t_i = 13$ days.

difficulties in evaluating the statistical significance of any differences between them. This issue notwithstanding, the close match does give one some confidence that our model will be useful in estimating seasonal fecundity in species where direct measures of seasonal fecundity are unavailable.

For the Black-capped Vireo data set, two nests were last observed several days before the expected fledging date; we had no additional information. To avoid making an arbitrary assumption, Table 4 reports two observed seasonal fecundities for Black-capped Vireos corresponding to both conceivable interpretations of the outcome of these two nesting attempts (i.e. nest predation or successful fledging).

We believe that the values for seasonal fecundity predicted from our model are no more subject to bias than are those obtained by directly following individuals through an entire breeding season. For example, Nolan (1978:418–420) obtained his direct estimate by counting the number of young fledged off an average territory during an entire breeding season, and was well aware of the possibility that his estimate could be biased because it assumes that production per territory equals production per female. The direct estimate of Black-capped Vireo seasonal fecundity obtained by following individuals through an entire breeding season may be biased low if some individuals moved off the study site and bred successfully after they were assumed to have finished breeding, and if monitoring late in the season was incomplete. The close match between the predicted and directly measured seasonal fecundities (Table 4) suggests that these biases are not important for these two species.

DISCUSSION

Most field workers interested in passerine breeding biology find nests and follow them for short periods of time. A few workers have followed individual females through the entire breeding season and, thereby, have measured directly seasonal fecundity (Nice 1937, 1943, Nolan 1978, Smith 1981). The paucity of empirical studies directly measuring seasonal fecundity does not reflect its lack of importance. Rather, the situation is a consequence of the difficulty and cost of conducting the more intensive study needed to directly measure the impact of nest predation and brood parasitism on seasonal fecundity and, hence, population growth. In addition, the accuracy and comparability of many empirical estimates of passerine nesting biology often are severely limited by small sample sizes, differences in observer capabilities and methodologies, and the need for considerable time and money. In considering whether our model's assumptions and conclusions are reasonable, they should be compared to the available empirical options.

The predicted seasonal-fecundity values for Prairie Warblers and Black-capped Vireos each rest on empirical estimates of 10 model parameters. One concern is that, with so many parameters, it would be relatively easy to tune the model to make the predicted and directly measured seasonal fecundities match. We are aware of this possibility and, consequently, regard the predictions of seasonal fecundity arising from the model as just that—predictions subject to further empirical test. Although a model with fewer parameters might increase one's qualitative understanding of passerine breeding biology, we believe our model has the minimum number of parameters needed to account quantitatively for the complexities of the available data.

How our approach extends existing methods.—Mayfield's (1975) method for calculating nest-failure rates quantifies the probability of nest failure per day that the nest is at risk. His measure of nest failure includes both predation and parasitism. We distinguish between these, and account for abandonment after parasitism. This refinement should help address hypotheses of general interest. To cite one example, the decline of Neotropical passerines in North America has been ascribed to increased levels of both nest predation and brood parasitism, among other factors (Terborgh 1989). Inasmuch as our model provides a standard way to quantify both of these risks, it should assist in testing hypotheses about their relative impact on passerine reproductive success.

Our method for predicting seasonal fecundity extends that developed by Nolan (1978: 390–395), who used a simulation model to predict seasonal fecundity from data obtained by following individual nests. The most substantial difference between our model and Nolan's is that he based his predictions on empirical estimates of the average life span of a nest, while we compute seasonal fecundity directly from empirical estimates of the nest-predation or brood-parasitism rates. (Although we have not done so, it would be straightforward to determine the average nest life span corresponding to a given set of model parameters.) For Prairie Warblers, our model's predicted seasonal fecundity (2.2) closely matches both Nolan's directly measured seasonal fecundity (2.2) and the seasonal fecundity predicted from his model (2.0).

May and Robinson's (1985) brood-parasitism models determined how small the intensity of brood parasitism must be in order for host reproduction to equal or exceed host mortality. Of the several models they present, the one for brood parasites that parasitize multiple hosts (e.g. cowbirds) is closest to ours. However, this model does not account for renesting of host females, and they admit to having considerable difficulty in estimating its parameters. We have not used our model to determine the level of parasitism at which the host population growth rate will be positive. However, this could be accomplished using the Leslie-matrix framework, our estimates of seasonal fecundity, and available survivorship estimates.

Ricklefs and Bloom (1977) developed a mathematical model for predicting seasonal fecundity from mean clutch size, breeding-season length, nest-failure rate, nest-initiation rate and other parameters, most of which closely parallel ours. They directly estimated their model's parameters from empirical data, and then used various regression methods to determine whether the relationship between seasonal fecundity and other model-parameters change across habitat types. Like Mayfield (1975), Ricklefs and Bloom (1977) combined nest predation and brood parasitism into a single measure of nest failure, and they do not account for differences in fecundity between parasitized and unparasitized nests.

Uses of model.—Although there are some excellent comprehensive studies of passerine breeding biology (e.g. Nice 1937, 1943, Nolan 1978, Smith 1981), most information on this topic is considerably more dispersed. Single papers in the literature often report information on only one or a few of the parameters in our model (Table 1), and they often do so in ways that are not readily comparable. Our model provides a means for standardizing the methods for estimating various parameters, and develops these methods with the ultimate goal of estimating a useful population parameter, seasonal fecundity. In much the same way that the Mayfield (1975) method has encouraged comparisons of nest success among different species and among data sets gathered using different protocols, our approach allows one to compare and evaluate many existing studies that contain information on parameters describing brood parasitism, nest predation, nest productivity, seasonal fecundity, the nesting cycle and the breeding season. Because this primary literature is so large, we refer the reader to available reviews (Nice 1957, Ricklefs 1969, Rothstein 1990).

Our model's applications extend from the design of studies measuring brood parasitism through analyses of such data. It defines, before a study is undertaken, the precise way in which its results can be extrapolated to estimates of seasonal fecundity, and the additional parameters needed to make this extrapolation. Additionally, by explicitly defining and identifying several commonly used measures of brood parasitism, we hope it will encourage researchers to be thorough in reporting the sampling methodologies they used to obtain a particular empirical measure of brood parasitism.

Our model can be used to make predictions, prior to a study's initiation, about what value of seasonal fecundity will be observed, using available data on brood-parasitism and nest-predation rates, as well as other model parameters. Thus, the consequences of experimental manipulations can be predicted prior to instigating time-consuming and expensive empirical studies. In addition, because empirical studies that tease apart the effects of various parameters on seasonal fecundity are difficult and expensive, and may provide a limited number of data points to depict complex interactions, use of the model to explicate these relations can be most beneficial. Our model should prove useful in general monitoring programs and in the management of endangered passerines, where the effects of manipulations need to be judged in a noninvasive and timely manner.

For endangered passerines subject to heavy brood parasitism, there is a possibility that manipulative experiments involving cowbird trapping would benefit the host species and simultaneously test our model. We expect the instantaneous parasitism rate to be approximately proportional to cowbird density. Thus, our model in conjunction with additional data on the effectiveness of cowbird traps in reducing cowbird densities could allow one to make *a priori* predictions about what effect a given density of cowbird traps will have on the intensity of brood parasitism, as well as on host seasonal fecundity. At present, many cowbird-trapping programs are undertaken with few or no prospective predictions about their effect. The ability to obtain such predictions should lead to more cost-efficient trapping programs.

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APPENDIX 1.
MAXIMUM-LIKELIHOOD PARAMETER ESTIMATES

Our maximum-likelihood method of estimating d_u, d_p, a_u, a_p, ρ_u and ρ_p uses data from nests found at various stages of the nesting cycle, and then revisited periodically. For example, this sample could contain all nests found in a study plot during an entire field season, and revisited every three days. The data give the contents and condition of every nest when found and each time the researcher revisits it. The method does not require all, or even most, nests to have been found during nest building.

There is one row in the computer program input matrix for each pair of consecutive visits to the same nest. For example, a nest visited on days 3, 6 and 15 of the nesting cycle would contribute two rows to the input matrix, corresponding to the intervals between days 3 and 6, and between days 6 and 15. Nests visited only once do not contribute to the analysis. The columns of the input matrix are: (1) day of nesting cycle of given visit; (2) nest status on this visit; (3) day of nesting cycle of next visit; and (4) nest status on next visit. The status of a nest is: unparasitized; parasitized with one parasite egg; parasitized with two parasite eggs; . . . ; abandoned with one parasite egg present; abandonded with two parasite eggs present; . . . ; or depredated (as defined in this paper). The computer program allows one to force $\rho_u = \rho_p$, $a_u = a_p$ and/or d_u

$= d_p$. The section on "ambiguities in data" makes recommendations for dealing with the difficulties always present in translating between field notes and the input data matrix.

Let $P(x_2, y_2 \mid x_1, y_1)$ be the probability that a nest with status x_1 on day y_1 of the nesting cycle will have status x_2 on day y_2 of the nesting cycle. To derive analytic formulas for these transition probabilities in terms of model parameters (Table 1), we set the partial derivatives with respect to s in Equations 4 and 9 equal to zero. Under the assumptions of the simple model, this results in a set of coupled piecewise linear ordinary differential equations, which can be solved in closed form. These equations describe the possible fates of a single female tracked from the start of a single nesting cycle, not allowing for renesting. The desired transition formulas follow directly from the solutions to these ordinary differential equations. These transition formulas extend Johnson's (1979) approach to estimating nest-failure rates. Our analysis increases the total number of possible states that a nest can change between so as to include "unparasitized," "parasitized with one parasite egg," and so forth. Unlike the situation Johnson considered, in our model multiple transitions between states can occur between two visits. For this reason, many of our transition formulas are extremely complicated algebraically; instead of reproducing them here, they are available from the authors on request. As well as being functions of y_1, y_2, x_1 and x_2, these transition probabilities are functions of ρ_u, ρ_p, a_u, a_p, d_u, d_p, t_e, t_i and t_f.

The likelihood function, L, is

$$L = \prod_{k=1}^{n} \mathrm{P}(z_{k4}, z_{k3} \mid z_{k2}, z_{k1}), \qquad (15)$$

where z_{ij} denotes the date or code in the i^{th} row and j^{th} column of the input data matrix, and n is the number of rows (transitions) in the input matrix.

Our computer program determines the values of ρ_u, ρ_p, a_u, a_p, d_u and d_p that maximize $\log_e L$. This program takes as input starting guesses of all parameters being estimated. It then goes through the input data matrix one row at a time, computing the transition probability for each observed transition, given the parameter values assumed. The transition probabilities for all rows are multiplied together, and their natural log taken, to give $\log_e L$. Next, the program slightly perturbs the value of one or more of the six parameters being maximized, and again computes $\log_e L$. It repeats this step until it finds a maximum of $\log_e L$. We used the "Amoeba" program of Press et al. (1988) to perform this maximization. Because this parameter-estimation problem is well posed, we expect that $\log_e L$ has only a single maximum. To test this hypothesis, we started the Black-capped Vireo parameter estimation from a variety of initial conditions. In all cases, the solution converged to the estimates in Table 3.

APPENDIX 2.
ANALYSIS OF PRAIRIE WARBLER AND BLACK-CAPPED VIREO DATA

Prairie Warbler.—Several issues arose in using Nolan's (1978:117, 149, 155, 169, 184, 189, 235–236, 239, 302–305, 388–389, 398 and 423) data to estimate our nesting-cycle, breeding-season and nest-productivity parameters (Table 2). First, Nolan defined the egg-laying and incubation periods so they overlap by a day, and the nestling period, as he defined it, overlaps by one-half day with both the incubation period and the period of parental care. These overlaps must be accounted for when computing our nesting-cycle parameters from his data. Second, Nolan sometimes gave both the mean and median of a time interval. We used the median when possible in computing the nesting-cycle and breeding-season parameters because, when the underlying distribution is skewed, it more accurately represents the experience of a typical individual. Third, we rounded Nolan's estimates to the nearest half day.

We estimated the brood-parasitism rate from Nolan's (1978:table 129) data showing 94 parasitism events in 1,922 days of observing nests between the inactive day after nest building and day two of incubation. Thus, $\rho = 94/1{,}922 = 0.049$ per day. Our estimate of the abandonment probability, $a = 0.46$, is based on Nolan's (1978:383) statement that 48 of 105 parasitism events (individual cowbird eggs) he observed caused the nest to be abandoned. We estimated the nest-predation rate from Nolan's (1978:table 138) data showing 189 nest failures in 2,823 days of observing nests between the inactive period at the end of nest building and the end of the period of nestling care, and his statement that cowbirds caused a fraction 0.179 of these nest failures. Using Equation 11, and noting that we have defined the nest-predation rate narrowly, so as not to include nest failures from cowbird parasitism, we have

$$\begin{aligned} d &= [1.0 - 0.179]\cdot[-(1/\Delta t)\log_e(1.0 - 189/2{,}823)] \\ &= 0.057 \text{ per day.} \end{aligned}$$

To predict Prairie Warbler seasonal fecundity under the model that allows parameter values to change during the nesting cycle and breeding season, we used Nolan's (1978) data showing: (1) how the nest-predation rate varies during the nesting cycle and breeding season (Nolan 1978:table 138); (2) how the productivity of unparasitized nests varies during the breeding season (Nolan 1978:389 and table 132); (3) how the brood-parasitism rate varies during the nesting cycle (Nolan 1978:table 129); and (4) the extent to which different females start the breeding season on different calendar days (Nolan 1978:184 and table 63).

To estimate the SEs of the brood-parasitism and nest-predation parameters, we assumed binomial sampling. For example, the SE of ρ is [(0.049)(1.0 −

$0.049)/1{,}922]^{0.5}$. Assuming a normal approximation to the binomial, the 95% confidence interval is the parameter estimate ±1.96 times its SE.

Nolan (1978:table 144) gave the empirically observed Prairie Warbler seasonal fecundity in Table 4. We estimated its SE as the standard deviation among individuals in number of offspring fledged, divided by the square root of sample size, quantities Nolan (1978:table 144) also gives.

We used equation 10.12 of Stuart and Ord (1987) to relate the SE of the predicted seasonal fecundity to the SEs of ρ, d and a, as well as the sensitivity (derivatives) of seasonal fecundity with respect to these parameters. We numerically determined the derivatives of the predicted seasonal fecundity with respect to ρ, a and d.

Black-capped Vireo.—We estimated t_e, t_i and t_f using Graber's (1961) data, her 1954 and 1955 field notes (from Caddo County, Oklahoma), and J.A.G.'s 1985 and 1986 data (from Kerr Wildlife Management Area [WMA], Kerr County, Texas). These observations involved closely monitored nests, and so represent a direct measurement of t_e, t_i and t_f. We estimated t_r using J.A.G.'s 1989 and 1990 Kerr data; these data include eight empirical observations of the time between when a single female fledged two broods, and four additional relevant observations (e.g. for one female, we knew the date her first brood fledged and date she completed construction of second nest). Although this estimate of t_r could be biased high because of failed nesting attempts between broods, we believe this is not a significant problem. The distribution of our 12 estimates of t_r is bimodal. Its overall median is 46.5, and the observations constituting the lower peak have a median of 44.

We estimated the median date at which first nesting attempts fledged young during 1989 and 1990 in the Kerr data as 23 May ($n = 42$ nests). The start of the breeding season is 35 days (i.e. t_f days) prior to this date, or 18 April. Based on J.A.G.'s qualitative assessment of the timing of molt, last-observed nest starts, and breeding activity of females, we estimate that 25 June is the end of the breeding season. These dates set s_s as 68 days.

We estimated f_u from successful unparasitized nests whose contents at fledging were known; these data included three such nests from 1985 and 1986 in the Kerr data, and seven nests from Graber's data. We estimated f_p from successful parasitized nests whose contents at fledging were known; these data included 12 such nests from 1985 and 1986 in the Kerr data, and 3 nests from Graber's data.

Ideally, we would have estimated all Black-capped Vireo nest-productivity, nesting-cycle and breeding-season parameters using only 1985 and 1986 Kerr data, since the estimates of ρ, a and d were obtained from this population. This was not possible because the Kerr population was so heavily parasitized in 1985 and 1986 that there were very few successful nests, drastically reducing the sample size available for estimating some parameters. Additionally, because Graber revisited nests daily while J.A.G. revisited nests less often, Graber's data are more suitable for estimating t_e, t_i and t_f.

Appendix 1 discusses our maximum-likelihood method for estimating ρ, a and d for Black-capped Vireos. We computed the SEs of these estimates using a bootstrap. This entailed constructing 1,000 artificial data sets on the computer, each one obtained by randomly drawing from the actual data set (with replacement) an artificial data set of the same size as the actual data set. We determined the maximum-likelihood estimates of ρ, a and d for each artificial data set. The confidence intervals reported in Table 3 for ρ, a and d encompass 95% of the 1,000 estimates of the respective parameter. We also saved each of these 1,000 triplets (ρ, a and d) in a file, and computed the seasonal fecundity corresponding to each one; the confidence interval for the predicted seasonal fecundity reported in Table 4 encompasses the middle 95% of these.

We computed the directly-observed Black-capped Vireo seasonal fecundity from 17 females followed on Kerr WMA during the entire 1985 breeding season and from 20 followed similarly in 1986. The estimate of 0.9 (Table 4) is based on 4 unparasitized nests that fledged 14 vireo young total, 12 successful parasitized nests that fledged 3 vireo young total, 5 vireo nesting attempts found after fledging that fledged at least one vireo each, and 2 vireo nesting attempts found after fledging which fledged at least one cowbird each. See the text and the first footnote to Table 4 for a discussion of how the estimate of 1.0 given in Table 4 differs. The broods found after fledging present a problem, since we have defined seasonal fecundity as the number of young fledged per female per breeding season. These broods could have suffered mortality of some young between fledging and when the broods were observed, and, additionally, there are difficulties in counting the number of offspring in a brood after it has fledged. We therefore assumed that broods found after fledging with at least one observed vireo young came from nests that fledged 3.4 vireos each (Table 2), and that broods found after fledging with at least one observed cowbird young came from nests that fledged no vireos. We computed the 95% confidence interval of the directly-observed seasonal fecundity as ±1.96 times its SE.

Document summary.—Computer programs that accomplish the following tasks are available on request: (1) obtain maximum-likelihood estimates of the nest-predation and brood-parasitism parameters from an input data matrix; (2) determine seasonal fecundity, given input values of the nest-predation, brood-parasitism, nest-productivity, nesting-cycle, and breeding-season parameters; (3) compute seasonal fecundity given input information on how model parameters and functions vary during the nesting cycle and/

or breeding season; and (4) compute the equilibrium snapshot and cohort parasitism fractions given input values of model parameters.

The following worksheets developed to analyze the Prairie Warbler and Black-capped Vireo data also are available: (1) description of methods used to estimate model parameters from Nolan's data; (2) empirical estimates used in simulation that allowed Prairie Warbler parameters to vary during the nesting cycle and/or breeding season; (3) description of methods used to estimate the nest-productivity, nesting-cycle and breeding-season parameters from Graber's and J.A.G.'s data; and (4) nest-by-nest account of the assumptions made in deriving the input matrix to estimate the nest-predation and brood-parasitism parameters from the 1985 and 1986 Kerr field notes.