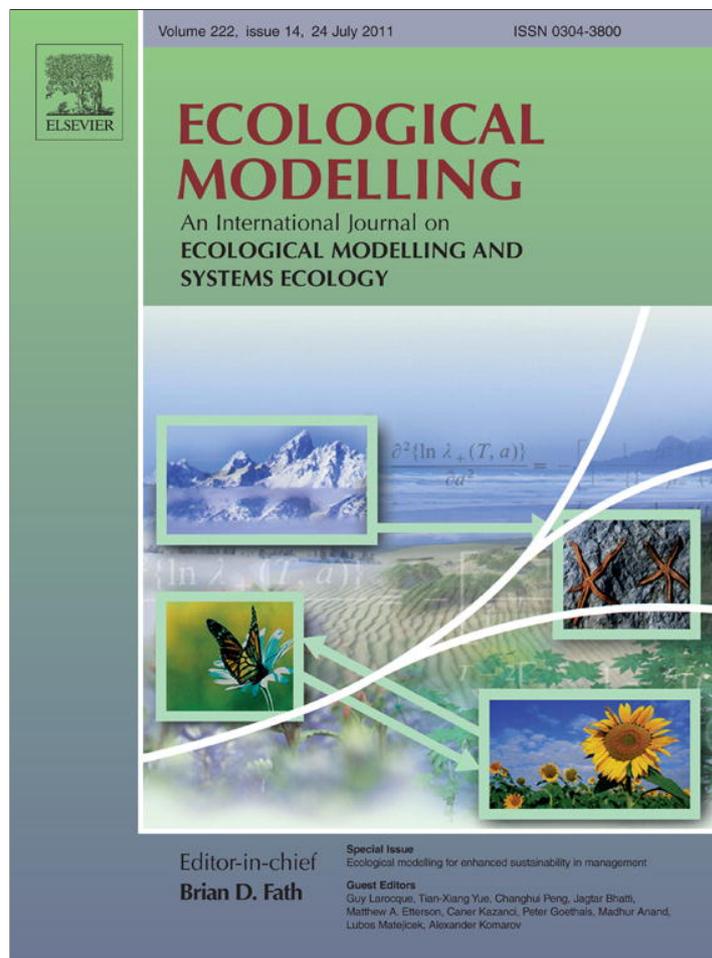


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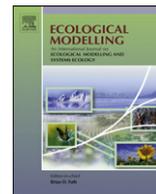
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## Modeling fecundity in birds: Conceptual overview, current models, and considerations for future developments

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## ABSTRACT

Fecundity is fundamental to the fitness, population dynamics, conservation, and management of birds. For all the efforts made to measure fecundity or its surrogates over the past century of avian research, it is still mismeasured, misrepresented, and misunderstood. Fundamentally, these problems arise because of partial observability of underlying processes such as reneating, multiple brooding, and temporary emigration. Over the last several decades, various analytical approaches have been developed to estimate fecundity from incomplete and biased data. These, include scalar arithmetic formulae, partial differential equations, individual-based simulations, and Markov chain methodology. In this paper, we: (1) identify component processes of avian reproduction; (2) review existing methods for modeling fecundity; (3) place these diverse models under a common conceptual framework; (4) describe the parameterization, validation, and limitations of such models; and (5) point out future considerations and challenges in the application of fecundity models. We hope this synthesis of existing literature will help direct researchers toward the most appropriate methods to assess avian reproductive success for answering questions in evolutionary ecology, natural history, population dynamics, reproductive toxicology, and management.

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### 1. Introduction

#### 1.1. Motivation

In birds, as in many other animals, fecundity is a hierarchical process in which the basic unit of reproduction (an egg) is contained within a collection of eggs (a clutch) laid by a female who may, in turn, lay multiple clutches in sequence during 1 year (a breeding season). Thus, individual reproductive success is the outcome of several linked steps extended over the course of a breeding season. It is a fundamental process underlying individual fitness and population persistence. Knowledge of how fecundity relates to environmental conditions and anthro-

pogenic disturbance can improve our understanding of population dynamics and help inform wildlife management and/or regulatory decisions (Cowardin and Johnson, 1979; Bennett and Etterson, 2007).

Fecundity, however, can be a very difficult process to study directly due to logistical and resource constraints upon field ornithologists. For example, tracking a female through multiple nesting attempts is often impossible, especially when females move to new locations to reneat. Moreover, many components of the avian reproductive cycle are only partially observable (due to concealed nests and cryptic behavior), making accurate empirical estimation of fecundity difficult or impossible. Thus, to estimate reproductive success in the presence of incomplete data, several researchers have developed models that integrate empirical observations of individual females throughout the breeding season. These models have employed several mathematical formalisms, including scalar arithmetic formulae, partial differential equations

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**Table 1**  
Common vocabulary used to describe avian fecundity\*.

Term	Definition	Source
<b>Fecundity – components</b>		
Clutch size	Number of eggs per nest	
Brood size	Number of offspring per nest, or fledged per nest	
Nest success	Probability that at least one young from a clutch will survive to fledging (altricial) or hatching (precocial)	Johnson (2007a,b)
<b>Fecundity – synonyms and variations</b>		
Fecundity	Number of offspring produced per female in a pre-defined period	This manuscript
Avian breeding productivity	Nestlings fledged per pair per breeding season	Ricklefs and Bloom (1977)
Annual reproductive success	Number of young reared during a breeding season	Murray (1991, 2000), Bennett and Etterson (2007)
Seasonal fecundity	Young fledged per female per breeding season	Pease and Grzybowski (1995), Etterson et al. (2009)
Breeding season productivity	Per capita number of young surviving to the end of the breeding season	Powell et al. (1999)
Annual fecundity	Young fledged per female per year	Farnsworth and Simons (2001), Nagy and Holmes (2005)
Breeding productivity	Young surviving to 1 week past fledging	Mattsson and Cooper (2007)

\* Fecundity is used here as a component of general reproductive success, the latter including fecundity and survival of those young to reproductive status (see Fig. 2).

(PDE), individual-based simulations (IB), and Markov chain theory (MC).

In the autumn of 2009, the authors participated in a symposium on modeling avian fecundity at the biennial meeting of the International Society for Ecological Modeling in Quebec City, Canada. The following synthesis assembles the collective thoughts of the participants on this topic. Emerging from this meeting was the recognition of an overwhelming need to synthesize existing knowledge regarding avian fecundity models under a common conceptual framework to facilitate their further development and application. Our current objective is to provide this synthesis. Our framework is not intended to be a unified model for performing analyses. Rather it is a unifying conceptual framework for considering different models under a similar nested process-oriented point of view.

### 1.2. What is avian fecundity?

Ornithologists use divergent terminology to characterize the concept of reproductive success. Indeed, fecundity is often defined in a contextually and taxonomically specific manner. For birds, which maintain parental investment after fertilization, *fecundity* is best expressed as the number of offspring per female reaching some stage of advanced maturation and/or independence. We distinguish it from *clutch size*, the number of eggs laid in a nest, and *brood size*, the number of hatchlings or fledglings produced in a nesting attempt (Table 1). The literature contains several terms used synonymously, or nearly so, with fecundity that differ only in the designated ending-points of maturation or independence (Table 1).

### 1.3. The avian nest cycle, breeding season, and recruitment into the breeding pool

A fundamental component of avian fecundity is the nesting cycle, which is a series of stages related to a single nesting attempt (Table 2). The *breeding season* is the period containing the set of all successful and failed nest cycles attempted by the females in a population in a single year (Fig. 1). The *breeding pool* is the set of females in the population that attempt to breed at least once in a given year. In most species, especially in the temperate zone, nest attempts are concentrated within a period lasting for a few months only. The breeding season includes all renesting attempts after both failed and successful nests (Fig. 1).

Fecundity is part of a larger process leading to the *recruitment* of individuals into the breeding population (Fig. 2). For a pair to replace itself, its young must not only survive to fledging, or inde-

pendence (identified here as fecundity), but also to the beginning of their first breeding season. *Juvenile survivorship* refers to survival from the marker at the end of fecundity (which varies among studies and taxa; Fig. 2, Table 1), to entry as breeding adults (recruitment) into the breeding population. Because the goals of this paper focus on fecundity, we will not consider juvenile survivorship or recruitment further.

## 2. Difficulties in measuring fecundity due to imperfect detection

The need to model fecundity, rather than measuring it directly, results from the simple fact that often one cannot directly observe many of the events that a population of females experiences in a breeding season (e.g. Olson et al., 2005; Williams et al., 2002; Pollock et al., 2004; MacKenzie et al., 2005). Imperfect detection of nests and females, unless explicitly incorporated in a model, may bias parameter estimates, resulting in biased predictions of fecundity. Common consequences of imperfect detection are described below.

### 2.1. Imperfect detection of nests

Searching for bird nests is difficult and requires trained observers (Martin and Geupel, 1993). Less skilled observers tend to find nests later in the nesting cycle. However, even the best observers will not discover all nests (Smith et al., 2009). For any given female, fledglings from undiscovered successful nests could be excluded from estimates of her reproductive output.

### 2.2. Imperfect detection of females in a breeding population

Female breeding behavior is often cryptic enough that some breeding females go entirely undetected (Olson et al., 2005). Consequently if some successful broods are first detected post-fledging, they may be incorrectly assigned to the wrong female. After a completed nesting attempt, females may move and reneest off-site (e.g., Lang et al., 2002), potentially biasing estimates of nest success and fecundity. Some females that are first discovered late in the breeding season may have just entered the breeding pool or their previous attempts may have been missed. If prior attempts were outside the sampling area, then those attempts would not have been observable (Kendall and Nichols, 2002). Females present on a study site, but whose breeding status is unknown, may also create difficulties in defining the population to which a fecundity estimate applies (Nolan, 1978; Grzybowski, unpubl. data).

**Table 2**  
Definitions of elements in avian fecundity models and ways in which they may be incorporated in these models.

Fecundity element	Definition	Usage in fecundity models
Population	Set of individuals (usually only females) for which a fecundity estimate is intended to apply	<ul style="list-style-type: none"> <li>•Often implicitly assumed rather than explicitly defined in fecundity models</li> <li>•This is also loosely considered the set of females that could be sampled for fecundity in an empirical study</li> </ul>
Breeding season	Period containing a series of complete and incomplete nest cycles for all females in a population	<ul style="list-style-type: none"> <li>•The starting and ending events depends on definition</li> <li>•Models are highly variable with respect to how the breeding season is defined</li> </ul>
Breeding pool	All females in a population that attempt to breed in a given season	<ul style="list-style-type: none"> <li>•Females in the breeding pool may enter and leave the actively breeding state over the course of the breeding season</li> <li>•Females that do not attempt to reproduce at all in a given season, are absent from the breeding pool for that year</li> </ul>
Nesting-cycle stages	Series of events related to a single nesting attempt	
•Pre-nest-building	Activity before nest-building, can include pair formation, prospecting for nest site	<ul style="list-style-type: none"> <li>•Often not explicitly included in fecundity models but related to the number of days between nesting attempts</li> </ul>
•Nest-building	The act of creating or maintaining a nest in preparation for eggs	<ul style="list-style-type: none"> <li>•Often not explicitly included in fecundity models but related to the number of days between nesting attempts</li> </ul>
•Egg-laying	Period between laying of first and last egg in a nest	<ul style="list-style-type: none"> <li>•May or may not be explicitly included in fecundity models</li> </ul>
•Incubation	Period when the female (or male) behaviorally modifies nest microclimate to alter egg temperature for optimal embryonic development	<ul style="list-style-type: none"> <li>•In warm environments, ambient temperatures might initiate development without parental body temperature</li> <li>•For Megapodes, decaying detritus incubates eggs</li> </ul>
•Post-hatching	Period between hatching and independence	<ul style="list-style-type: none"> <li>•Typically used only for precocial species</li> </ul>
•Nestling	Hatched young occupying a nest	<ul style="list-style-type: none"> <li>•Only applies to altricial species</li> </ul>
•Fledging	Period when hatched young leave nest or develop functional flight feathers to become independent	<ul style="list-style-type: none"> <li>•Often not explicitly included in fecundity models but related to the number of days between nesting attempts for multi-brooded species</li> <li>•Multiple markers can be used for precocial or altricial species to depict time of independence</li> </ul>
Recruitment	When young (normally) from previous breeding season enter breeding pool	<ul style="list-style-type: none"> <li>•Females of smaller or short-lived species usually breed at 1 year of age</li> <li>•Females of larger or longer-lived species may delay breeding for several years, which reduces breeding propensity in the population</li> </ul>

### 2.3. Temporary emigration

A special female-detection problem can occur in some long-lived bird species where experienced individuals may not attempt to breed every year. This occurs either because of extreme environmental conditions, such as late spring snow-melt in arctic-nesting geese, extended drought in tropical birds (Grant et al., 2000; Reed et al., 2004), or because of a lengthy breeding cycle as in several seabird species (Weimerskirch et al., 1997; Jenouvrier et al., 2008). Non-breeding individuals may be difficult to detect either because their behavior differs from breeders or because they are physically absent from their normal breeding area in those years. For instance, non-breeding seabirds remain at sea to forage, and non-breeding geese migrate to molting areas (Reed et al., 2003). This transition from a breeding to a non-breeding state for an entire breeding season is sometimes referred to as temporary emigration (Kendall et al., 1997; Fujiwara and Caswell, 2002). Temporary emigrants do not enter the breeding pool, and may or may not be present on the breeding grounds. In the former case, in which non-breeders are present, their behavior may make them less available for detection (e.g., if breeding females are detected through observation of breeding behaviors). Failure to consider breeding propensity (i.e., the probability that an individual will attempt to breed in a given year) will lead to over-estimation of annual fecundity.

### 3. Use and limitations of indices

Given the difficulty of directly measuring fecundity or estimating it from incomplete observations, some researchers have substituted statistics that are readily estimable as putative indices

of fecundity, such as nest contents (i.e., clutch or brood size), nest survival (or nest success), or adult to juvenile ratios. While some of these metrics have been commonly collected and reported, there are compelling reasons to doubt their reliability as indices of avian fecundity. Later (Section 4), we describe explicit approaches to modeling fecundity that integrate the major components described immediately below.

#### 3.1. Clutch size

The simplest index of annual fecundity is clutch size (Table 1). This metric is of limited value, however, because clutch size is an individual nest statistic and does not predict seasonal egg totals. Its estimation may also be biased by seasonal variation (i.e., late-season clutches are usually smaller; e.g., Klomp, 1970; Olsen et al., 2008). Clutch size becomes a questionable index of brood size, and even more so of fecundity, when one considers that partial clutches can be lost from inviability of eggs and brood reduction before fledging (Robinson and Rodden-Robinson, 2001; Ackerman et al., 2003; Ellis-Felege et al., in press).

#### 3.2. Brood size

The average number of offspring fledged per successful nest (brood size, Table 1) is also an individual nest statistic. Renestings and nest-detection issues (Mayfield, 1961, 1975; see below) make it an unacceptable index of fecundity except in the special case where females make only one nesting attempt per year. Brood size fails to account for the females in a population that attempt multiple nests and multiple broods in a single breeding season.

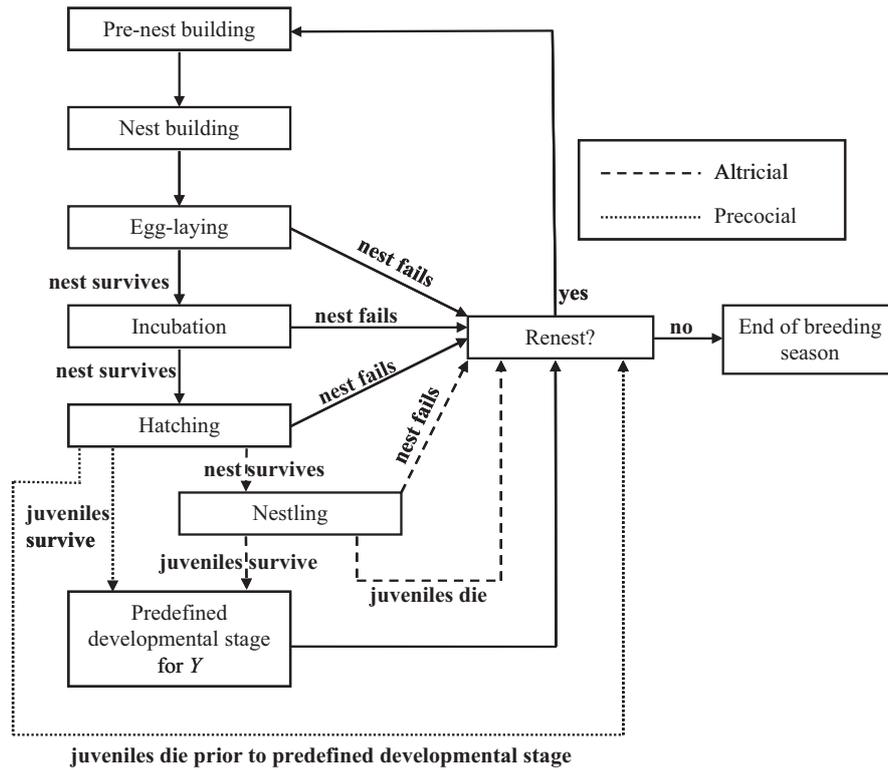


Fig. 1. Conceptual diagram of the stages of a nesting cycle that comprise a breeding season in a fecundity model (see Table 2 for definitions).

3.3. Nest success

The most commonly used index of fecundity is nest success (Cowardin and Johnson, 1979; Murray, 2000; Thompson et al., 2001), defined as the probability that a nest will successfully fledge at least one young. However, empirical estimates of nest success (*S* in Section 4 below) are often positively biased because nests discovered later in the nesting cycle are more likely to succeed (because they must survive fewer days to fledging than nests discovered earlier), and some early nesting-cycle failures will go undetected, a sampling artifact often referred to as discovery bias (Mayfield, 1961, 1975).

While estimates of nest success can be corrected for discovery bias, these estimates still fail to account for renesting or multiple brooding and are thus inadequate indices of fecundity (Dzubin and Gallop, 1972; Cowardin and Johnson, 1979; Pease and Grzybowski, 1995; Farnsworth and Simons, 2001). Nest success estimates may also be subject to within-season temporal variation (Grant et al., 2005; Etterson et al., 2007b), and variation in nest survival probability among individuals; the latter may be the result of within-season tradeoffs or alternative reproductive tactics among individuals

(Slatkin, 1974; Kroll and Haufler, 2009; Winkler and Allen, 1996; Olofsson et al., 2009).

Several studies have examined the relationship between estimates of nest success and of fecundity (reviewed in Anders and Marshall, 2005) and generally found the correlation poor. Nagy and Holmes (2004) provide an empirical example for black-throated blue warblers (*Dendroica caerulescens*); data from a long-term study of marked individuals showed that nest success rates explained only 29% of variation in fecundity among years. Subsequent analyses in the same population showed that, while nest success and fecundity are positively correlated, the use of regression analysis to predict fecundity from nest survival rates underestimated true fecundity by 33% (Jones et al., 2005). Grzybowski and Pease (2000) used a modeling approach to show how the relationship between nest success and seasonal fecundity is non-linear (except for species where females make only one nesting attempt per season).

3.4. Other indices

Another statistic that has been proposed as an index of fecundity is the proportion of juveniles to adults in a population (e.g., DeSante

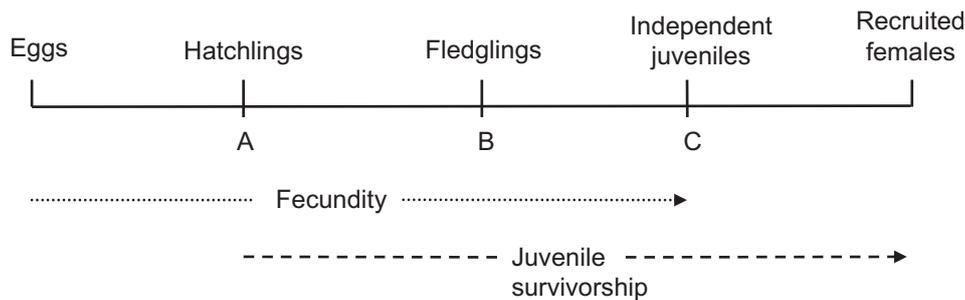


Fig. 2. Timelines over which reproductive success is evaluated with respect to fecundity and juvenile survivorship. Potential end points for fecundity and starting points for juvenile survivorship include hatching (for precocial only; A), fledging (for altricial only; B), or when young become independent (C).

et al., 1995). The inverse (adult to juvenile ratio) has been used as a measure of productivity in waterfowl management (Lynch and Singleton, 1964) and may be correlated with fecundity. However, these ratios leave the causes of variation in reproductive success unexplained.

Vickery et al. (1992) created a rank-score system for behaviors related to breeding (presence of territorial male, birds carrying nest material, etc.) to develop a reproductive index that they subsequently related to habitat quality. However, Morgan et al. (2010) evaluated the Vickery et al. (1992) index in a breeding population of savannah sparrows (*Passerculus sandwichensis*) in which nests were also carefully monitored. They found inconsistencies among workers in how index values were scored, and a poor correlation between index values and either nest or territory success. In summary, there are empirical and theoretical reasons to believe that these indices will often perform poorly as comparative estimates of fecundity.

#### 4. Fecundity models

The need to understand the mechanisms driving reproductive success (Section 1), the logistical and practical difficulties in measuring fecundity directly (Section 2), and the inadequacy of indices (Section 3) all highlight the need to develop models that can integrate events during the breeding season into a complete estimate of fecundity. Such models should incorporate data on measurable variables while simultaneously making assumptions about unobservable or cryptic processes (e.g., dates for the beginning and end of the breeding season, fraction of experienced breeders in the breeding pool, nest success). Below, we provide a conceptual model of avian fecundity and illustrate how its components are integrated under several mathematical formalisms that have been used to develop fecundity models.

##### 4.1. A working definition of fecundity

We define *fecundity* as the number of offspring produced per female in a given population within a breeding season or year. This definition is intentionally general to accommodate the different life stages through which fecundity is estimated (e.g., hatching, fledging or independence; Fig. 2). The life stage used may depend on a species' specific life history traits and/or the particular research questions posed by investigators. Nevertheless, existing fecundity models share a fundamental structure and organization that we describe below.

##### 4.2. Scalar model: a unifying framework

Herein we generalize and modify Ricklefs and Bloom's (1977) scalar model of avian fecundity (their Eq. 1), to obtain the following conceptual and heuristic framework for existing fecundity models.

$$F = YSN \quad (1a)$$

In Eq. (1a),  $F$  = fecundity,  $Y$  = expected number of young per successful nest raised to a specified level of development,  $S$  = expected probability that a nest fledges at least one fledgling (i.e., probability that the nest is successful), and  $N$  = expected number of nest attempts per breeding female. Note that our parameter definitions, especially for  $Y$  and  $S$ , differ from those of Ricklefs and Bloom (1977). The latter authors define  $S$  to be the proportion of young that fledge and they define  $C$  (clutch size, their analog to our  $Y$ ) to be the number of eggs laid per nest. Thus, their definitions combine nest loss from total nest failure with partial nest loss through partial predation, nest parasitism, brood reduction, and any other causes, into a single nest success parameter ( $S$ ). We deviate from their defini-

tions, in part to maintain consistency with current methods for nest survival estimation (Section 5.2 below).

Empirical measures of fecundity might combine one or more of the above processes into a single estimated parameter, but researchers should not ignore the relationships among them. For example, writing  $F = (YS)N$ , we would interpret  $YS$  as the expected number of young produced per nesting attempt (including both successful and unsuccessful nesting attempts). Alternatively, writing  $F = S(YN)$ , we would interpret  $YN$  as the expected number of young produced per female across all of her successful nesting attempts. Writing  $F = Y(SN)$ , we would interpret  $SN$  as the expected number of successful nests per breeding female per breeding season. These joint quantities ( $SY$ ,  $YN$ , and  $SN$ ) could plausibly be empirically estimated in some circumstances (although they may not be independent, see below).

In Eq. (1a),  $F$  is the expected number of offspring produced per breeding female. However, in many populations, some females do not breed (see Section 2.3 above and Section 5.5 below). Thus a more general conceptual model would employ four parameters:

$$F = YSNP \quad (1b)$$

In Eq. (1b),  $F$ ,  $Y$ ,  $S$ , and  $N$  are defined as above, and  $P$  is the probability that a female attempts to breed in a season (breeding propensity). As with Eq. (1a), Eq. (1b) admits to further intuitive understanding by considering combinations of component parameters (although, for brevity, we consider only one such combination). In particular, writing  $F = (YS)(NP)$  shows that  $YS$  and  $NP$  are related expected values.  $Y$  is the expected number of young fledged to a given developmental stage conditional on a nest fledging at least one young ( $S$ ). Thus  $YS$  is the expected number of young fledged per nest (whether successful or not). Similarly,  $N$  is the expected number of nest attempts that a female makes, conditional on her attempting at least one nest ( $P$ ). Thus  $NP$  is the expected number of nest attempts per female per season (whether she breeds or not). Finally, Eq. (1b) states that fecundity is the product of the expected number of young fledged per nest attempt and the expected number of nest attempts per female per season. In our conceptual models above (Eqs. (1a and 1b)) we present  $F$ ,  $Y$ ,  $S$ ,  $N$ , and  $P$  as expected values (and thus implicitly assume independence among parameters). Yet our empirical models, when fit to actual data, typically include subtle dependencies, especially between  $S$  and  $N$  (see Section 5.4 below).

Despite (or perhaps because of) their simplicity, Eqs. (1a and 1b) have several important properties that help to clarify and unify avian fecundity models. First, they capture and integrate three or four basic processes into which fecundity can be separated. Second, Eqs. (1a and 1b) strike an appropriate balance between the parsimony required of a useful conceptual model and the realism required to capture the interdependent processes that together determine avian fecundity. While versions of Eqs. (1a and 1b) with one or more of the component parameters (i.e.,  $Y$ ,  $S$ ,  $N$  or  $P$ ) set to unity serve for some species with unique life-histories, simpler equations will not achieve the generality among species that is possible with Eq. (1b).

Equations (1a and 1b) also serve to highlight important differences among existing fecundity models. The underlying processes represented by  $Y$ ,  $S$ ,  $N$ , and  $P$  may be, and often are, further subdivided. For example, whether and how brood reduction is modeled differs among fecundity models. In many species,  $Y$  is the end result of partial predation and brood parasitism on an initial clutch size (see Sections 5.1 and 5.3 below). Similarly, nest survival,  $S$ , is the probability that a nest succeeds in the face of many potential causes of failure (competing risks), and these have been modeled in diverse ways (see Section 5.2 below). The parameter,  $P$ , is often assumed to be equal to unity (i.e., all females are assumed to breed) in models

for socially monogamous, altricial passerines, which dominate the fecundity literature.

The fourth process, describing the number of nest attempts,  $N$ , can rarely be directly observed and measured. Although some models make transparent (and sometimes simplistic) assumptions about  $N$ , most generate  $N$  implicitly based on other model parameters (Grzybowski and Pease, 2005; Etersson et al., 2009), making it difficult to know exactly what assumptions various models are making with respect to  $N$ , and complicating comparisons that can be made between models (reviewed in Section 5.4 below).

#### 4.3. Mathematical formalisms employed in avian fecundity models

Equations (1a and 1b) represent perhaps the simplest possible conceptual model of avian fecundity. See Murray (1991, 2000) for a more general scalar approach for non-monogamous birds. Importantly, however, when analyzing empirical data, it is necessary to employ a model that dynamically links  $Y$ ,  $S$ ,  $N$ , and,  $P$  for each individual. Such dynamic models necessarily specify how these parameters are functionally dependent, as opposed to employing Eqs. (1a and 1b), which imply conditional independence. These models include the partial differential equations (PDE) model of Pease and Grzybowski (1995); the individual-based (IB) models of Powell et al. (1999) and Mattsson and Cooper (2007); and the Markov chain (MC) models of Bennett and Etersson (2007) and Etersson et al. (2009).

The PDE, IB, and MC models we reviewed (employing three different mathematical formalisms) all use some variation of the same fundamental algorithm. In its most general form, this algorithm starts by characterizing each female in the population with a vector,  $\mathbf{x}_t$ , describing her time-specific state (where  $\mathbf{x}_0$  represents her initial state); for example,  $\mathbf{x}_t = [x_1, x_2, x_3, \dots]$ , where  $x_1$  = breeding or floater,  $x_2$  = age of nest, if breeding,  $x_3$  = number of previously successful nest attempts, etc. This is perhaps most intuitively seen in the MC models, where the transition matrix elements are daily probabilities of transition among states (Bennett and Etersson, 2007). For each specified time interval during the breeding season (e.g., day), this algorithm uses model parameters (e.g., transition matrix elements in the MC formalism) to estimate the number of individuals that transition between various states. The algorithm iteratively works through the full breeding season using the outcome of day 1 to predict the system status on day 2, and so forth. Upon completion of this algorithm, the final state is to have completed breeding for the season at which point the mean (PDE, MC) or distribution (IB) of fecundity is calculated. All PDE, IB, and MC models that we reviewed are similar in assuming the Markov property that the future state of the system depends only on its current state.

In practice, however, only the IB models keep track of separate state vectors for each individual. Both the PDE and MC models work with probabilistic state vectors for the full population. In essence, the PDE and MC models simplify the problem by focusing on the mean (first moment) of the predicted distribution of  $F$ . Under some circumstances, the variance (second moment) may also be estimable with PDE and MC models, albeit under restrictive assumptions (e.g., Etersson et al., 2009). In contrast, by tracking each individual separately, IB models can incorporate general forms of process variation in the underlying parameters.

The apparent differences in mathematical formalism between PDE, IB, and MC methods are more superficial than substantive. First, different models use different state variables. For example, some models allow nests to be parasitized (Pease and Grzybowski, 1995; Powell and Knutsen, 2006), but other models do not include parasitism status as a state variable. Other models include states of disturbance by chemical stressors (Roelofs et al., 2005; Bennett and Etersson, 2007). This choice of state variables does not depend on

the formalism employed. Second, all IB and MC models published to date take a discrete-time approach (e.g., Powell et al., 1999; Mattsson and Cooper, 2007). PDE models (Pease and Grzybowski, 1995; Grzybowski and Pease, 2005) treat time as continuous, although computer implementations of the PDE models necessarily treat time as discrete. Third, IB models (e.g., Mattsson and Cooper, 2007) explicitly treat model parameters as random variables and are well-suited for studying the variance in fecundity arising from arbitrary types of process variation. Yet, process variation, especially in  $N$  (the number of nest attempts per female) is implicit in both the PDE and MC models. However, the mathematically well-developed diffusion literature could readily be employed to incorporate further process variation into PDE models of avian fecundity (see e.g., Karlin and Taylor, 1981; Lande, 1993). Similarly, demographic stochasticity is readily modeled using the MC models (Etersson et al., 2009).

Still, detailed comparisons among various published PDE, IB, and MC models are hindered by mathematically complicated and often implicit dependencies among model parameters. As a consequence, only very rarely is the explicit mathematical relation among fecundity models ever explored (Grzybowski and Pease, 2005; Mattsson and Cooper, 2007; Etersson et al., 2009). Further, seemingly minor differences in assumptions may have a substantial impact on results. Different models also are framed using different (but closely related) parameters. This can make direct comparison of the assumptions of models difficult, and obscure the reasons why two different models produce different predictions of seasonal fecundity when applied to the same data (e.g., Mattsson and Cooper, 2007).

## 5. Issues in parameterizing fecundity models

Depending on the nature of the system to which a fecundity model is applied, investigators also may need to consider other processes such as brood parasitism or other mechanisms of brood reduction. Below, we discuss considerations for parameterizing fecundity models in the context of Eqs. (1a and 1b).

### 5.1. Clutch size, brood size, and the number of young produced in a breeding attempt ( $Y$ )

Clutch size (the number of eggs laid in a given nest attempt; Table 1) may be arguably the most studied demographic parameter in birds (e.g., Moreau, 1944; Lack, 1948, 1968; Skutch, 1949; Ricklefs, 1970a, 1980; reviewed by Martin, 2004). Indeed, studies of avian clutch size and brood size have greatly advanced life history optimality theory (Partridge and Harvey, 1988). However, several issues must be addressed to estimate  $Y$  (the number of young raised to a specified level of development from a successful nest) from either clutch or brood size.

Clutch size generally overestimates the mean number of young hatched or fledged per nest attempt because it does not accommodate: (1) egg inviability (Gnam and Rockwell, 1991; Ortiz-Catedral and Brunton, 2008); and (2) partial clutch or brood loss (Peterson et al., 1998). The latter can occur due to many causes, including nest parasitism, partial predation, starvation, and interspecific competition. Other potential issues in the estimation of clutch and brood size include: (3) inter- or intra-specific brood parasitism (Fletcher et al., 2006; Zanette et al., 2007); (4) extra-pair fertilizations (for estimates of male fecundity: Trivers, 1972); and (5) biased sampling of high-quality individuals (Verhulst and Nilsson, 2008). Furthermore, mean clutch size typically changes over the course of a breeding season, either decreasing (Klomp, 1970) or increasing (Crick et al., 1993; Zicus et al., 2003); inadequate sampling of this change could result in biases of unknown direction.

## 5.2. Nest success ( $S$ )

There are two major ways in which eggs or young may be lost before fledging: (1) loss of individual eggs or young (i.e., Section 5.1), and (2) loss of an entire nest, the latter often referred to as “nest predation” or “nest failure” and defined to include the loss of an entire nest due to any and all causes. While, loss of individual eggs or young in a nest frequently occurs (e.g., Mattsson and Cooper, 2007), a nest is considered successful even if it only produces a single fledgling. This definition of nest success ( $S$ ) as the probability that a nest produces at least one young has a long history (e.g., Johnson, 2007a), and it would be confusing and counter-productive to redefine it here. Thus we maintain consistency with the existing literature by defining nest success to be the probability that a nest produces at least one fledgling. We subsume loss of individual eggs and young (while other eggs or young yet survive) into the set of causes leading from clutch size to brood size to the number of young per successful nest raised to a specified level of development ( $Y$ ).

Regardless of the ambiguity between egg versus nest success,  $S$  is a critical component in all avian fecundity models, and there is a rich literature on its estimation (see Johnson, 2007a for an historical overview). Virtually all modern methods are based on the key insight of Mayfield (1961, 1975) and involve estimating a daily probability of nest survival ( $s$ ), which is then exponentiated to estimate  $S$  (e.g., as  $S = s^a$ , where  $a$  = the age of nests at hatching for precocial birds or fledging for altricial birds). A few researchers have employed instantaneous hazard rate estimates (Nur et al., 2004; Heisey et al., 2007). Major topics in the nest survival literature include the importance of nest encounter probabilities, the adequacy of the assumption that nest survival rates are constant over time, age of nest, and among nests, and, more generally, the analysis of covariates to nest survival rates (reviewed by Johnson, 2007a). While our conceptual model(s) (Eqs. (1a and 1b)) employs the parameter  $S$ , all of the specific avian fecundity models we reviewed actually use estimates of  $s$  derived using a formal method for nest survival analysis. Johnson (2007b) provides a guide to such methods.

One key empirical problem, with particular relevance to fecundity estimation, is that of estimating probabilities of nest mortality due to different causes, or competing risks (Pease and Grzybowski, 1995; Powell et al., 1999; Etterson et al., 2007a,b). There is a rich general literature on estimation of competing risks (Crowder, 2001; Pintillie, 2006), though the topic has received limited attention in wildlife ecology (Heisey and Patterson, 2006) and nest survival estimation (Johnson, 2007a). This is in part because nest failures can be very difficult to assign to cause (Manolis et al., 2000; Stanley, 2004; Etterson and Stanley, 2008). However, predation, parasitism, adverse weather, nest abandonment, and egg failure due to toxins all “compete” as causes of nest mortality, and fecundity models that incorporate such causes must appropriately treat them as competing risks. Methods for estimating competing risks from nest monitoring data include procedures that exclude all causes of failure except the one of interest (Vander Haegen et al., 2002), multinomial logistic regression models (Thompson and Burhans, 2004), and multinomial Markov chain methods (Etterson et al., 2007a,b; Etterson and Stanley, 2008).

## 5.3. Brood parasitism

Brood parasitism acts as a competing risk for nest survival and also creates several differing effects on  $S$  and  $F$  separate from predation (Pease and Grzybowski, 1995; Post van der Burg et al., 2009). Grzybowski and Pease (2000) found complicating and intertwining effects of brood parasitism on seasonal fecundity that were dependent on the level of nest predation, level of brood reduction, abandonment probability, and breeding-season length. Specifi-

cally, brood parasitism can cause brood reduction (thus reducing  $F$ ) in any of the following cases: (1) the adult brood parasite removes host eggs; (2) the parasite nestlings displace host young; or (3) the host nestlings are killed during competition with parasite young (summarized in Johnsgard, 1997). Some adult brood parasites may completely supplant host young, effectively depre-dating nests (Arcese et al., 1996), thus causing host adults to re-nest. Separately, host individuals that abandon parasitized nests, events occurring early in the nesting cycle, incur a very limited cost to  $F$  compared to hosts that complete a nesting cycle but rear only parasite young, an effective nest failure (Grzybowski and Pease, 2000).

Some fecundity models have incorporated parasitism as a binary random variable (i.e., parasitized or not parasitized; e.g., Powell and Knutson, 2006). However, this does not capture the process of brood reduction, or the likelihood or impact of repeat parasitism events in the same nesting cycle. The fecundity model of Pease and Grzybowski (1995) implicitly incorporated the effects of repeat parasitism events and the effects of those events on number of re-nesting events and thus fecundity. Likewise, Post van der Burg et al. (2009) statistically estimate parasitism risk, and then incorporate that risk into a stochastic dynamic programming model (Post van der Burg et al., unpublished data), allowing clutch size to be a state variable that can change stochastically according to the probability of a parasitism event.

## 5.4. Number of nest attempts ( $N$ )

One of the most difficult fecundity parameters to measure empirically is the annual number of breeding attempts by females. The PDE, IB, and MC models take two fundamentally different approaches to re-nesting. The first characterizes the breeding season length explicitly as a temporal window within which females may nest and re-nest after either failed or successful nesting attempts. This approach was first taken by Ricklefs (1970b) and Ricklefs and Bloom (1977). It has been subsequently employed by Pease and Grzybowski (1995), Powell et al. (1999) and Bennett and Etterson (2007). The second approach characterizes the breeding-season length implicitly, as arising from a series of re-nesting decisions governed by simple rules or probabilities deciding whether females re-nest or quit breeding after each nest attempt. This approach was first taken by Cowardin and Johnson (1979). It has been subsequently employed (in various forms) by Schmidt and Whalen (1999) and Etterson et al. (2009). Farnsworth and Simons (2005) and Mattsson and Cooper (2007) combined approaches by employing re-nesting probabilities within a temporal breeding window.

The use of a temporal window to implicitly define  $N$  requires knowledge of the length of time (typically in days) required for a successful nest (the duration of an unsuccessful nest is governed by the daily nest failure rate,  $s$ ), the amount of time required between a completed nest attempt and a subsequent attempt, and the length of the breeding season. The first of these parameters is readily estimable from individual nest records (e.g., Stanley and Newmark, 2010); the other two are more difficult to assess. Estimating the time interval between nests requires knowledge of the exact end dates and subsequent starts dates for sequential nests by a given female, and also requires that nest attempts not be missed between the two known attempts. The length of the interval may also depend on whether or not the previous attempt was successful (Pease and Grzybowski, 1995; Walk et al., 2004; Kershner et al., 2004).

Estimating the length of the breeding season is also challenging. Using simply the dates of the first and last observed eggs (nests) in a sample obviously results in overestimates of  $N$  because many females do not breed for the full interval spanned by extreme dates. Ricklefs and Bloom (1977) accounted for this issue using the entropy equation from information theory. Alternatively, Pease and

Grzybowski (1995), in their simple case, defined the limits of the breeding season to be the points at which 50% of females had initiated (start of the season) or ceased (end of season) breeding for the year and provide several options for determining these points. Nolan (1978) used female molt to assess ending times for a breeding season. Ettore et al. (2009) compared several measures of breeding-season length estimated from samples of first and last egg dates among females within populations.

The use of reneesting probabilities to implicitly define  $N$  requires knowledge of a female's reneesting status subsequent to each successful or failed nest. In its simplest form (with temporally invariant reneesting probabilities), the method overestimates the true length of the breeding season, though resulting biases in  $F$  may be slight (Cowardin and Johnson, 1979; Ettore et al., 2009). In practice, many investigators employing reneesting probabilities have imposed additional constraints, for example by directly limiting the number of successful broods (Martin, 1995) or by simultaneously constraining the number of successful broods and the number of reneesting attempts (e.g., Donovan et al., 1995; Schmidt and Whalen, 1999; see also Table 2 of Grzybowski and Pease, 2005).

Ettore et al. (2009) used empirical data on nests of eastern meadowlark (*Sturnella magna*) and dickcissel (*Spiza americana*) to compare the methods of constraining  $N$  via limited breeding-season length or via reneesting probabilities. They found the method employing reneesting probabilities to be slightly more accurate, although not qualitatively better. However, Grzybowski and Pease (2005) demonstrated that fixed values for reneesting may create unreliable estimates of fecundity that are highly dependent on levels of nest predation and nest parasitism (which implicitly constrain or extend effective breeding-season length).

### 5.5. Breeding propensity ( $P$ )

In our conceptual model (Eq. (1b)), we have defined breeding propensity ( $P$ ) to be the proportion of females in a population that will attempt at least one nest in any given year. Implicit in our definition is the idea that not all females in the population will enter the breeding pool in a given year, and, among females that do, not all will necessarily be actively breeding at any given time. In some typically large single-brooded species, two common issues arise: 1) the effects of delayed maturation and how it influences entry into the breeding pool; and 2) the propensity of mature individuals to breed in any given breeding season. In some cases, the parameter  $P$  is assumed to be equal to 1 and can be ignored in Eq. (1b). However, in species with a long breeding cycle or a short breeding season, a substantial proportion of the population may not breed in any given year. For these species,  $P < 1$ .

Estimating breeding propensity (or its complement, the probability of temporarily emigrating away from the breeding population) is difficult and requires an elaborate sampling scheme with large sample sizes. Useful modeling approaches can incorporate capture–mark–recapture designs (Lebreton et al., 1992) such as the robust design (Kendall et al., 1997; Williams et al., 2002). In these robust design models, secondary (within-season) capture occasions spanning a short time (i.e., several consecutive days) are interspersed between primary (between-season) capture occasions separated by longer intervals (i.e., 1 year). Models for closed populations applied to the secondary occasions allow estimation of capture probability conditional on being present at the site ( $p^*$ ), which in turn allows capture probability to be separated from temporary emigration at the primary occasion level. Slinger et al. (2001) provides an example applying this method to the estimation of breeding propensity in black brants (*Branta bernicla*). However, the robust design requires several restrictive assumptions, and some parameters in the model may not be identifiable (Kendall and Nichols, 2002).

Another approach involves the use of ancillary information. For instance, the presence of radio-marked individuals in the population may provide an independent estimate of  $p^*$ , thereby allowing the estimation of temporary emigration. Reed et al. (2004) used this approach to estimate breeding propensity in greater snow geese (*Chen caerulescens atlantica*).

Recent developments in multistate capture–recapture models also offer the possibility to estimate breeding propensity. In this case, non-breeding is modeled as a non-observable state (Lebreton and Pradel, 2002). Jenouvrier et al. (2008) and Gauthier et al. (2010) provide a complex set of capture–mark–recapture models that can accommodate prebreeders as well as older individuals skipping a breeding season. Although this approach has been applied with some success in seabirds it also requires restrictive assumptions and may lead to identifiability problems in parameter estimation. As with the robust design, the use of ancillary information could help to address these problems.

### 5.6. Defining the population

Implicit in an estimate of  $F$  is the sample of females under consideration, which also needs to be representative of the population under study. Many investigations define sampling areas in regions where the species under study is most common. However, this may not capture the age-distribution and the differential fecundity of different age classes appropriately (Grzybowski and Fazio, unpubl. data). Some females within a population may move between different nesting efforts to new mates beyond the designated study area, and produce successful nesting efforts that go undetected (Nolan, 1978; Grzybowski, unpubl. data). One could assume that compensatory within-season immigration occurs, but this may not hold in small populations. Some females observed in a study area may be non-breeding individuals, or may just be transients between other points where they do breed. Including or excluding these females will affect fecundity estimates. In large measure, these concerns are not yet considered in fecundity studies, or only marginally so (Williams et al., 2002; Pollock et al., 2004; MacKenzie et al., 2005).

### 5.7. The ending marker for maturation/independence of young

$Y$ , and hence  $F$ , is defined to some marker of maturation or independence of the young (Fig. 2). Most frequently these markers are to hatching (precocial species) or fledging (altricial species). However, because a significant level of juvenile mortality occurs in the window from fledging to independence, some authors argue the need for an extended period of parental dependence to be included in fecundity (Murray, 1991; Powell et al., 1999; Anders and Marshall, 2005; Mattsson and Cooper, 2007). However, obtaining data on juvenile survival after hatching (precocial) or fledging (altricial) is difficult and typically requires careful monitoring, often with radio-telemetry (Schmidt et al., 2008).

## 6. Model use and analysis

Fecundity models have many applications, among them estimating reproductive success, predicting fecundity under various alternative parameter values, understanding the biological processes inherent in avian reproduction, and managerial and regulatory decision-making. For these applications, estimating uncertainty around model predictions is required to assess the degree of confidence we should place in model-based inferences.

### 6.1. Applications of expected values

The fundamental goal of many avian fecundity models is to provide estimates of the expected number of offspring produced

per female per season or year (i.e.,  $F$ ). These estimates of  $F$  can be compared among species (Ricklefs and Bloom, 1977), under alternative management proposals (Cowardin and Johnson, 1979; Pease and Grzybowski, 1995), or along environmental gradients (Etterson et al., in press). Marshall et al. (2002) used the Pease and Grzybowski (1995) model to assess the effects of experimentally manipulated prey abundance on  $F$ , and Roelofs et al. (2005) and Bennett and Etterson (2007) developed models to extrapolate the estimated effects of chemicals from laboratory tests to potential field effects on  $F$  in natural populations. The resulting estimates of mean fecundity from these models may be the final model output, or may serve, in turn, as inputs for population-projection models when combined with information about adult and juvenile survival (e.g., Cowardin and Johnson, 1979; Etterson et al., in press).

### 6.2. Sampling variance of fecundity estimates

Whatever the desired use for estimates of fecundity, their value is greatly enhanced by an associated estimate of precision. Early models did not include measures of precision (Ricklefs and Bloom, 1977; Cowardin and Johnson, 1979). More recently, models have reported a measure of precision, either as confidence intervals or standard error estimates, as in Pease and Grzybowski (1995), Powell et al. (1999) and Etterson et al. (2009). These estimates of sampling variance (or SE, 95% CI) of  $F$  are conditional on the sampling variance of input parameters. Properly interpreted, such measures tell us how well we understand  $F$  given the empirically estimated parameters upon which  $F$  depends.

### 6.3. Process variation

In addition to the standard errors described above, many fecundity models also include some process variation. Though it is straightforward to build a model that incorporates distinct types of process variation, obtaining empirical estimates of demographic stochasticity, environmental stochasticity, and other sources of natural variation is difficult. To date, investigation of general forms of process variance has been largely, but not entirely, restricted to groups working on IB models. For example, Mattsson and Cooper (2007) hypothesized distributions among individuals for input parameters, and interpreted the resulting variation in fecundity as a measure of among-individual variance. Etterson et al. (2009) computed estimates of demographic stochasticity for a restricted set of models with constant parameters.

### 6.4. Sensitivity analysis

Sensitivity analyses are crucial for examining how model output changes when input values vary, and they encompass both finite and infinitesimal perturbations. When modeling fecundity, some breeding components will be more important than others for making accurate predictions. Key parameters may be identified by perturbing input values for a single parameter across biologically plausible ranges (Pease and Grzybowski, 1995; Powell et al., 1999; Mattsson and Cooper, 2007), or for multiple parameters simultaneously. For example, predictions from the Mattsson and Cooper (2007) model suggested that Louisiana waterthrush (*Seiurus motacilla*) fecundity varies more in response to changes in nest survival rates than to changes in reneesting parameters. However, patterns of sensitivities may, in turn, depend on other aspects of life history, as demonstrated by Grzybowski and Pease (2000), who showed that the relative importance of egg-loss due to brood parasitism versus nest predation depends on the intensity of brood parasitism and the propensity for females to abandon nests following parasitism events.

### 6.5. Validation

Ideally, we would like to be able to validate predictive models by comparing predictions against independently collected data (*sensu* Williams et al., 2002). This is often not practical, which makes assessment of model validity more difficult. That said, several researchers have compared predicted fecundity to observed fecundity for a limited number of data sets (Pease and Grzybowski, 1995; Simons et al., 2000; Mattsson and Cooper, 2007; Etterson et al., 2009). Such analyses are not a full model validation, as the same data used to calculate fecundity empirically were also used to obtain the model prediction. Even so, these are non-trivial and useful exercises, as the predicted and observed values of  $F$  sometimes diverge (Mattsson and Cooper, 2007; Etterson et al., 2009). Comparison of model outputs and empirical results have been done perhaps most often using the PDE model of Pease and Grzybowski (1995) with high consistency (e.g., Woodworth, 1999; DeCecco et al., 2000; Marshall et al., 2002; Mattsson and Cooper, 2007). Clark and Mangel (2000) suggest using quantitative measures of model predictions compared to data. Many candidate metrics exist, including various measures of squared error between the data and the model (Hilborn and Mangel, 1997; Etterson et al., 2009).

## 7. Future considerations and challenges

The fecundity models we discuss here were developed largely for temperate-breeding, socially monogamous songbirds. The various models we reviewed have been tested against empirical data from numerous species with the latter life history and have generally performed well. However, there is considerable diversity among aspects of avian life history strategies with respect to reproduction such as large variation in clutch size, development of young, level and type of parental care, and mating systems. These considerations may pose special challenges for data collection and subsequent parameterization of fecundity models. While many of these life history features can be incorporated into the current framework of models, others of the examples listed below would challenge existing models, and require alternative approaches. Below, we offer thoughts on some of the remaining challenges to further generalization of avian fecundity models.

### 7.1. Latitudinal and climate variations

Life history strategies can vary with latitude, and most cases simply require adjustments for model input parameters. For instance, the common loon (*Gavia immer*) breeds across a broad latitudinal range from temperate to Arctic regions that will affect the length of the breeding season and the probability of reneesting for failed breeders (Evers et al., 2010). Similarly, James and Shugart (1974) found for each degree of increasing latitude in the Eastern United States, American robins (*Turdus migratorius*) nested on average 3 days later. Perhaps more complicating, however, northern bobwhites (*Colinus virginianus*) across their temperate and semi-tropical range have breeding seasons that vary in both timing and duration based upon weather limitation (e.g., wet-dry seasons of Texas, lengthy seasons of the southeast; Guthery, 2000). In addition to breeding-season length, Greenberg et al. (2006) found latitudinal clines in nest flooding rates, nest predation rates, and clutch size in salt marsh sparrows, suggesting that latitudinal variation probably involves a complex tradeoff among different reproductive traits.

### 7.2. Food availability

While breeding seasons are inextricably linked to food availability, which in turn is frequently dependent on climatic conditions, special cases challenge our generalized modeling approach. Red

crossbills (*Loxia curvirostra*), for example, are opportunistic breeders that can nest any month of the year, but maintain breeding windows spanning 9 months; their breeding phenology is determined by photoperiod and unpredictable food supplies (cone crops) encountered in their wanderings (Hahn, 1995). In specialist predators, such as many boreal owl species that consume small mammals, breeding activity may depend on the phase of their cyclic prey (Brommer et al., 2002; Gauthier et al., 2004).

### 7.3. Other variations in breeding-season length(s), timing, and duration

In extreme environments, breeding may be event driven. For example, in many arctic-nesting species, the probability of breeding may depend on the timing of snow-melt in spring (Reed et al., 2004). Similarly, wet–dry seasons in the tropics trigger many breeding-season phenologies (Gill, 2007; Poulin et al., 1992). In a similar vein, some species are capable of breeding well outside their usual season (Koenig and Stahl, 2007) or engaging in multiple breeding seasons within the same annual cycle that may occur at separate breeding locations hundreds to thousands of kilometers apart (Rohwer et al., 2009). Similarly, some species, for example barn owls (*Tyto alba*) and ruddy ground-doves (*Columbina talpacoti*) can initiate first brood any month of the year (Marti et al., 2005; Snow and Snow, 1964, respectively).

### 7.4. Lifespan, breeding propensity, and age of first reproduction

Short-lived birds, such as most passerines, mature early in life, start breeding at 1 year of age, and are frequently multiple-brooded. In contrast, long-lived species are frequently single-brooded; individuals may take several years to recruit into the breeding population and may not breed every year once they have been recruited (e.g., common loons; Evers et al., 2010). In other cases, breeding propensity may be fairly predictable, as in some albatrosses that will invariably skip breeding the year following successful reproduction, though birds experiencing nest failure may or may not re-nest the following year (Gauthier et al., 2010).

Correctly estimating the age of first reproduction is also challenging in species with delayed maturation because one can rarely be sure that individuals encountered for the first time on a study area have never bred before (though distinct plumages make this possible in rare cases). While some advanced capture–recapture methods (e.g., multistate models, reverse encounter histories; Pradel et al., 1997; Pradel and Lebreton, 1999) partially address this problem, potential issues associated with the determination of annual fecundity in long-lived birds are still quite different than in short-lived species (see Section 5.5).

### 7.5. Special considerations for precocial species

Much of the work on avian fecundity models has focused on birds with altricial young. Precocial species, where young may leave the nest within hours of hatching, have received less attention. The distinction between altricial and precocial is itself an oversimplification of extremes in developmental states (Gill, 2007). Generally applicable models such as those of Ricklefs and Bloom (1977), or more specialized forms, such as those of Murray (1991) for polyandrous species, are data demanding.

While hatching can be used as a marker for fecundity, estimating post-hatch chick survival to some maturation point such as developing flying ability (see Figs. 1 and 2) requires more intensive sampling techniques. These may include marking of chicks at hatch in the nest and application of standard capture–recapture methods (e.g., Lepage et al., 2000), or radio-telemetry (e.g., Mauser et al., 1994; Larson et al., 2001) to generate estimates of survival.

Following success of a nest, precocial, multi-clutch birds typically brood young for some time before initiating a subsequent nesting attempt (unless the male participates in brooding activities).

### 7.6. Non-monogamous mating strategies

Many mating strategies exist among birds, and socially monogamous strategies (as opposed to genetically monogamous relationships where extra-pair copulations are not observed) have been found to be the primary mating strategy in many avian species (Gill, 2007). In some species, such as northern bobwhites, males can incubate a substantial number of nests in a given year (up to 30% within a defined population), as well as participate in brood-rearing activities after young hatch (Curtis et al., 1993; Burger et al., 1995). Researchers have documented female bobwhites engaging in rapid multi-clutch polygamy where both sexes attempt to increase fitness by simultaneously incubating two clutches (Curtis et al., 1993; Burger et al., 1995). Additionally, male bobwhites that participate in brood-rearing activities can dramatically reduce the time between nests to just 1–2 days (Brennan, 1999).

Other complex breeding systems will lead to similar complications in the estimation of fecundity: they include such examples as polygyny (Kroodsma and Verner, 1997); polyandry, which is prevalent in many shorebirds (e.g., Oring et al., 1994); and polygynandry, which occurs in some passerines such as the Dunnock (*Prunella modularis*; Davies, 1992) and Bicknell's thrush (*Catharus bicknelli*; Goetz et al., 2003). These systems create modeling challenges and may lead to underestimation of fecundity by only monitoring and incorporating female activities (Burger et al., 1995). Parameterization of models for these mating systems would require careful monitoring of marked individuals throughout the season.

### 7.7. Brood parasitic species

While several current modeling efforts (e.g., Pease and Grzybowski, 1995) can deal with the effects of brood parasitism on host species, the fecundity of brood parasitic species presents a special challenge. Obligate brood parasitism, where parasites lay their eggs in the nests of host species, is found in at least seven unrelated taxa (Johnsgard, 1997). Some are host specific, forming specialized relations with their host species (e.g., Cuculidae), while others are host generalists, laying eggs in the nests of many host species (e.g., some cowbirds). Further complicating this topic are groups such as waterfowl which exhibit dual strategies, laying eggs parasitically prior to incubating their own nest when environmental conditions are favorable (Sorenson, 1991). Although estimates of egg success can be obtained (Johnsgard, 1997), the problems of establishing and tracking effective “clutches” (Scott and Ankney, 1983) or relating nest success among an array of host species for most brood parasites extends beyond both current empirical and analytical capabilities, and requires an array of assumptions and inferences not normally included in fecundity models.

### 7.8. Time-lags in application of statistical techniques

The application of appropriate statistical and modeling techniques has frequently suffered long time-lags between state-of-knowledge and state-of-general application. Concepts embedded in the Mayfield corrections for estimating nest success were first proposed in 1961, presented explicitly in 1975; yet by 1999, only about 30% of studies that could benefit from their application considered them (Thompson et al., 2001). Even with the introduction of concept and models directed at seasonal fecundity (Ricklefs, 1973; Ricklefs and Bloom, 1977; Pease and Grzybowski, 1995), much of the current literature on reproductive success in birds still focuses on nest success (e.g., Martin, 1995; Dinsmore et al., 2002; Shaffer,

2004) rather than annual or seasonal fecundity. This transfer of perception and mathematical techniques between biometricians and biologists (or managers) involving numerical applications more broadly (Clobert and Lebreton, 1991) remains a long-standing challenge today requiring communication in both directions.

## 8. Summary

The fundamental purpose of our symposium and consequent synthesis was to lead researchers, ourselves included, to a better understanding of the issues, processes, problems, solutions, and challenges of assessing avian reproductive success. To do so, we have relied heavily on a simple conceptual model (Eqs. (1a and 1b)) that serves to broadly unify existing models of avian fecundity. Though of limited use for data analysis, our simple model lays bare the essential component processes of avian fecundity, something that has been missing from the fragmented and complicated literature. Our conceptual model also serves to highlight the general kinds of data that must be collected and reported to parameterize a seasonal fecundity model. Such data are often missing from published accounts of reproductive life history.

We focus on fecundity, the number of young produced per female within a defined period of time, because of its paramount importance as a critical parameter in understanding and answering questions of evolutionary fitness, population dynamics, natural history, ecotoxicology, and regulatory and management decisions. Among the current issues to which we direct attention are the misconceptions and inadequacies of commonly used metrics and indices of reproductive success and the need to adequately capture and assess reneesting and breeding-season length in fecundity assessments. Our hope here is to direct researchers and managers toward a more comprehensive understanding of the issues, problems, and value of properly modeling fecundity.

While the modeling approaches we describe in this paper differ in many ways, these differences obscure the fact that these models have all been constructed using a similar conceptual algorithm, incorporating the basic parameters ( $Y$ ,  $S$ ,  $N$  and  $P$ ) of Eqs. (1a and 1b). Thus, most fecundity models are more similar than they first appear. The differences among the fecundity models we have described herein (Pease and Grzybowski, 1995; Powell et al., 1999; Mattsson and Cooper, 2007; Etterson et al., 2009) reflect the mathematical formalisms in which they are written and the circumstances and scientific questions to which they are applied.

The explicit recognition of avian fecundity as a stochastic process composed of interacting sub-processes provides a common conceptual framework for further development of avian fecundity models. The above framework suggests that new developments can be made in improving how to measure, estimate, and include these basic sub-processes in new studies. Such studies could include, but are not limited to, those that focus on developing statistical methods to estimate and control for partial observability, partitioning sampling and process variance in parameter estimates, assessing competing risks, and expanding the scope of models to encompass diverse life history strategies, and environmental conditions.

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## References

- Ackerman, J.T., Eadie, J.M., Loughman, D.L., Yarris, G.S., McLandress, M.R., 2003. The influence of partial clutch depredation on duckling production. *J. Wildl. Manage.* 67, 576–587.
- Anders, A.D., Marshall, M.R., 2005. Increasing the accuracy of productivity and survival estimates in assessing land bird population status. *Conserv. Biol.* 19, 66–74.
- Arcese, P., Smith, J.N.M., Hatch, M.L., 1996. Nest predation by cowbirds, and its consequences for passerine demography. *Proc. Natl. Acad. Sci. USA* 93, 4608–4611.
- Bennett, R.S., Etterson, M.A., 2007. Incorporating results of avian toxicity tests into a model of annual reproductive success. *Integr. Environ. Assess. Manag.* 3, 498–507.
- Brennan, L.A., 1999. Northern bobwhite (*Colinus virginianus*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America* 397. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington.
- Brommer, J.E., Pietiäinen, H., Kolunen, H., 2002. Reproduction and survival in a variable environment: Ural owls (*Strix uralensis*) and the three-year vole cycle. *Auk* 119, 544–550.
- Burger Jr., L.W., Ryan, M.R., Dailey, T.V., Kurzejeski, E.W., 1995. Reproductive strategies, success, and mating systems of northern bobwhite in Missouri. *J. Wildl. Manage.* 59, 417–426.
- Clark, J., Mangel, M., 2000. *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford Univ Press, New York.
- Clobert, J., Lebreton, J.D., 1991. Estimation of demographic parameters in bird populations. In: Perrins, C.M., Lebreton, J.D., Hiron, G.J.M. (Eds.), *Bird Population Studies: Relevance to Conservation and Management*. Oxford Univ. Press, Oxford, pp. 75–104.
- Cowardin, L.M., Johnson, D.H., 1979. Mathematics and mallard management. *J. Wildl. Manage.* 43, 18–35.
- Crick, H.Q.P., Gibbons, D.W., Magrath, R.D., 1993. Seasonal changes in clutch size in British birds. *J. Anim. Ecol.* 62, 263–273.
- Crowder, M., 2001. *Classical Competing Risks*. Chapman and Hall, Boca Raton.
- Curtis, P.D., Mueller, B.S., Doerr, P.D., Robinette, C.F., DeVos, T., 1993. Potential polygamous breeding behavior in northern bobwhite. *Third Natl. Quail. Symp.* 3, 55–63.
- Davies, N.B., 1992. *Dunnock Behaviour and Social Evolution*. Oxford Univ. Press, Oxford.
- DeCecco, J.A., Marshall, M.R., Williams, A.B., Gale, G.A., Cooper, R.J., 2000. Comparative seasonal fecundity of four Neotropical migrants in middle Appalachia. *Condor* 102, 653–663.
- DeSante, D.F., Burton, K.M., Saracco, J.F., Walker, B.L., 1995. Productivity indices and survival rate estimates from MAPS, a continent-wide programme of constant-effort mist-netting in North America. *J. Appl. Stat.* 22, 935–948.
- Dinsmore, S.J., White, G.C., Knopf, F.L., 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83, 3476–3488.
- Donovan, T.M., Thomson, F.R., Faaborg, J., Probst, J., 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conserv. Biol.* 9, 1380–1395.
- Dzubin, A., Gallop, J.B., 1972. Aspects of mallard breeding ecology in Canadian parkland and grassland. In: Smith, R.L., Palmer, J.R., and Baskett, T.S. (Eds.), *Population Ecology of Migratory Birds*. U.S. Fish Wildl Serv Research Report no. 2, pp. 113–152.
- Ellis-Felege, S.N., Miller, A., Burnam, J.S., Wellendorf, S.D., Sisson, D.C., Palmer, W.E., Carroll, J.P. Parental decisions following partial depredation on northern bobwhite (*Colinus virginianus*) nests. *Stud. Av. Biol.*, in press.
- Etterson, M.A., Olsen, B.J., Greenberg, R., Shriver, G. Sources, sinks and model accuracy. In: Liu, J., Hull, V., Morzillo, A., Wiens, J. (Eds.), *Sources, Sinks, and Sustainability*. Cambridge Univ Press, in press.
- Etterson, M.A., Nagy, L.R., Rodden-Robinson, T., 2007a. Partitioning risk among different causes of nest failure. *Auk* 124, 432–443.
- Etterson, M.A., Olsen, B.J., Greenberg, R., 2007b. The analysis of covariates in multi-fate Markov chain nest-failure models. *Stud. Av. Biol.* 34, 55–64.
- Etterson, M.A., Stanley, T.R., 2008. Incorporating classification uncertainty in competing-risks nest-failure analysis. *Auk* 125, 687–699.
- Etterson, M.A., Bennett, R.S., Kershner, E.L., Walk, J.W., 2009. Markov chain estimation of avian seasonal fecundity. *Ecol. Appl.* 19, 622–630.
- Evers, D.C., Paruk, J.D., McIntyre, J.W., Barr, J.F., 2010. Common loon (*Gavia immer*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*, No. 313. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington.
- Farnsworth, G.L., Simons, T.R., 2001. How many baskets? Clutch sizes that maximize annual fecundity of multiple-brooded birds. *Auk* 4, 973–982.

- Farnsworth, G.L., Simons, T.R., 2005. Relationship between Mayfield nest-survival estimates and seasonal fecundity: a cautionary reply. *Auk* 122, 1000–1001.
- Fletcher, R.J., Koford, R.R., Seaman, D.A., 2006. Critical demographic parameters for declining songbirds breeding in restored grasslands. *J. Wildl. Manage.* 70, 145–157.
- Fujiwara, M., Caswell, H., 2002. A general approach to temporary emigration in mark-recapture analysis. *Ecology* 83, 3266–3275.
- Gauthier, G., Bêty, J., Giroux, J.-F., Rochefort, L., 2004. Trophic interactions in a high arctic snow goose colony. *Integr. Comp. Biol.* 44, 119–129.
- Gauthier, G., Milot, E., Weimerskirch, H., 2010. Small-scale dispersal and survival in a long-lived seabird, the wandering albatross. *J. Anim. Ecol.* 79, 879–887.
- Gill, F.B., 2007. *Ornithology*, 3rd ed. W.H. Freeman, New York.
- Gnam, R., Rockwell, R.F., 1991. Reproductive potential and output of the Bahama parrot (*Amazonia leucocephala bahamensis*). *Ibis* 133, 400–405.
- Goetz, J.E., McFarland, K.P., Rimmer, C.C., 2003. Multiple paternity and multiple male feeders in Bicknell's thrush (*Catharus bicknelli*). *Auk* 120, 1044–1053.
- Grant, P.R., Grant, B.R., Keller, L.F., Petren, K., 2000. Effects of El Niño events on Darwin's finch productivity. *Ecology* 81, 2442–2457.
- Grant, T.A., Shaffer, T.L., Madden, E.M., Pietz, P.J., 2005. Time-specific variation in passerine nest survival: new insights into old questions. *Auk* 122, 661–672.
- Greenberg, R., Elphick, C., Nordby, J.C., Gjerdrum, C., Spautz, H., Shriver, G., Schmelting, B., Marra, P., Nur, N., Olsen, B.J., Winter, M., 2006. Flooding and predation: trade-offs in the nesting ecology of tidal-marsh sparrows. *Stud. Av. Biol.* 32, 96–109.
- Grzybowski, J.A., Pease, C.M., 2000. Comparing the relative effects of brood parasitism and nest predation on seasonal fecundity in passerine birds. In: Smith, J.M.N., Cook, T.L., Robinson, S.K., Rothstein, S.I., Sealy, S.G. (Eds.), *Ecology and Management of Cowbirds and their Hosts*. Univ Texas Press, Austin, pp. 145–155.
- Grzybowski, J.A., Pease, C.M., 2005. Renesting determines seasonal fecundity in songbirds: what do we know? What should we assume? *Auk* 122, 280–291.
- Guthery, F.S., 2000. *On Bobwhites*, 1st ed. Texas A&M Univ Press, College Station.
- Hahn, T.P., 1995. Integration of photoperiodic and food cues to time changes in reproductive physiology by an opportunistic breeder, the red crossbill, *Loxia curvirostris* (Aves: Carduelinae). *J. Exp. Zool.* 272, 213–226.
- Heisey, D.M., Patterson, B.R., 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *J. Wildl. Manage.* 70, 1544–1555.
- Heisey, D.M., Shaffer, T.L., White, G.C., 2007. The analysis of covariates in multi-fate Markov chain nest failure models. *Stud. Avian Biol.* 34, 55–64.
- Hilborn, R., Mangel, M., 1997. *The Ecological Detective: Confronting Models with Data*. Princeton Univ Press, Princeton.
- James, F.C., Shugart Jr., H.H., 1974. The phenology of the nesting season of the American robin (*Turdus migratorius*) in the United States. *Condor* 76, 159–168.
- Jenouvrier, S., Tavecchia, G., Thibault, J.C., Choquet, R., Bretagnolle, V., 2008. Recruitment processes in long-lived species with delayed maturity: estimating key demographic parameters. *Oikos* 117, 620–628.
- Johnsgard, P.A., 1997. *The Avian Brood Parasites; Deception at the Nest*. Oxford Univ Press, New York.
- Johnson, D.H., 2007a. Methods of estimating nest success: an historical tour. *Stud. Av. Biol.* 34, 1–12.
- Johnson, D.H., 2007b. Estimating nest success: a guide to the methods. *Stud. Av. Biol.* 34, 65–72.
- Jones, J., Doran, P.J., Nagy, L.R., Holmes, R.T., 2005. Relationship between Mayfield nest-survival estimates and seasonal fecundity: a cautionary note. *Auk* 122, 306–312.
- Karlin, S., Taylor, H.E., 1981. *A Second Course in Stochastic Processes*. Academic Press, San Diego.
- Kendall, W.L., Nichols, J.D., 2002. Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. *Ecology* 83, 3276–3284.
- Kendall, W.L., Nichols, J.D., Hines, J.E., 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78, 563–578.
- Kershner, E.L., Walk, J.W., Warner, R.E., 2004. Postfledging movements and survival of juvenile eastern meadowlarks (*Sturnella magna*) in Illinois. *Auk* 121, 1146–1154.
- Klomp, H., 1970. Determination of clutch-size in birds – a review. *Ardea* 58, 1–7.
- Koenig, W.D., Stahl, J.T., 2007. Late summer and fall nesting in the acorn woodpecker and other North American terrestrial birds. *Condor* 109, 334–350.
- Kroll, A.J., Haufler, J.B., 2009. Age and clutch size variation in Dusky Flycatcher nest survival. *J. Ornithol.* 150, 409–417.
- Kroodsma, D.E., Verner, J., 1997. Marsh wren (*Cistothorus palustris*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*, No. 308. Academy of Natural Sciences, Philadelphia, PA, American Ornithologists' Union, Washington.
- Lack, D., 1948. The significance of clutch size. Part 3. Some interspecific comparisons. *Ibis* 90, 25–45.
- Lack, D., 1968. *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* 142, 911–927.
- Lang, J.D., Powell, L.A., Kremetz, D.G., Conroy, M.J., 2002. Wood thrush movements and habitat use: effects of forest management for red-cockaded woodpeckers. *Auk* 119, 109–124.
- Larson, M.A., Clark, M.E., Winterstein, S.R., 2001. Survival of ruffed grouse chicks in northern Michigan. *J. Wildl. Manage.* 65, 880–886.
- Lebreton, J.D., Burnham, K.P., Clobert, J., Anderson, D.R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62, 67–118.
- Lebreton, J.D., Pradel, R., 2002. Multistate recapture models: modelling incomplete individual histories. *J. Appl. Stat.* 29, 353–369.
- Lepage, D., Gauthier, G., Menu, S., 2000. Reproductive consequences of egg-laying decisions in snow geese. *J. Anim. Ecol.* 69, 414–427.
- Lynch, J.J., Singleton, J.R., 1964. Winter appraisals of annual productivity in geese and other water birds. *Wildfowl Trust Annu. Rep.* 15, 114–126.
- MacKenzie, D.L., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2005. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Academic Press, Burlington, MA.
- Manolis, J.C., Anderson, D.E., Cuthbert, F.J., 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* 117, 615–626.
- Marshall, M.R., Cooper, R.J., Strazanac, J.S., Butler, L., 2002. Effects of experimentally reduced prey abundance on the breeding ecology of the Red-eyed Vireo. *Ecol. Appl.* 12, 261–280.
- Marti, C.D., Poole, A.F., Bevier, L.R., 2005. Barn owl (*Tyto alba*). In: Poole, A. (Ed.), *The Birds of North America Online*. Cornell Laboratory of Ornithology; the Birds of North America online database, Ithaca, <http://bna.birds.cornell.edu/BNA/account/BarnOwl>.
- Martin, T.E., 1995. Avian life-history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* 65, 101–127.
- Martin, T.E., 2004. Avian life-history evolution has an eminent past: does it have a bright future? *Auk* 121, 289–301.
- Martin, T.E., Geupel, G.R., 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *J. Field Ornith.* 64, 507–519.
- Mattsson, B.J., Cooper, R.J., 2007. Which life-history components determine breeding productivity for individual songbirds? A case study of the Louisiana Waterthrush (*Seiurus motacilla*). *Auk* 124, 1186–1200.
- Mausser, D.M., Jarvis, R.L., Gilmer, D.S., 1994. Survival of radio-marked Mallard ducklings in northeastern California. *J. Wildl. Manage.* 58, 82–87.
- Mayfield, H.F., 1961. Nesting success calculated from exposure. *Wilson Bull.* 73, 255–261.
- Mayfield, H.F., 1975. Suggestions for calculating nesting success. *Wilson Bull.* 87, 456–466.
- Moreau, R.E., 1944. Clutch size: a comparative study with reference to African birds. *Ibis* 86, 286–347.
- Morgan, M.R., Normant, C., Runge, M.C., 2010. Evaluation of a reproductive index for estimating productivity of grassland breeding birds. *Auk* 127, 86–93.
- Murray Jr., B.G., 1991. Measuring annual reproductive success, with comments on the evolution of reproductive-behavior. *Auk* 108, 942–952.
- Murray Jr., B.G., 2000. Measuring annual reproductive success in birds. *Condor* 102, 470–473.
- Nagy, L.R., Holmes, R.T., 2004. Factors influencing fecundity in migratory songbirds: is nest predation the most important? *J. Avian Biol.* 35, 487–491.
- Nagy, L.R., Holmes, R.T., 2005. Food limits annual fecundity of a migratory songbird: an experimental study. *Ecology* 86, 675–681.
- Nolan Jr., V., 1978. The ecology and behavior of the prairie warbler, *Dendroica discolor*. *Ornithol. Monogr.* 26.
- Nur, N., Holmes, A.L., Geupel, G.R., 2004. Use of survival time analysis to analyze nesting success in birds: an example using Loggerhead Shrikes. *Condor* 106, 457–471.
- Olofsson, H., Ripa, J., Jonzen, N., 2009. Bet-hedging as an evolutionary game: the trade-off between egg size and number. *Proc. R. Soc. B* 276, 2963–2969.
- Olsen, B.J., Felch, J.M., Greenberg, R., Walters, J.R., 2008. Causes of reduced clutch size in a tidal marsh endemic. *Oecologia* (Heidelberg) 15, 421–435.
- Olson, G.S., Anthony, R.G., Forsman, E.D., Ackers, S.H., Loschl, P.J., Reid, J.A., Dugger, K.M., Glenn, E.M., Ripple, W.J., 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. *J. Wildl. Manage.* 69, 918–932.
- Oring, L.W., Reed, J.M., Alberico, J.A.R., 1994. Mate acquisition tactics in polyandrous Spotted Sandpipers (*Actitis macularia*): the role of age and experience. *Behav. Ecol. Sociobiol.* 5, 9–16.
- Ortiz-Catedral, L., Brunton, D.H., 2008. Clutch parameters and reproductive success of a translocated population of red-crowned parakeet (*Cyanoramphus novaezelandiae*). *Aust. J. Zool.* 56, 389–393.
- Partridge, L., Harvey, P.H., 1988. The ecological context of life-history evolution. *Science* 241, 1449–1455.
- Pease, C.M., Grzybowski, J.A., 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerines birds. *Auk* 112, 343–363.
- Peterson, M.J., Grant, W.E., Silvy, N.J., 1998. Simulation of reproductive stages limiting productivity of the endangered Attwater's prairie chicken. *Ecol. Model.* 111, 283–295.
- Pintillie, M., 2006. *Competing Risks: A Practical Perspective*. John Wiley & Sons, West Sussex.
- Pollock, K.H., Marsh, H., Bailey, L.L., Farnsworth, G.L., Simons, T.R., Alldredge, M.W., 2004. Separating components of detection probability in abundance estimation: an overview with diverse examples. In: Thompson, W.L. (Ed.), *Sampling Rare and Elusive Species: Concepts, Designs and Techniques for Estimating Population Parameters*. Island Press, Washington, pp. 43–58.
- Post van der Burg, M., Powell, L.A., Tyre, A.J., 2009. Modeling parasitism rate and parasitism risk: an illustration using a colonially nesting songbird, the red-winged blackbird (*Agelaius phoeniceus*). *J. Av. Biol.* 40, 263–270.
- Poulin, B., Lefebvre, G., McNeil, R., 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology* 73, 2295–2309.
- Powell, L.A., Conroy, M.J., Kremetz, D.G., Lang, J.D., 1999. A model to predict breeding-season productivity for multibrooded songbirds. *Auk* 116, 1001–1008.
- Powell, L.A., Knutsen, M.G., 2006. A productivity model for parasitized, multibrooded songbirds. *Condor* 108, 292–300.

- Pradel, R., Johnson, A.R., Viallefont, A., Nager, R.G., Cézilly, F., 1997. Local recruitment in the greater flamingo: a new approach using capture-mark-recapture data. *Ecology* 78, 1431–1445.
- Pradel, R., Lebreton, J.D., 1999. Comparison of different approaches to the study of local recruitment of breeders. *Bird Study* 46, 74–81.
- Reed, E.T., Bêty, J., Mainguy, J., Gauthier, G., Giroux, J.-F., 2003. Molt migration in relation to breeding success in greater snow geese. *Arctic* 56, 76–81.
- Reed, E.T., Gauthier, G., Giroux, J.-F., 2004. Effects of spring conditions on breeding propensity of greater snow goose females. *Anim. Biodivers. Conserv.* 27, 35–46.
- Ricklefs, R.E., 1970a. Clutch size in birds: outcome of opposing predator and prey adaptations. *Science* 168, 559–560.
- Ricklefs, R.E., 1970b. The estimation of a time function of ecological use. *Ecology* 51, 508–513.
- Ricklefs, R.E., 1973. Fecundity, mortality, and avian demography. In: Farner, D.S. (Ed.), *Breeding Biology*. National Academy of Sciences, Washington.
- Ricklefs, R.E., 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* 97, 38–49.
- Ricklefs, R.E., Bloom, G., 1977. Components of avian breeding productivity. *Auk* 94, 86–96.
- Robinson, W.D., Rodden-Robinson, T., 2001. Observations of predation events at bird nests in central Panama. *J. Field Ornith* 72, 43–48.
- Roelofs, W., Crocker, D.R., Shore, R.F., Moore, D.R.J., Smith, G.C., Akcakaya, H.R., Bennett, R.S., Chapman, P.F., Clook, M., Crane, M., Dewhurst, I.C., Edwards, P.J., Fairbrother, A., Ferson, S., Fischer, D., Hart, A.D.M., Holmes, M., Hooper, M.J., Lavine, M., Leopold, A., Luttik, R., Mineau, P., Mortenson, S.R., Noble, D.G., O'Connor, R.J., Sibly, R.M., Spendriff, M., Springer, T.A., Thompson, H.M., Topping, D.C., 2005. Case study part 2: probabilistic modeling of long-term effects of pesticides on individual breeding success in birds and mammals. *Ecotoxicology* 14, 895–923.
- Rohwer, S., Hobson, K.A., Rohwer, V.G., 2009. Migratory double breeding in Neotropical migrant birds. *Proc. Natl. Acad. Sci.* 106, 19050–19055.
- Shaffer, T.L., 2004. A unified approach to analyzing nest success. *Auk* 121, 526–540.
- Schmidt, K.A., Whalen, C.J., 1999. The relative impacts of nesting predation and brood parasitism on seasonal fecundity in songbirds. *Conserv. Biol.* 13, 46–57.
- Schmidt, K.A., Rush, S.A., Ostfeld, R.S., 2008. Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. *J. Anim. Ecol.* 77, 830–837.
- Scott, D.M., Ankney, C.D., 1983. The laying cycle of brown-headed cowbirds: Passerine chickens? *Auk* 100, 583–592.
- Sedinger, J.S., Lindberg, M.S., Chelgren, N.D., 2001. Age-specific breeding probability in black brant: effects of population density. *J. Anim. Ecol.* 70, 798–807.
- Simons, T.R., Farnsworth, G.L., Shriner, S.A., 2000. Evaluating great smoky mountains national park as a population source for wood thrush. *Conserv. Biol.* 14, 1133–1144.
- Skutch, A.F., 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91, 430–455.
- Slatkin, M., 1974. Hedging ones evolutionary bets. *Nature* 250, 704–705.
- Smith, P.A., Bart, J., Lanctot, R.B., McCaffery, B.J., Brown, S., 2009. Probability of detection of nests and implications for survey design. *Condor* 111, 414–423.
- Snow, D.W., Snow, B.K., 1964. Breeding seasons and annual cycles of Trinidad land-birds. *Zoologica* 49, 1–39.
- Sorenson, M.D., 1991. The functional significance of parasitic egg laying and typical nesting in redhead ducks: an analysis of individual behavior. *Anim. Behav.* 42, 771–796.
- Stanley, T.R., 2004. When should mayfield data be discarded? *Wilson Bull.* 116, 267–269.
- Stanley, T.R., Newmark, W.D., 2010. Estimating length of avian incubation and nestling stages in afro-tropical forest birds from interval-censored nest records. *Auk* 127, 79–85.
- Thompson, B.C., Knadle, G.E., Brubaker, D.L., Brubaker, K.S., 2001. Nest success is not an adequate estimate of avian reproduction. *J. Field Ornith* 75, 527–536.
- Thompson III, F.R., Burhans, D.E., 2004. Differences in predators of artificial and real songbird nests: evidence of bias in artificial nest studies. *Conserv. Biol.* 18, 373–380.
- Trivers, R.L., 1972. Parental investment and sexual selection. In: Campbell, B. (Ed.), *Sexual Selection and the Descent of Man*. Aldine-Atherton, Chicago, pp. 136–179.
- Vander Haegen, W.M., Schroeder, M.A., DeGraaf, R.M., 2002. Predation on real and artificial nests in shrubsteppe landscapes fragmented by agriculture. *Condor* 104, 496–506.
- Verhulst, S., Nilsson, J.A., 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 363, 399–410.
- Vickery, P.D., Hunter Jr., M.L., Wells, J.V., 1992. Use of a new reproductive index to evaluate relationship between habitat quality and breeding success. *Auk* 109, 697–705.
- Walk, J.W., Wentworth, K., Kershner, E.L., Bollinger, E.K., Warner, R.E., 2004. Renesting decisions and annual fecundity of female Dickcissels (*Spiza americana*) in Illinois. *Auk* 121, 1250–1261.
- Weimerskirch, H., Brothers, N., Jouventin, P., 1997. Population dynamics of wandering albatross (*D. exulans*) and Amsterdam albatross (*D. amsterdamensis*) in the Indian Ocean and their relationship with long-line fisheries: conservation implications. *Biol. Conserv.* 79, 257–270.
- Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. *Analysis and Management of Animal Populations*. Academic Press, San Diego.
- Winkler, D.W., Allen, P.E., 1996. The seasonal decline in avian clutch size: strategy or physiological constraints? *Ecology* 77, 922–932.
- Woodworth, B.L., 1999. Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. *Conserv. Biol.* 13, 67–76.
- Zanette, L., Haydon, D.T., Smith, J.N.M., Taitt, M.J., Clinchy, M., 2007. Reassessing the cowbird threat. *Auk* 124, 210–223.
- Zicus, M.C., Fieberg, J., Rave, D.P., 2003. Does mallard clutch size vary with landscape composition: a different view. *Wilson Bull.* 115, 409–413.