

A CLUTCH AND BROOD SURVIVAL MODEL THAT DISCRIMINATES RANDOM AND CORRELATED MORTALITY

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Abstract. Quantitative conservation methodologies such as Population Viability Analysis (PVA) require reliable estimates of life history parameters such as breeding success. The utility of such metrics for egg-laying species is complicated by the fact that the mortality of eggs and juveniles can occur both randomly and independently over time, or catastrophically, as in the sudden loss of a clutch or brood. Not knowing the nature of mortality caused by either or both of abiotic (e.g., weather) and biotic (e.g., predation) events limits our ability to confidently assess a population's demography and sustainability, or rank competing hypotheses. To address this deficiency, we describe a statistical model that estimates egg and juvenile survival rates continuously from laying to fledging based on periodic observations of individual clutches and broods. Adjunct data on environmental or predation threats can be included in the model as covariate series potentially affecting juvenile survival. Our model can statistically characterize mortality between the extremes of random and catastrophic mortality and can determine if unwitnessed mortalities occurred independently or were correlated (i.e., overdispersed, where catastrophe is extreme overdispersion). Overdispersion is estimated as a parameter of the beta-binomial probability distribution of survival outcomes, which differs from its treatment in Program MARK where overdispersion is an a posteriori diagnostic referred to as \hat{c} . We used data for the sea duck Barrow's Goldeneye to illustrate our model. Specifically, we contribute to the argument that a larger brood confers a fitness advantage to a tending hen by concluding that brood size on hatch day is positively correlated with a juvenile's probability of surviving to fledge.

Key words: beta-binomial; breeding success; brood amalgamation; catastrophe; clutch parasitism; Mayfield method; mortality; overdispersion; Program MARK; survival.

INTRODUCTION

One of the key methodologies for assessing a population's sustainability over time is population viability analysis (PVA; Beissinger and McCullough 2002, Morris and Doak 2002). Effective use of analyses such as PVA requires that an analyst have confidence in the life history parameter estimates and their uncertainties that enter such models. However, expressions of uncertainty often tacitly assume that survival estimates arise from a simple binomial process where individuals independently either live or die, and whose rate may or may not change over time. The three most well-known statistical tools for estimating survival rates for bird clutches and broods are the Kaplan-Meier product-moment survival estimator (Kaplan and Meier 1958), the Mayfield method (Mayfield 1961, 1975), and Program MARK (White and Burnham 1999; available on-

line).⁵ The Mayfield method for nest success has found wide use in bird demographics over the last four decades, and some authors have modified or refined the Mayfield method to adapt it to their particular data (Johnson 1979, Johnson and Shaffer 1990, Grand and Flint 1997, Stanley 2000, Manly and Schmutz 2001, Dinsmore et al. 2002). The Kaplan-Meier product-moment survival estimator has found broad generic applicability in survival analysis and hypothesis testing in a variety of fields from medicine to demography. However, like the Mayfield method, it assumes that the deaths of individuals are random and follow a binomial probability distribution.

A well-known contemporary analytical tool for population demographers is Program MARK (White and Burnham 1999). Program MARK offers a suite of options for survival estimation and modeling using observational or capture-mark-recapture (CMR) data that includes a nest survival model (Dinsmore et al. 2002) that has evolved from the Mayfield method. The principal contribution of Program MARK is its capacity

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⁵ (<http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>)

for robust and realistic, though potentially highly parameterized, survival models, and its ability to empirically deal with overdispersion, i.e., the tendency for individual mortality events to be correlated. Program MARK exploits the contemporary availability of powerful computers to undertake data analyses that were impractical in the recent past. Perhaps more important, it has implemented contemporary theory for model ranking based on the information-theoretic approach to model selection and interpretation (Burnham and Anderson 2002). Thus it has the ability to estimate survival rates and their uncertainty for direct use in demographic population models or for hypothesis ranking among competing models.

Despite the robustness of analytical tools such as Program MARK, there remain many circumstances where specific hypotheses or particular data structures are not well suited to the suite of statistical options available in the literature. One key deficiency concerns a lack of robustness in accommodating the distributional characteristics of clutch and brood mortalities. In particular, it has been recognized by demographers that a survival rate is not a generic metric, but integrates an individual's success at avoiding mortalities due to random biotic (e.g., predation) and abiotic (e.g., weather) events (Morris and Doak 2002). Such predation or weather events are not likely to affect all eggs in a clutch, or all juveniles in a brood, independently. For example, a predator may attack more than one juvenile in a brood of ducklings, or a violent weather event may destroy an entire brood. Overall survivorship of eggs and juveniles will represent an individual's success at enduring all of these threats.

The model we present here addresses two limitations of the Mayfield, Kaplan-Meier, and Program MARK methodologies. None of the above models deals explicitly with overdispersion during the parameter estimation phase of model fitting (though Program MARK deals with overdispersion as an a posteriori correction). Likewise, none accommodates the reality that an individual's survival likely results from enduring a mixture of random (independent) and correlated (overdispersed) mortality processes. Specifically, our model offers two advantages for modeling breeding success from laying to fledging. First, survivorship is statistically partitioned into random and correlated mortality profiles. Thus the assumption that mortality events be statistically independent, i.e., binomially distributed, is relaxed. The overdispersed partition may range from partial to full (catastrophic). This nonindependence of mortality events is accommodated by use of the beta-binomial probability distribution for model prediction error (Mood et al. 1985, McCullagh and Nelder 1989). Second, survivorship estimates can be measured from laying through hatching, then from hatching to fledging without the need to observe hatching.

A potential constraint of our approach is that survivorship curves are parameterized to follow a Weibull probability distribution (Walpole et al. 1998). As such, our model trades off the advantages of our parsimonious approach against robustness in survivorship curves offered by distribution-free models such as those offered by Program MARK. However, our more flexible error structure can reduce the need for flexibility in the survivorship model. Goodness-of-fit (GOF) assessments can be used to judge any consequences of this trade-off. Our model incorporates the information-theoretic features of model ranking and GOF testing (Burnham and Anderson 2002) that would be familiar to users of Program MARK and are key to parsimonious model selection, hypothesis ranking, and adjudication of the quality of a model's fit to data.

Researchers can judge the utility of the clutch and brood survivorship model we describe here for their scientific inquiries by addressing the following features of their hypotheses and data. If (a) your purpose is (1) to estimate clutch and/or brood survival rates, their uncertainty and distributional (random or correlated) characteristics for use in a demographic or simulation model, or (2) to rank models or test hypotheses concerning the survival rate of eggs in a clutch or juveniles in a brood (i.e., investigate the effects of predators, weather, pesticides, etc.), and (b) you have data on steady or declining clutch and/or brood sizes periodically over time, clutch and/or brood age, and optionally a brood covariate series (e.g., weather, or a stage or condition variable), and (c) you are comfortable with assuming almost synchronous hatching of all eggs in a clutch, specifying a laying age and/or a fledging age, assuming negligible measurement error, and assigning all eggs or juveniles (precocial or altricial) observed to a family, then: you can estimate clutch and/or brood survival rates and their uncertainty, have survival rates vary with age or time, relate survival to a covariate data series, and partition mortality into its random and correlated components.

Our model was motivated in part by demographic questions concerning the breeding success of the sea duck Barrow's Goldeneye (*Bucephala islandica*) in the central interior (Chilcotin-Cariboo) region of British Columbia, Canada. Our particular interest in Barrow's Goldeneye in this region stems from the unique grassland and fragmented forest mosaic habitat near Riske Creek, British Columbia (see Plate 1). This habitat is rare and unique in British Columbia and is geographically isolated from similar habitat to the east, particularly in Canada's prairie provinces. Decades of forestry and fire suppression have resulted in this unique habitat being further diminished by timber harvesting and forest encroachment upon the grassland.

Conservation concerns for the Chilcotin-Cariboo population of Barrow's Goldeneye initially arose due to their being secondary cavity nesters that lay 4–15 eggs (Godfrey 1986), primarily in cavities excavated



PLATE. 1. Aerial view portraying landscape characteristics of the Chilcotin-Cariboo region near Riske Creek, British Columbia (B.C.), Canada. Photo credit: W. S. Boyd.

by Pileated Woodpeckers (*Dryocopus pileatus*; Evans et al. 2002). Barrow's Goldeneye tend to choose cavities roughly 12 m above the ground and in aspen or fir trees within ≈ 100 m of a small, shallow pond (Evans 2003). Their choice of such cavities helps minimize egg predation by black bears and small mammals (Evans et al. 2002). Hatching of all eggs in a clutch occurs synchronously, with the hatched young undergoing a coordinated freefall from their cavity and then being led to an adjacent pond by the hen. The territoriality of Barrow's Goldeneye usually results in each small pond accommodating a single brood, with larger ponds sometimes accommodating multiple, but isolated, broods (Savard 1982, 1984). Brood rearing occurs on ponds shallow enough for the young to dive for invertebrate prey (Evans 2003). While on or around the pond the young are vulnerable to avian and mammalian predators and harsh weather events such as heavy rain or hailstorms.

The key scientific queries concern the potential loss of riparian areas as a source of cavities due to forestry, the possibility that climate change would alter the productivity (invertebrate biomass) of the ponds for foraging juveniles, and that a changing landscape from forest encroachment would increase predation threats, particularly from avian predators, on juveniles (Evans 2003). Consequently, over the past two decades Barrow's Goldeneye has attracted research attention from both conservation and behavioral scientists. Conservation questions addressed, for example, whether the use of nest boxes would increase clutch survivorship by providing greater protection from predation, resulting in more and larger clutches (Savard 1988, Evans et al. 2002). Similarly, behavioral ecologists ques-

tioned the evolutionary advantage of the high prevalence of conspecific clutch parasitism (Eadie and Fryxell 1992, Eadie and Lyon 1998, Eadie et al. 1998, Lyon and Eadie 2000) and brood amalgamation (Savard 1987) in Barrow's Goldeneye and related species.

Much of the scientific argument concerning the evolutionary consequences of these behaviors has relied on theoretical models (Johnstone 2000, Broom and Ruxton 2002a, b, Öst et al. 2003) and genetic sampling and interpretation (Andersson and Åhlund 2000, Lyon and Eadie 2000). Given this backdrop, we applied our clutch and brood survivorship model to observations of known clutches and broods made in 1995, and 1997 to 2000, at Riske Creek to empirically address two hypotheses related to Barrow's Goldeneye conservation. Hypothesis I: Is there is a different probability of surviving to fledge for juvenile Barrow's Goldeneye hatched in larger vs. smaller broods? Hypothesis II: Does the foraging quality of a brood-rearing pond (as measured by invertebrate biomass) affect the probability that a juvenile in a brood using that pond will fledge?

SURVIVORSHIP MODEL

Our model was developed on the premise that the survival rate of eggs in a clutch, or juveniles in a brood, can vary with age (a), and in the case of broods (b), in relation to abiotic and biotic covariates. A full description of the model is presented in the Appendix, whereas here we describe the model conceptually and with only sufficient detail and parameter definitions to enable a reader to qualitatively interpret the results we present for Barrow's Goldeneye.

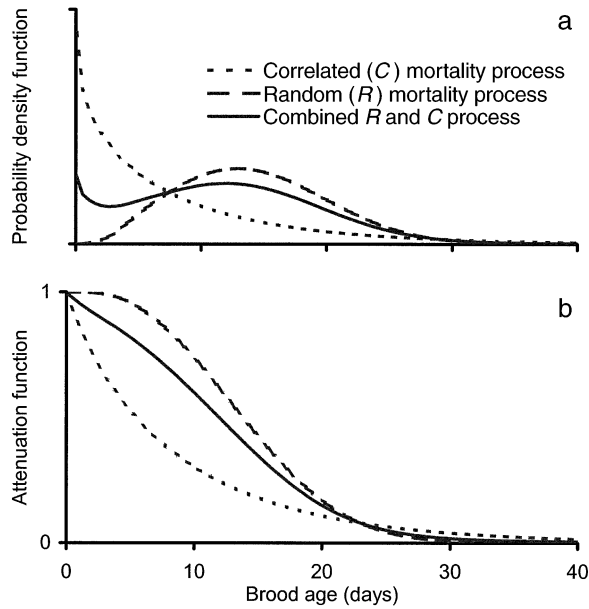


FIG. 1. Example plots of (a) probability density functions (pdf) and (b) their associated survivorship attenuation functions for random (R) and correlated (C) mortality processes and both additively combined (R and C). The functions for R and C portray situations with an initial period when young juveniles experience a high rate of correlated mortality (perhaps catastrophic losses of broods) that diminishes with time as the rate of random mortality increases, then diminishes with age. The parameter values for this example are: $\alpha_{B,R} = 0.001$, $\beta_{B,R} = 2.5$, $\alpha_{B,C} = 0.1$, $\beta_{B,C} = 0.9$, $c_B = 0.7$, and $f_B = 0.05$.

We developed our model using the Weibull probability density function (pdf) as a tractable and flexible model of survivorship probabilities over time (Walpole et al. 1998). In its simplest formulation it represents a constant survival rate with an exponential distribution of survivorship,

$$\omega(a; \alpha, \beta) = \alpha\beta a^{\beta-1}e^{-\alpha a^\beta} \quad (1)$$

($\alpha > 0$; $\beta > 0$) with its attenuation, or survivorship, function ($1 -$ cumulative probability function) $A(a)$ being described by

$$A(a) = e^{-\alpha a^\beta}. \quad (2)$$

When the shape parameter $\beta = 1$, survivorship is constant at the instantaneous rate α . Values for $\beta \neq 1$ introduce age dependence in survivorship.

A key feature of our model is its ability to partition survivorship into random (R) and correlated (C) components. To achieve such a model we chose to construct a new pdf as a contagious mixture of two Weibull distributions representing the random and correlated components of mortality independently for both clutches (or nests, N) and broods (B). The two scenarios of random (R) and correlated (C) mortalities are additive (Fig. 1) for both clutches and broods such that

$$A(a) = (1 - v(a))A_{R,C}(a) + v(a)A_{C,C}(a) \quad (3)$$

where the subscript “dot” can represent exclusively either clutches (N) or broods (B), and $v(a)$ represents the proportion of a clutch or brood vulnerable to a correlated mortality process at age a .

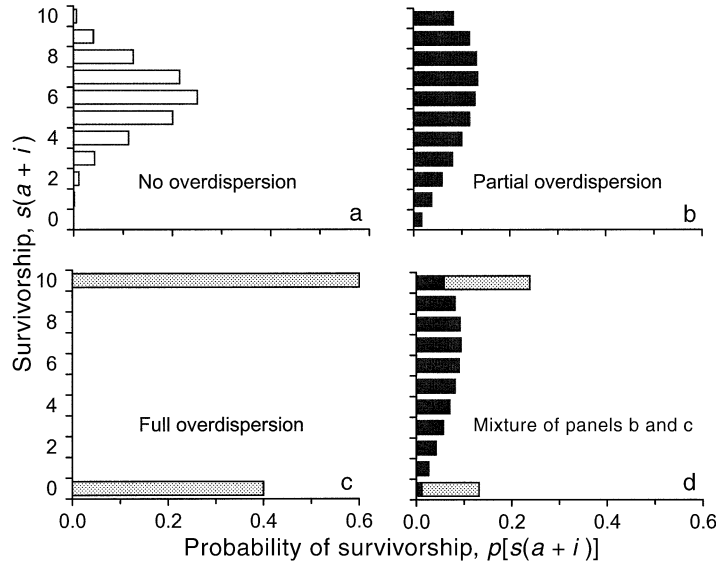
The survivorship function for both clutches and broods (Eq. 3) must be bounded in time. By defining $a = 0$ to correspond to the age that a clutch hatches, increasingly negative ages apply to increasing younger clutches, while positive ages apply to broods. We therefore define a negative number of days (I), corresponding to the age all clutches in the dataset are initiated. Likewise, for broods we define a positive number of days corresponding to the age (D) beyond which the disappearance of a juvenile from a brood might be due to fledging rather than mortality. Consequently, the age range for clutches is $a = I$ to 0, while that for broods is $a = 0$ to D . The proportion of clutches and broods, respectively, vulnerable to a correlated mortality process at age $a = I$ and $a = 0$, respectively, are defined by c_N and c_B , and diminish with age at instantaneous rates f_N and f_B .

One goal of our model was to allow both the random and correlated survivorship profiles for broods to be functions of external factors, our so-called brood covariates. We identified two potential brood covariates directly associated with basic data collection: expected brood size on hatch day ($E_{N,b}[a = 0]$) and the day of the year that hatching occurred, t . We refer to these as intrinsic brood covariates. Additionally, one or several adjunct brood covariates may have also been measured. Our model allows these covariates and their coefficients to operate on the Weibull parameters $\alpha_{B,\cdot}$ and $\beta_{B,\cdot}$ (yielding $\alpha'_{B,\cdot,b}$ and $\beta'_{B,\cdot,b}$) to modify the shape of the survivorship function (Eq. 3), where the subscript “dots” can represent either random (R) or correlated (C) mortality. Note that any covariates operating upon $\beta_{B,\cdot}$ introduce age dependence in survivorship.

A key model assumption is no, or more practically, negligible measurement error. That is, we assume that counts of the number of eggs in a clutch or juveniles in a brood are accurate. Therefore all data records (r , $r = 1$ to \mathfrak{R}) for each clutch or brood must exhibit a steady or declining number of individuals over time. As such, our model error structure presumes that deviations from predicted survivals arise from actual stochastic outcomes. Further, we consider the basic sampling or observational unit to be a clutch or brood followed through time, with their eggs and juveniles, respectively, being considered elements of the sample. Survivorship estimates are therefore inherently weighted by clutch or brood size. We also make the point here that our implementation of the model treats individuals alive on hatch day as juveniles in a brood.

Readers should also recognize that our definition of a clutch or brood is robust in the sense that an analyst is free to create the analyst’s own definition of a clutch or brood. For example, an analyst might choose to define a brood before and after an amalgamation event

FIG. 2. Examples of plausible probability mass distributions of survivorship outcomes, $p[s(a+i)]$, for $n(a) = 10$, $\mu_{s(a+i)} = 0.6$, and $v = 0$. (a) No overdispersion, $\theta_{s(a+i)}^2(a) = 0$, generates a binomial distribution of survivorship outcomes; (b) partial overdispersion, $\theta_{s(a+i)}^2(a) = 0.2$, generates a greater spread of possible survivorship outcomes according to a beta-binomial distribution; while (c) full overdispersion, $\theta_{s(a+i)}^2(a) = 1.0$, generates a beta-binomial distribution with only two possible outcomes, either all $n(a)$ individuals survive or die. Plot (d) portrays an example in which 70% of the mortalities follow a random mortality process (C), while 30% of mortalities ($c = 0.3$; $f = 0$) are correlated (C) and fully overdispersed as per plot (c).



as two separate broods, and perhaps accompany the analysis with a categorical brood covariate that indicates whether or not the brood resulted from an amalgamation. Likewise, an analyst may choose to define a brood that has moved between two ponds, as two separate broods.

To address the deficiency of traditional models to accommodate the nonindependence of mortality events we chose the beta-binomial probability mass function (pmf) to model prediction error. The advantage of the beta-binomial pmf is that its definition includes a parameter, $\theta_{s(a+i)}^2(a)$, that explicitly accommodates overdispersed (i.e., correlated) outcomes when $\theta_{s(a+i)}^2(a) > 0$. Here the subscript dots represent the four survivorship scenarios $N, R; N, C; B, R$; and B, C . If $\theta_{s(a+i)}^2(a) = 0$ there is no overdispersion and the distribution limits to the binomial pmf; thus by our definition $\theta_{s(a+i)}^2(a) = 0$ always. If, in the extreme, $\theta_{s(a+i)}^2(a) = 1$, the beta-binomial distribution is fully overdispersed such that the $n(a)$ individuals in a clutch or brood either all survive or none survive; by our definition a catastrophic outcome at a survival rate of $\mu_{s(a+i)}$ over the time interval i . Note that we have made $\theta_{s(a+i)}^2(a)$ a function of age,

$$\theta_{s(a+i)}^2(a) = \theta_{s(a+i)}^2(0)e^{-v_{s(a+i)}a} \quad (4)$$

to accommodate the probable scenario that the degree of correlated mortality (C) is likely to diminish with age, especially for juveniles in a brood. Our survivorship model predicts a probability, $p[s(a+i)]$, of observing $s(a+i)$ of $n(a)$ individuals surviving a time interval i . For illustration, we draw attention to the graphic examples (Fig. 2) illustrating random and overdispersed survivorship outcomes.

Recognizing that even a determined observer is unlikely to witness many clutches hatching, we realized that some of the robustness of our model would rest with its ability to accept data for clutches and broods

lacking observations of the number of eggs or juveniles alive on hatch day. Our model was therefore constructed to calculate the expected number of eggs hatched ($E_{N,B}[0]$) during the clutch to brood transition ($N|B$) as a probabilistic mixture of $R|R$, $R|C$, $C|R$, and $C|C$ survivorships.

Once the probabilities of observing any outcome $s(a+i)$ have been defined, we can calculate the negative ln-likelihood of each possible outcome for each data record r using

$$\lambda_{F_r[s(a+i)]} = -2\ln[p[s(a+i)]] \quad (5)$$

where $F_r[s(a+i)] = 1$ if the outcome $s(a+i)$ for prediction $\mu_{s(a+i)}$ was observed, else $F_r[s(a+i)] = 0$. We include the factor 2 to make Eq. 5 equivalent to the G statistic for evaluation using likelihood ratio tests (Burnham and Anderson 2002). The likelihood of the model is therefore,

$$L[s(a+i)] = \sum_{r=1}^{\Re} \sum_{s(a+i)=0}^{n(a)} \lambda_{F_r[s(a+i)]} \times F_r[s(a+i)] \quad (6)$$

where \Re is the number of observations of $F_r[s(a+i)] = 1$. The maximum-likelihood parameter estimates and their covariance matrix are obtained when L is minimized (L_{\min}). The quality of model fit (GOF) was diagnosed by parametric bootstraps, which also yielded confidence limits for the derived survival estimates and an a posteriori estimate of overdispersion \hat{c} (White and Burnham 1999).

HYPOTHESES, DATA PREPARATION, UTILE METRICS

Our purpose is to report on two hypotheses concerning survivorship to fledging of Barrow's Goldeneye juveniles, primarily to illustrate our model. However, our results have implications both for Barrow's Goldeneye conservation, and our understanding of the

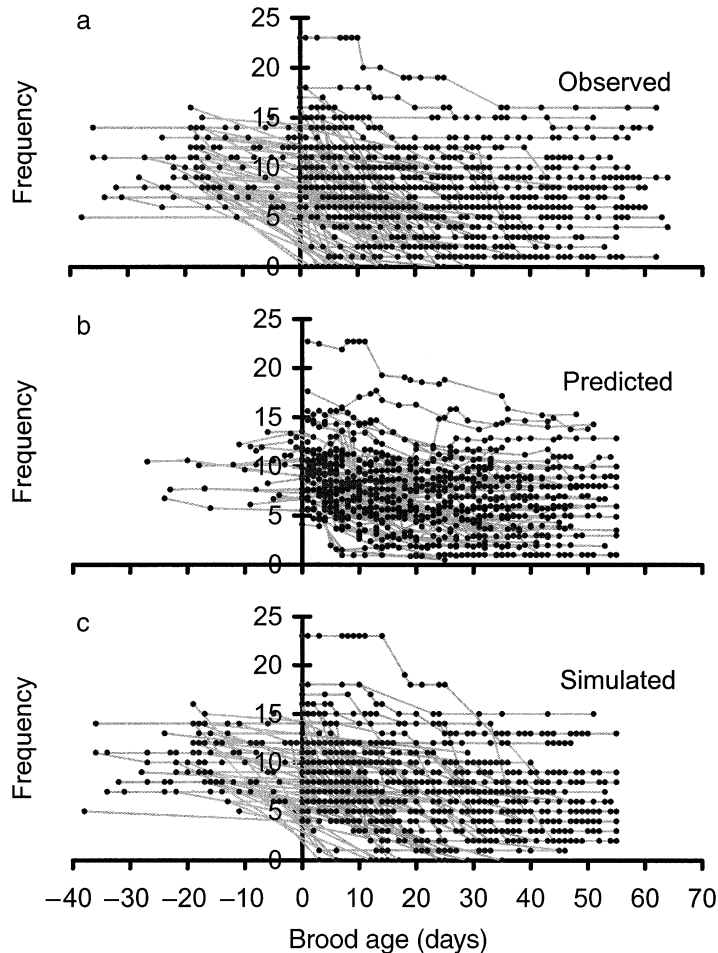


FIG. 3. Typical (a) observed, (b) predicted, and (c) simulated profiles of the observed number of eggs (brood ages $a < 0$) in a clutch and juveniles (brood ages $a \geq 0$) in a brood. Clutches and broods for each tending hen are connected by gray lines. The observed data (a) are those for the years 1995 and 1997–1999. These data were analyzed to investigate Hypothesis I ($N = 1090$). It is evident that many more broods were observed than clutches. Note that the observed data are truncated at a brood age of 56 days corresponding to the analyst's choice of $D = 56$ for age at fledging. The model predictions (b) are those provided by Model 1 of Table 1. Likewise, the simulated data (c) are one realization using the maximum-likelihood estimated parameters of Model 1 of Table 1.

fitness implications of the reproductive behaviors of clutch parasitism and brood amalgamation. Hypothesis I concerns possible differences in the probability of surviving to fledge among juveniles reared in broods of different sizes, as measured or inferred on the day the eggs hatched (hatch day). Hypothesis II concerns possible differences in the probability of surviving to fledge among juveniles reared on ponds with differing productivities, as measured by estimates of invertebrate biomass (Evans 2003). Invertebrate biomass (milligrams per sample) was estimated from benthic core samples and pelagic activity traps collected among 20 ponds in 1995 and 1997 to 1999 a priori qualitatively judged to be of low, medium, and high invertebrate productivity (Evans 2003). An estimated interannual correlation of 93% among ponds supported that this measure had merit as a reliable index of pond productivity. Invertebrate biomass varied by roughly an order of magnitude among the ponds sampled, all of which were observed to support Barrow's Goldeneye broods in at least one of the years sampled.

We had available for analysis a set of observations of the number of eggs in a clutch and juveniles in a brood for individually followed families (Fig. 3a). Off-

spring associated with an adult tending hen, identified by her unique nasal disc pairing, allowed each egg or juvenile observed to be assigned to a specific hen. However, clutches may have been parasitized, so we generally did not know if a family was composed of eggs from more than one hen. Typically broods were observed and counted every 2–5 days, but sometimes more or less frequently. Clutches were observed much less frequently than broods. The calendar date (t) of all observations was recorded and used to calculate clutch and brood ages. If clutches were not observed at, or just before, hatch, as was typically the case, calendar hatch date was usually inferred from the observed stage of juvenile development when broods were first observed on a pond (Gollop and Marshall 1954). Our analyzed dataset included egg counts only for dates on or after the date the maximum number of eggs in a cavity was observed. Our dataset did not include broods that we knew underwent brood amalgamation or for which hatch date, and therefore clutch and brood age, could not be confidently calculated. Further, observations of clutches outside the age range $I \leq a$, $a + i \leq D$ were excluded from our dataset. Within the subset of data that qualified for analysis (Fig. 3a), a few fam-

ilies were first followed as clutches, while most were not followed until they were first seen as broods on a pond. We chose $I = -40$ days and $D = 56$ days for the analyses we present. We also clarify that for Barrow's Goldeneye I refers to the age the tending hen began to incubate her full clutch in order to assure synchronous hatching. Egg laying for any hen will have taken place over several days. Fewer data records qualified for investigating Hypothesis II ($\mathfrak{N} = 659$) than for Hypothesis I ($\mathfrak{N} = 1090$) since Hypothesis I could use data from families on ponds for which there was no estimate of pond productivity.

For an accepted model fit, we consider three metrics to be of special interest to many analysts, and appear in our results. One is the probability, at age a , that a juvenile will fledge at age D . For hatch day (i.e., $a = 0$), $A_{B,R}(0)$ and $A_{B,C}(0)$ represent survivorships to age a with their corresponding vulnerabilities to random [$1 - v(0)$] or correlated mortalities [$v(0)$],

$$p[\text{fledge}(0, D)] = \frac{[1 - v(0)]A_{B,R}(0)\mu_{B,R}(D) + v(0)A_{B,C}(0)\mu_{B,C}(D)}{A_B(0)} \quad (7)$$

This metric has particular utility for expressing the relative effect of model covariates on a juvenile's propensity to fledge.

A second metric is expected brood size on hatch day, $E_{N,b}[0]$. This metric provides an estimate of the number of juveniles alive in brood b on hatch day when there is at least one observation of the number of eggs alive prior to hatch. In this study we use $E_{N,b}[0]$ as an intrinsic covariate to investigate Hypothesis I. It has particular value in that it mitigates an observer's inability to count the number of juveniles in a nest on hatch day. It is worth noting that for some interpretations $E_{N,b}[0]$ might be considered a better metric than an actual count of juveniles on hatch day if the analyst's purpose is to infer a hen's intended initial brood size; i.e., analyses drawing fitness interpretations; however, the two metrics will tend to be very highly correlated.

Lastly, we present a measure of dispersion more intuitive than $\theta_{\cdot,\cdot}^2$, specifically

$$EIU = 1 + \theta_{\cdot,\cdot}^2(a) \times (n(a) - 1). \quad (8)$$

This metric calculates the "effective independent unit" (EIU), a statistical measure of the number of individual eggs or juveniles that tend to associate as a single mortality event such that the hypothetical outcomes of such mortality events would follow a binomial distribution. An EIU value of, say 2.3, for juveniles might be interpreted to mean that a predator tends to take, on average, 2.3 juveniles per mortality event. This metric has proven informative in other sampling applications where individual birds within a flock do not associate independently (Iverson et al. 2004). Conversely, when $\theta_{\cdot,\cdot}^2 > 0$ the "ef-

fective independent sample size" (EISS) for a clutch or brood observation is reduced from $n(a)$ to

$$EISS = \frac{n(a)}{1 + \theta_{\cdot,\cdot}^2(a) \times [n(a) - 1]}. \quad (9)$$

When interpreting our results we entertained both the information-theoretic and hypothesis-testing paradigms for adjudicating our two key hypotheses and their alternatives (Anderson et al. 2000, Burnham and Anderson 2002). We first used AIC_C to assess the weight of evidence in our data for each hypothesis (model ranking). We then used likelihood ratio tests to execute probabilistic comparisons among paired competing models differing only in a single main effect.

RESULTS

Competitive model trials to investigate Hypotheses I and II using our data from all ponds produced a distinct ranking of models (Tables 1 and 2). The highest ranked models for both hypotheses narrowly passed parametrically bootstrapped GOF diagnostics of model adequacy ($p \pm 1 \text{ SE} = 0.03 \pm 0.02$ for Hypothesis I; $p \pm 1 \text{ SE} = 0.06 \pm 0.02$ for Hypothesis II). More satisfying values for p could have been obtained had we chosen to remove a few outlier data points that contributed disproportionately to model deviance (L_{MIN}). However, we had confidence that our relatively large number of data records (\mathfrak{N}) effectively neutralized any bias from these outliers. Our choice not to censor outliers resulted also in bootstrapped estimates of $\hat{c} \pm 1 \text{ SE}$ slightly greater than unity, at 1.08 ± 0.04 and 1.06 ± 0.05 for the best ranked models (Model 1) for Hypotheses I and II, respectively. The quality of the fit for Model 1 concerning Hypothesis I can be visualized in the survivorship predictions (Fig. 3b) and by comparing the observed data (Fig. 3a) with a simulated realization (Fig. 3c) generated using the maximum-likelihood parameter estimates for Model 1.

With respect to Hypothesis I, the second highest ranked model, Model 2 (ignoring Model 1 with function $\theta_{B,C}^2(a)$ for the moment), strongly supports a parametrically and statistically strong relationship between the probability, on hatch day, that a juvenile will fledge at age $D = 56$ days, $p[\text{fledge}(0, D)]$, and expected brood size on hatch day, $E_{N,b}[0]$. Model 2 is an ≈ 500 times more probable fit to our data than its direct competitor, Model 6 (Pair A in Table 1, Fig. 4), lacking $E_{N,b}[0]$ as a covariate. A likelihood ratio test favored Model 2 ($p[\text{Model 2} \equiv \text{Model 6}] = 0.0004$, $\Delta L_{\text{MIN}} = 20.53$, $df = 4$). Model 2 also identifies strong year-effects, with the effect of $E_{N,b}[0]$ varying among years to the extent that little effect is evident in 1997, while in other years there is a distinct tendency for $p[\text{fledge}(0, D)]$ to increase as $E_{N,b}[0]$ increases. Model 2, with year-effects, is $\approx 10^4$ times a more probable fit to our data than its competitor, Model 7, that lacks year-effects (Pair B in Table 1). A likelihood ratio test sig-

TABLE 1. Models ranked by increasing AIC_c , and associated statistics for Hypothesis I: Are there differences in the probability of surviving to fledge among juveniles reared in broods of different sizes as measured or inferred on their hatch day?

Model	Pair	Model description	ΔAIC_c	K	w	L_{MIN}
1	C	NULL + YEAR _R + E _{N,b} [0] _{RC} with $\theta_{B,C}^2(a)$	0.00	14	0.99	1522.67
2	A, B, C	NULL + YEAR _R + E _{N,b} [0] _{RC}	14.40	13	0.01	1539.09
3		NULL + YEAR _R + AGE _R + E _{N,b} [0] _{RC}	16.26	14	0.00	1538.93
4		NULL + YEAR _R with $\theta_{B,C}^2(a)$	21.02	10	0.00	1551.72
5		NULL + YEAR _R + AGE _R	24.10	10	0.00	1554.80
6	A	NULL + YEAR _R	26.91	9	0.00	1559.62
7	B	NULL + E _{N,b} [0] _{RC}	32.64	10	0.00	1563.34
8		NULL + AGE _R + E _{N,b} [0] _{RC}	34.29	11	0.00	1562.99
9		NULL + AGE _R	36.86	7	0.00	1573.57
10		NULL (E _C , J _{RC})	42.30	6	0.00	1581.02

Notes: The baseline NULL (E_C, J_{RC}) model identifies a constant mortality rate with a correlated mortality (C) process for both eggs (E) and juveniles (J) and, in the case of juveniles, also statistically identifies a random mortality process (R). The following symbols represent those covariates challenged with explaining our clutch and brood data: YEAR, among-year differences in juvenile survivorship; AGE, age-dependent differences in juvenile survivorship; E_{N,b}[0], juvenile survivorship differences with expected brood size on hatch day; PP, juvenile survivorship differences among ponds with different invertebrate productivities. The symbol $\theta_{B,C}^2(a)$ indicates that the degree of correlated mortality among juveniles can diminish with brood age. "Pair" identifies, using shared characters, paired rank comparisons referred to in the text; blank cells in this column indicate that the model was not paired with another model; K represents the number of estimated parameters; w represents AIC_c weights; and L_{MIN} is the model deviance. Models are described by their ln-linear additive covariates that operate on the Weibull parameters α and β .

Hypothesis I model fit summaries and sampling statistics: number of clutches plus broods, 117; number of eggs, 990; number of juveniles, 7707; number of clutch predictions made and evaluated, 45; number of brood predictions made and evaluated, 894. The bootstrapped estimates of $\hat{c} \pm 1$ SE for the null and best models are 1.07 ± 0.04 and 1.08 ± 0.04 , respectively, indicating minimal overdispersion. The best model ($AIC_c = 1550.73$) passed the parametric bootstrap diagnostic for GOF.

nificantly favors Model 2 ($p[\text{Model 2} = \text{Model 7}] < 0.0001$, $\Delta L_{MIN} = 24.25$, $df = 3$).

Competitive model trials to investigate Hypothesis II using our data from those fewer ponds for which we had covariate data on pond productivity also produced a distinct ranking of models (Table 2). As for the original dataset used to investigate Hypothesis I, Model 3 investigating Hypothesis II also strongly supported a positive relationship between $p[\text{fledge}(0, D)]$ and E_{N,b}[0], again with year-effects (Fig. 5a), though the statistical strength of the relationship is weaker due to the smaller dataset. Indeed, Model 3 excluded pond productivity as a covariate, indicating insufficient statistical support for the hypothesis that, among the ponds sampled, $p[\text{fledge}(0, D)]$ is influenced by pond productivity. The direct competitor of Model 3, Model

5 (Pair D in Table 2), was approximately five times poorer at explaining our data than was Model 3. Model 7, which included pond productivity, but not E_{N,b}[0], as a covariate, ranked poorly as a putative model to explain our data, though there is a slight tendency for the $p[\text{fledge}(0, D)]$ to increase with pond productivity in years other than 1997 (Fig. 5b).

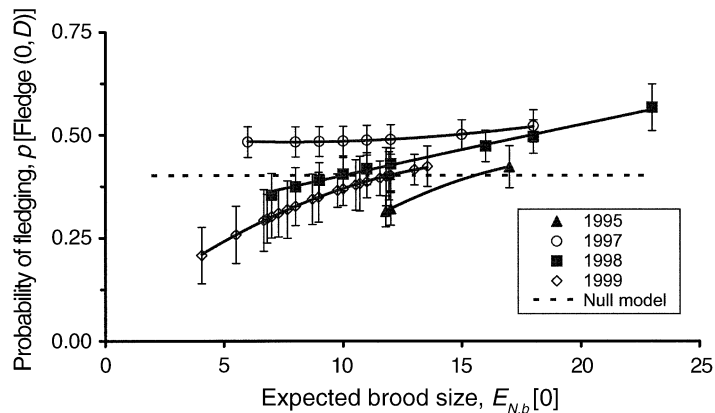
The best ranked models investigating Hypotheses I and II include the function $\theta_{B,C}^2(a)$ (Eq. 4) with $v_B > 0$, indicating that the degree of correlated mortality among juveniles (and the EIU, Fig. 6a) diminished with brood age as, incidentally, did their vulnerability to correlated mortality (Fig. 6b). The models that included $v_B > 0$ were ≈ 1300 and 14 times more probable than their competitors with $v_B = 0$, for Hypotheses I (Pair C in Table 1) and II (Pair E in Table 2), respectively. Like-

TABLE 2. Models ranked by increasing AIC_c , and associated statistics for Hypothesis II: Are there differences in the probability of surviving to fledge among juveniles reared on ponds with different invertebrate productivities as measured by estimates of invertebrate biomass on selected ponds?

Model	Pair	Model description	ΔAIC_c	K	w	L_{MIN}
1	E	NULL + YEAR _R + E _{N,b} [0] _{RC} with $\theta_{B,C}^2(a)$	0.00	14	0.77	849.05
2		NULL + YEAR _R + PP _R + E _{N,b} [0] _{RC} with $\theta_{B,C}^2(a)$	3.50	16	0.13	848.53
3	D, E	NULL + YEAR _R + E _{N,b} [0] _{RC}	5.29	13	0.06	856.35
4		NULL + YEAR _R + AGE _R + E _{N,b} [0] _{RC}	7.13	14	0.02	856.18
5	D	NULL + YEAR _R + PP _R + E _{N,b} [0] _{RC}	8.52	15	0.01	855.56
6		NULL + YEAR _R + PP _R	20.87	11	0.00	875.95
7		NULL + YEAR _R + PP _R with $\theta_{B,C}^2(a)$	21.40	12	0.00	874.47
8		NULL (E _C , J _{RC})	24.47	6	0.00	889.59

Notes: Definitions are as in Table 1. Hypothesis II model fit summaries and sampling statistics: number of clutches plus broods, 61; number of eggs, 574; number of juveniles, 5408; number of clutch predictions made and evaluated, 39; number of brood predictions made and evaluated, 536. The bootstrapped estimates of $\hat{c} \pm 1$ SE for the null and best models are 1.05 ± 0.05 and 1.06 ± 0.05 , respectively, indicating minimal overdispersion. The best model ($AIC_c = 877.14$) passed the parametric bootstrap diagnostic for GOF.

FIG. 4. The probability (with 95% confidence intervals), on hatch day, that a juvenile Barrow's Goldeneye will fledge at $D = 56$ days, $p[\text{fledge}(0, D)]$, as a function of expected brood size on hatch day, $E_{N,b}[0]$. The values portrayed are those reported by the highest ranked model (Model 1) of those used to investigate Hypothesis I (Table 1). Year effects are clearly evident. There is no evidence that $p[\text{fledge}(0, D)]$ is influenced by $E_{N,b}[0]$ in 1997, whereas in other years there is a clear tendency for juveniles hatched into larger broods to have an increased $p[\text{fledge}(0, D)]$.



likelihood ratio tests affirmed the statistical contribution of $v_B > 0$ to model fit (Hypothesis I: $p[v_B = 0] < 0.0001$, $\Delta L_{\text{MIN}} = 16.41$, $\text{df} = 1$; Hypothesis II: $p[v_B = 0] = 0.007$, $\Delta L_{\text{MIN}} = 7.30$, $\text{df} = 1$). This was anticipated since juveniles would be expected to behave more independently of their siblings as they aged, thereby lessening group vulnerability to predation or weather threats. The inclusion of $\theta_{B,C}^2(a)$ in all competitive model pairs significantly improved the fit of these models but did not change the relative ranking of models based on the covariates of age, year, $E_{N,b}[0]$, or pond productivity.

For neither Hypotheses I nor II was there statistical evidence of an age-effect on juvenile survivorship independent of any putative covariates, i.e., no support for either $\beta_{B,R} \neq 1$ or $\beta_{B,C} \neq 1$. Nevertheless, our highest ranked models for both hypotheses (Model 1) included intrinsic brood-effect parameters operating on $\beta_{B,R}$ and $\beta_{B,C}$, respectively, such that $\beta'_{B,R,b} \neq 1$ and $\beta'_{B,R,b} \neq 1$. Thus an effect of $E_{N,b}[0]$ was to change daily survivorship with age among broods. The tendency was for young broods with higher values for $E_{N,b}[0]$ to experience higher survivorships early in life (Fig. 7), which eventually resulted in a higher overall $p[\text{fledge}(0, D)]$ for those broods.

Finally, Model 1 concerning Hypothesis II afforded us an opportunity to look for a relationship between $E_{N,b}[0]$ and pond productivity for those clutches and broods for which we had adjunct data on pond productivity. However, we found no evidence that the $E_{N,b}[0]$ for Barrow's Goldeneye hens using particular ponds may be determined in part by the pond's productivity. Such evidence would support an hypothesis that hens obtain some nutrition for egg production exogenously once having arrived on the breeding grounds.

DISCUSSION

Our clutch and brood survivorship model successfully evaluated two key hypotheses concerning the breeding success of Barrow's Goldeneye in British Columbia. We confidently concluded that the probability

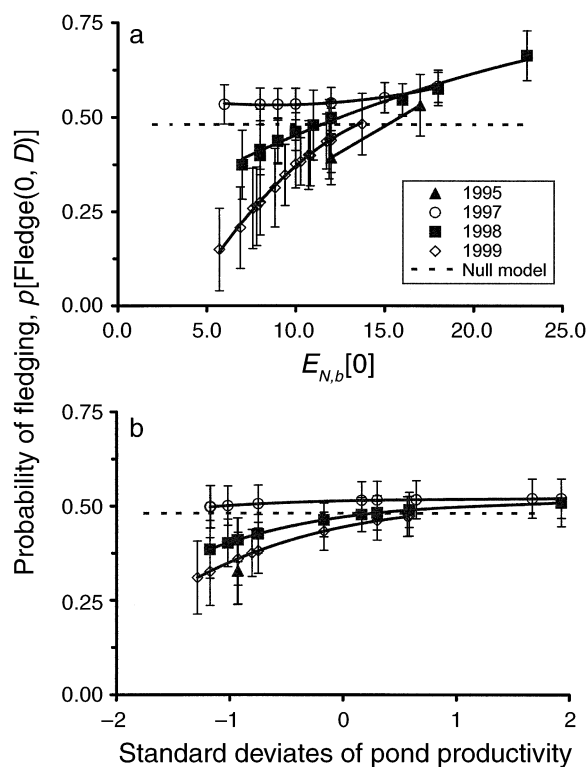


FIG. 5. (a) The probability (with 95% confidence intervals), on hatch day, that a juvenile Barrow's Goldeneye will fledge at $D = 56$ days, $p[\text{fledge}(0, D)]$, as a function of expected brood size on hatch day, $E_{N,b}[0]$. The values portrayed are those reported by the highest ranked model (Model 2) of those models used to investigate Hypothesis II that include pond productivity as a covariate (Table 2). This result is similar to that portrayed in Fig. 4, which is based on a larger sample size. (b) The $p[\text{fledge}(0, D)]$ (with 95% confidence intervals) as a function of standard deviates of pond productivity measured as mean invertebrate biomass per pond-year (milligrams per sample). The values portrayed are those reported by Model 7 of those used to investigate Hypothesis II. The results indicate both parametrically and statistically weak evidence for the $p[\text{fledge}(0, D)]$ to be higher on the more productive ponds. The inadequacy of this relationship is emphasized by the very low rank of this model when compared to models including $E_{N,b}[0]$ as a covariate.

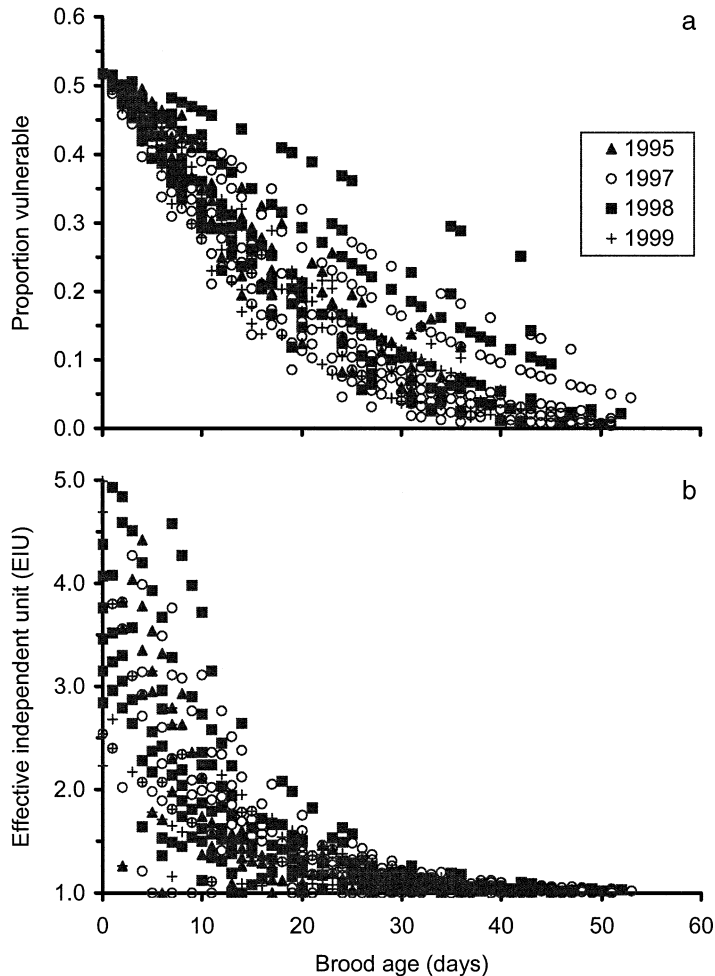


FIG. 6. (a) The predicted proportion of juveniles alive at the plotted brood age that are vulnerable to a correlated mortality process. This proportion will diminish with brood age when $f_b \geq 0$, as in this result for Model 1, challenging Hypothesis I. (b) The effective independent unit (EIU) vs. brood age. EIU will diminish with $n_b(a)$ as well as with brood age when $v_b \geq 0$ as in this result for Model 1, challenging Hypothesis I. The scatter within and among years for both panels (a) and (b) arises from differences among broods in their expected brood size on hatch day, $E_{N,b}[0]$ and, for panel (b), also from differences in the number of juveniles alive at brood age a , $n_b(a)$.

that a juvenile would survive to fledge was positively related to brood size on hatch day in some years, but found little support for the argument that pond productivity affected juvenile survival. More generally, we think this demonstration of our model introduces an-

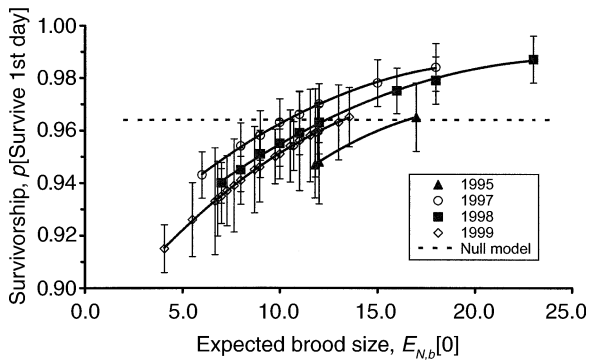


FIG. 7. Daily survivorship (with 95% confidence intervals) of juveniles during the first day after hatch, and according to year, vs. expected brood size on hatch day, $E_{N,b}[0]$, for Model 1, challenging Hypothesis I.

other robust analytical tool for investigating environmental effects (e.g., pesticides, predation, habitat alterations, weather, etc.) on the reproductive success of birds, or for providing high-quality parameter estimates and a measure of their uncertainty for inclusion in population viability (PVA) or similar analyses. With respect to similar analyses, we have used our model successfully on a previously published dataset of our colleagues (Gill et al. 2000, 2003) to challenge the null hypothesis that pesticides do not affect the reproductive success of American Robins (*Turdus migratorius*) nesting in fruit orchards of the Okanagan Valley, British Columbia. As we expected, we found no detectable effect of pesticides on reproductive success in accordance with the authors' original interpretations using the Mayfield method (Mayfield 1961, 1975) and Program MARK's nest survival model (White and Burnham 1999, Dinsmore et al. 2002). The reason for our expectation arises from our recognition that overdispersion in a dataset acts to reduce the effective independent sample size (EISS, Eq. 9) and thus appropriately decreases the power to falsely detect a significant effect. That is, our model reduces the probability of

making a Type II error (Walpole et al. 1998) when survivorship outcomes are not independent. A corollary to this benefit of our model is that analyses that do not explicitly account for overdispersion run a higher risk of falsely detecting statistical correlations, which can ultimately lead to fictitious interpretations of cause and effect.

Readers may have perceived that our model is not limited in application to demographic analyses of bird reproduction, but can be applied to any species where an interpretation of its reproductive life history is analogous to that of birds, e.g., egg-laying reptiles. Indeed, when there is no need to model the clutch-to-brood transition, our model can be applied to any species where an integer number of offspring in a brood can be accurately counted over time, there is a desire to explicitly account for overdispersion, and the model's caveats and assumptions stated in the *Introduction* are acceptable to the analyst.

We illustrated our model using data on Barrow's Goldeneye clutch and brood survivorship to challenge two hypotheses. (Incidentally, in preliminary analyses we found no support for the hypothesis that juvenile survivorship was influenced by hatch day of the year, *t*). Our modeling results clearly supported that a juvenile's probability of surviving to fledge at 56 days increased with its expected brood size on hatch day in some years. This finding supports the life history argument that conspecific clutch parasitism has a fitness advantage for the juveniles (Eadie and Lyon 1998, Eadie et al. 1998, Lyon and Eadie 2000) and perhaps also for the recipient hen (Eadie and Lumsden 1985, Eadie et al. 1988). The juveniles of both the tending hen, and the hen that deposited her eggs in that tending hen's nest, are conferred a survivorship advantage by having their offspring as members of larger broods. However, this interpretation must be tempered by the realization that the tending hen is probably not indifferent to the parentage of the brood she is tending. There is evidence in Common Eiders (*Somateria mollissima*) that a tending hen, or her ducklings, may act to preferentially increase their fitness over that of the other ducklings in amalgamated broods (Öst and Bäck 2003), a so-called "selfish herd" behavior (Hamilton 1971, Eadie et al. 1988). We point out that we did not have information on which, if any, of the broods in our analysis were formed through clutch parasitism, but this seems certain to be true for the largest of broods (i.e., those with brood sizes on hatch day of 20–25 juveniles [Evans et al. 2002; J.-P. Savard, *personal communication*]). Likewise, we did not follow the survivorship of broods that were observed to increase in size by brood amalgamation. However, our interpretations of a higher probability of surviving to fledge in larger broods endorses the fitness value of brood amalgamation (Savard 1987).

A conservation interpretation of increased juvenile survival in larger broods is that increasing the size of

broods in a region, such as the Riske Creek region of our study, appears to be a conservation option if survival to fledge is considered to limit population growth. Thus our results add another question to conservation planning. That is, what is the trade-off between providing nest boxes to increase the number of Barrow's Goldeneye nesting opportunities in underutilized ponds, vs. increasing the survivorship of offspring in currently used ponds? The answer is not evident with our current knowledge. However, Barrow's Goldeneye have invested in the life history fitness option of relinquishing offspring to the care of another, perhaps more established or closely related (Andersson and Åhlund 2000, Lyon and Eadie 2000) hen. This suggests that this option might be preferable to a hen raising her own offspring in a more risky habitat, perhaps despite nesting opportunities provided by artificial nest boxes. Though nest boxes have proven successful, large-mammal (e.g., bears) and small-mammal (e.g., squirrels) predation can defeat their efficacy (Evans et al. 2002), perhaps more so in less preferred habitat. However, our study supplements the findings of Evans et al. (2002), which demonstrate a significantly increased clutch size for nest boxes over natural cavities. Notwithstanding unconsidered factors, our results imply that such increases in clutch size can disproportionately increase the expected number of juveniles fledged.

Had our data supported a positive relationship between pond productivity and the probability of juveniles surviving to fledge, we would have been able to provide guidance as to which ponds would have the highest priority for nest boxes. Unfortunately, we found no convincing evidence of such a relationship, possibly because there was insufficient contrast in pond productivity, with no pond having a productivity below a critical threshold affecting juvenile survival. Supporting this interpretation of adequate productivity, we also found no evidence of a relationship between expected brood size on hatch day and pond productivity, given that it has recently been established that Barrow's Goldeneye hens from the Riske Creek region acquire the vast majority of their nutrition for egg development locally (Hobson et al. 2004). Our failure to detect such a relationship must be interpreted with the understanding that only ponds that supported at least one brood were included for consideration in this analysis. Clearly ponds depauperate of prey biomass would be poor choices for brood rearing. More positively, there appears to be a considerable range of pond productivities that support successful rearing of Barrow's Goldeneye broods.

We conclude by emphasizing the key contributions of our model for advancing our understanding of the dynamics of reproduction in birds and perhaps other egg-laying species. Principally, we provide a method and model application for measuring and statistically evaluating survivorship during the critical life history

phase of egg-laying to fledging. We particularly want to emphasize two elements of our modeling approach. First, we demonstrate the utility of our model for statistically discriminating between random and correlated mortality events. We think this is a key advance that reinforces the need for demographic models, including population viability models, to strive for realism concerning survivorship dynamics. Second, our emphasis on overdispersion (correlated mortality) reinforces that mortality events are unlikely to be random events, particularly in young broods, and indeed may be fully correlated, i.e., catastrophic. We implore investigators to recognize this potential feature of brood survivorship when they draw statistical inferences from their similar data. To that end we have also introduced the concept of the effective independent sample size (EISS, Eq. 9; see *Hypotheses, data preparation, utile metrics*), which we trust will motivate readers to take heed of the potential for nonindependence of individual mortalities.

Finally, despite the benefits of our statistical modeling approach for the hypotheses challenged here, there potentially remain with our model the same subtle suite of biases that can also plague studies relying on the more traditional Mayfield (Mayfield 1961, 1975) and Kaplan-Meier (Kaplan and Meier 1958), or the more contemporary Program MARK (White and Burnham 1999) methodologies. Since we can only draw statistical interpretations from the data we collected, clutches or broods that failed before they were witnessed by an observer introduce interpretive biases to which a researcher must be astute. We consider such biases in our particular study to be minimal because of the dutiful nature of data collection and the easily observed brood rearing by Barrow's Goldeneye hens. Our most overt bias is our compulsory selection only of ponds supporting broods for challenging Hypothesis II. As with all modeling interpretations, our ultimate conclusions are conditional upon the constraints that determined what data were collected and the circumstances under which they were collected.

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APPENDIX

A detailed mathematical description of the clutch and brood survivorship model associated with the study is available in ESA's Electronic Data Archive: *Ecological Archives* A015-008-A1.