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A statistical model discriminating random and correlated mortality from laying to

fledging: Barrow's Goldeneye as an example

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4   Quantitative conservation methodologies such as Population Viability Analysis (PVA) require

5   reliable measurements of life history parameters such as breeding success. The utility of such

6   metrics for egg-laying species is complicated by our knowledge that the mortality of eggs in a

7   clutch and juveniles in a brood can occur both randomly and independently over time, or

8   catastrophically, such as in the sudden loss of a clutch or brood. Not knowing the nature of

9   breeding mortality events caused by either or both of abiotic (e.g., weather, pesticides) and biotic

10 (e.g., predation, habitat alteration) circumstances limits our ability to confidently assess a

11 population's demography and sustainability, or test competing hypotheses. Using the seaduck

12 Barrow's Goldeneye as an example, we describe a multinomial likelihood model that estimates

13 egg and juvenile survival rates continuously from laying to fledging based on periodic

14 observations of individual clutches and broods. Adjunct data, such as environmental or

15 predation threat measurements, can be included as covariate series for evaluating their influence

16 on the predicted survival rates of juveniles in a brood. In our example we conclude that expected

17 brood size on hatch day is strongly positively correlated with the probability a juvenile Barrow's

18 Goldeneye will survive to fledge. We also discuss how knowledge of the effect of an

19 environmental variable on breeding success interpreted from our model can guide conservation

20 strategies that manipulate that variable. Our model has a distinctive ability to statistically

21 characterize mortality between the extremes of random and catastrophic mortality; and can

22 determine if unwitnessed mortalities occurred independently or were correlated (i.e.,

23 overdispersed, where catastrophe is extreme overdispersion). Overdispersion is estimated as a

1   parameter of the beta-binomial probability distribution of survivals, and thus differs from its

2   treatment in Program MARK where overdispersion is an *a posteriori* diagnostic referred to as $\hat{C}$.

3

4   Key words: beta-binomial, breeding success, brood, brood amalgamation, catastrophe, clutch,

5   clutch parasitism, Mayfield, mortality, overdispersion, Program MARK, survival

1   **INTRODUCTION**

2   One of the key methodologies for assessing a population's sustainability over time is

3   population viability analysis (PVA, Beissinger and McCullough 2002, Morris and Doak 2002).

4   Effective use of analyses such as PVA require that an analyst has confidence in the life history

5   parameters that enter such models. Uncertainty in the mean value of a rate parameter such as

6   survival is generally expressed in confidence limits. However, such expressions of uncertainty

7   often tacitly assume that survival estimates arise from a simple binomial process where

8   individuals independently either live or die, and whose rate may or may not change over time.

9   The three most well-known statistical tools for estimating survival rates for bird clutches and

10   broods are the Kaplan-Meier product-moment survival estimator (Kaplan and Meier 1958), the

11   Mayfield method (Mayfield 1961, 1975), and Program MARK (White and Burnham 1999,

12   http://www.cnr.colostate.edu/~gwhite/mark/mark.htm). The Mayfield method for nest success

13   has found wide use in bird demographics over the last four decades, and some authors have

14   modified or refined the Mayfield method to adapt it to their particular data (Johnson 1979,

15   Johnson and Shaffer 1990, Grand and Flint 1997, Dinsmore et al. 2002). The Kaplan-Meier

16   product-moment survival estimator has found broad generic applicability in survival analysis and

17   hypothesis testing in a variety of fields from medicine to demography. However, like the

18   Mayfield method, it assumes that mortality events, i.e. the death of individuals, are random and

19   follow a binomial probability distribution.

20   A well known contemporary analytical tool for population demographers is Program

21   MARK (White and Burnham 1999). Program MARK offers a suite of options for survival

22   estimation and modeling using observational or capture-mark-recapture (CMR) data that includes

23   a 'Nest Survival' module that has evolved from the Mayfield method. The principal contribution

1   of Program MARK is its capacity for robust and realistic, though potentially highly

2   parameterized, survival models, and its ability to empirically deal with overdispersion; i.e., the

3   tendency for individual mortality events to be correlated. Program MARK exploits the

4   contemporary availability of powerful computers to undertake data analyses that were impractical

5   in the recent past. Perhaps more importantly, it has implemented contemporary theory for model

6   ranking based on the information-theoretic approach to model selection and interpretation

7   (Burnham and Anderson 2002). Thus it has the ability to estimate survival rates and their

8   uncertainty for direct use in demographic population models or for hypotheses testing among

9   competing models.

10   Despite the robustness of analytical tools such as Program MARK, there remain many

11   circumstances where specific hypotheses or particular data structures are not well suited to the

12   suite of statistical options available in the literature. One key deficiency concerns the breeding

13   success of egg-laying species, notably birds. A reliable assessment of the viability of a defined

14   bird population requires an understanding of the survival dynamics of offspring from laying,

15   through hatching, to fledging. In demographic and statistical terms, this understanding includes

16   estimation of survival rates, their uncertainty, and distributional characteristics. It has also been

17   recognized by demographers that a survival rate is not a generic metric, but integrates an

18   individual's success at avoiding mortalities due to random biotic (e.g., predation) and abiotic

19   (e.g., weather) events (Morris and Doak 2002). Likewise, such predation or weather events are

20   not likely to affect all eggs in a clutch, or all juveniles in a brood, independently. For example, a

21   predator may attack more than one juvenile in brood of ducklings, or a violent weather event may

22   destroy an entire brood. Overall survivorship of eggs and juveniles will represent an individual's

23   success at enduring all of these threats.

1   The model we present here addresses two limitations of the Mayfield, Kaplan-Meier and

2 Program MARK methodologies. None of the above models deals explicitly with overdispersion

3 during the parameter estimation phase of model fitting (though Program MARK deals with

4 overdispersion as an *a posteriori* correction). Likewise, none accommodates the realism that an

5 individual's survival likely results from enduring of a mixture of random (independent) and

6 correlated (overdispersed) mortality processes. A key feature of our model is that it explicitly

7 incorporates both of these processes into survival estimation and has the ability to partition these

8 two separable mortality profiles. Specifically, our model addresses two components of breeding

9 success as expressed by offspring survivorship from laying to fledging. First, survivorship is

10 statistically partitioned into random and correlated mortality profiles. Thus the assumption that

11 mortality events be statistically independent, i.e., binomially distributed, is relaxed. The

12 overdispersed partition may range from partial to full (catastrophic). This non-independence of

13 mortality events is accommodated by use of the beta-binomial probability distribution for model

14 prediction error (Mood et al. 1985, McCullagh and Nelder 1989). Whereas the first two

15 moments (mean and variance) of the binomial distribution are defined by n (the number of

16 individuals at risk of mortality over a specific time period) and the survival rate (μ); the beta-

17 binomial distribution is further defined by a variance inflation parameter (θ^2), that explicitly

18 measures overdispersion. Second, survivorship estimates can be measured from laying through

19 hatching, then from hatching to fledging without the need to observe hatching. Our model also

20 incorporates the information-theoretic features of model ranking (Burnham and Anderson 2002)

21 that would be familiar to users of Program MARK and are key to model selection and hypothesis

22 testing.

1   Researchers can judge the utility of the clutch and brood survivorship model we describe

2   here for their scientific inquiries by addressing the following features of their hypotheses and

3   data. If…

4   (a) your purpose is (i) to estimate clutch and/or brood survival rates, their uncertainty and

5   distributional (random or correlated) characteristics for use in a demographic or simulation

6   model, or (ii) to rank models or test hypotheses concerning the effect of covariates on the

7   survival rate of juveniles in a brood (i.e., test the effects of predators, weather, pesticides, etc.),

8   and

9   (b) you have data on steady or declining clutch and/or brood sizes periodically over time, clutch

10   and/or brood age, and optionally a covariate series (e.g., weather, or a stage or condition

11   variable), and

12   (c) you are comfortable with assuming almost synchronous hatching of all eggs in a clutch,

13   specifying a laying age and/or a fledging age, assuming negligible measurement error, and

14   assigning all eggs or juveniles observed to a family, then

15   you can estimate clutch and/or brood survival rates and their uncertainty, have survival rates vary

16   with age or time, relate survival to a covariate data series, and partition mortality into its random

17   and correlated components.

18   *Fig. 1 near here*

19   Our model was motivated in part by demographic questions concerning the breeding

20   success of the seaduck Barrow's Goldeneye in the central interior (Chilcotin-Cariboo) region of

21   British Columbia, Canada. From a conservation perspective, the western population of Barrow's

22   Goldeneye is judged secure, with breeding occurring throughout British Columbia and the Yukon

1   Territory, but the eastern Canadian population is federally listed as a species of 'Special Concern'

2   by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC;

3   http://www.cosewic.gc.ca). COSEWIC is the scientific body which adjudicates the status of

4   species listed or proposed as candidates for protection under Canada's Species-at-Risk Act. Our

5   particular interest in Barrow's Goldeneye in this region stems from the unique grassland and

6   fragmented forest mosaic habitat near Riske Creek, British Columbia. This habitat is rare and

7   unique in British Columbia and is geographically isolated from similar habitat to the east,

8   particularly in Canada's prairie provinces. Decades of forestry and fire suppression have resulted

9   in this unique habitat being further diminished by timber harvesting and forest encroachment

10   upon the grassland.

11   Conservation concerns for the Chilcotin-Cariboo population of Barrow's Goldeneye

12   initially arose due to their being secondary cavity nesters that lay 4-15 eggs (Godfrey 1986)

13   primarily in cavities excavated by Pileated Woodpeckers (*Dryocopus pileatus*, Evans et al.

14   2002). Barrow's Goldeneye tend to choose cavities roughly 12 m above the ground and in aspen

15   or fir trees within ≈100 m of a small, shallow pond (Evans 2003). Their choice of such cavities

16   helps minimize egg predation by black bears and small mammals (Evans et al. 2002). Hatching

17   of all eggs in a clutch occurs somewhat synchronously with the hatched young undergoing a

18   coordinated freefall from their cavity and then being led to an adjacent pond by the hen. The

19   territoriality of Barrow's Goldeneye usually results in each small pond accommodating a single

20   brood, with larger ponds sometimes accommodating multiple, but isolated, broods (Savard 1982,

21   1984). Brood rearing occurs on ponds shallow enough for the young to dive for invertebrate prey

22   (Evans 2003). While on or around the pond the young are vulnerable to avian and mammalian

23   predators and harsh weather events such as heavy rain or hailstorms.

1   The key scientific queries concern the potential loss of riparian areas as a source of

2   cavities due to forestry, the possibility that climate change would alter the productivity

3   (invertebrate biomass) of the ponds for foraging juveniles, and that a changing landscape from

4   forest encroachment would increase predation threats, particularly from avian predators, on

5   juveniles (Evans 2003). Consequently, over the past two decades Barrow's Goldeneye have

6   attracted research attention from both conservation and behavioral scientists. Conservation

7   questions addressed, for example, whether the use of nest boxes would increase clutch

8   survivorship by providing greater protection from predation, resulting in more and larger clutches

9   (Savard 1988, Evans et al. 2002). Similarly, behavioral ecologists questioned the evolutionary

10   advantage of the high prevalence of conspecific clutch parasitism (Eadie and Fryxell 1992, Eadie

11   and Lyon 1998, Eadie at al. 1998, Lyon and Eadie 2000) and brood amalgamation (Savard 1987)

12   in Barrow's Goldeneye and related species. The model we present here is particularly well suited

13   to challenge some aspects of such questions. For example, it can challenge the null hypothesis

14   that a Barrow's Goldeneye juvenile has the same probability of surviving to fledge regardless of

15   whether it hatched in a small or large clutch.

16   We point out that with respect to clutch parasitism and brood amalgamation, an

17   experimental approach to detecting the subtle fitness implications of brood size is difficult

18   because experimental protocols require unnatural manipulation of brood sizes, and the labor

19   intensiveness of executing such experiments limits sample sizes. As such, much of the scientific

20   argument concerning the evolutionary consequences of these behaviors has relied on theoretical

21   models (Johnstone 2000, Öst et al. 2003, Broom and Ruxton 2002a,b) and genetic sampling and

22   interpretation (Andersson and Åhlund 2000, Lyon and Eadie 2000). Here we offer a statistical

23   modeling approach to the analysis and interpretation of data gathered to improve our

1   understanding of the biology of clutch parasitism and brood amalgamation. A statistical

2   modeling approach benefits from potentially large sample sizes and no need to manipulate

3   nature, but carries the philosophical disadvantage of an inability to sanction categorical

4   conclusions concerning alternate hypotheses. Statistical interpretations are limited to

5   adjudicating the relative support of competing models for explaining observed data within an

6   information-theoretic approach to model selection.

7   With these concepts in mind we applied our clutch and brood survivorship model to

8   observations of known clutches and broods made in 1995, and 1997 to 2000, at Riske Creek.

9   Simultaneously we collected data on covariate series such as pond productivity, and where

10   possible, brood size on hatch day. We used our model to challenge two hypotheses. Hypothesis

11   I: There is a different probability of surviving to fledge for a juvenile Barrow's Goldeneye

12   hatched in a large versus a small brood. Hypothesis II: The foraging quality of a brood-rearing

13   pond (as measured by invertebrate biomass) affects the probability that a juvenile in a brood

14   using that pond will fledge. In challenging these biological questions our model simultaneously

15   identifies the statistical nature (random or correlated) and mixture of the clutch and brood

16   survivorship profiles. Such partitioning improves the ability of the model to statistically

17   discriminate between mortality processes resulting from abiotic and biotic processes, and

18   increases the prospect for realism in any subsequent demographic models for Barrow's

19   Goldeneye.

20   We perceive the value of our statistical model of clutch and brood survivorship to rest

21   with its availability and robustness as a statistical tool for researchers addressing biological and

22   conservation questions similar to our own. As such our model was developed as a Microsoft

23   Visual Basic © application with a user-friendly interface and the flexibility to handle datasets

1   similar to ours and which meet the requirements we describe above. The model and its

2   documentation may be downloaded from http://www.sfu.ca/biology/wildberg/bdsmith.html

3   (available soon).

4   **SURIVORSHIP MODEL**

5   As with all statistical models, our model is defined by a deterministic component for

6   generating survival predictions, and a statistical error component that evaluates observed survival

7   outcomes with respect to these predictions. Model estimates are derived by minimizing, in a

8   probabilistic sense, the discrepancy between the predicted and observed survivorships using the

9   principle of maximum likelihood.

10   *Deterministic model*

11   The deterministic component of our model was developed on the premise that the

12   survival rate of eggs in a clutch, or juveniles in a brood, can vary with age (a), and in the case of

13   broods (b), in relation to abiotic and biotic covariates. We developed our model using the

14   Weibull probability density function (pdf) as a tractable and flexible model of survivorship

15   probabilities over time (Walpole et al. 1998). The Weibull distribution has a sound theoretical

16   basis for modeling survivorship both in biological and engineering systems. In its simplest

17   formulation it represents a constant survival rate with an exponential distribution of survivorship.

18   The Weibull pdf, $\omega(a)$, is described by

19   [1] $$\omega(a;\alpha,\beta) = \alpha\beta a^{\beta-1} e^{-\alpha a^{\beta}}$$

20   with its attenuation, or survivorship, function (1-cumulative probability function) $A(a)$ being

21   described by

1 [2] $A(a) = e^{-\alpha a^{\beta}}$.

2 When $\beta = 1$ survivorship is a constant instantaneous rate α.

3 A key feature of our model is that it has the ability to partition survivorship into random

4 (R) and correlated (C) components. As such it is necessary to define a mean survival rate from

5 age a to age $a+i$, $u[a+i]$, as a function of the mixture of random and correlated mortality

6 processes. To achieve such a model we chose to construct a pdf as a contagious mixture of two

7 Weibull distributions representing the random and correlated components of mortality for both

8 clutches (or nests, N) and broods (B). We found it both biologically reasonable and

9 mathematically tractable to model the new distributions, $\omega_{\bullet}(a)$, by

$$\omega_N(a) = c_N e^{-f_N(a-I)^{\beta_{N,C}}} \alpha_{N,C} \beta_{N,C} (a-I)^{(\beta_{N,C}-1)} e^{-\alpha_{N,C}(a-I)^{\beta_{N,C}}}$$

10 [3a]

$$+ (1 - c_N e^{-f_N(a-I)^{\beta_{N,R}}}) \alpha_{N,R} \beta_{N,R} (a-I)^{(\beta_{N,R}-1)} e^{-\alpha_{N,R}(a-I)^{\beta_{N,R}}}$$

11 and

$$\omega_B(a) = c_B e^{-f_B a^{\beta'_{B,C,b}}} \alpha'_{B,C,b} \beta'_{B,C,b} a^{(\beta'_{B,C,b}-1)} e^{-\alpha'_{B,C,b} a^{\beta'_{B,C,b}}}$$

12 [3b]

$$+ (1 - c_B e^{-f_B a^{\beta'_{B,R,b}}}) \alpha'_{B,R,b} \beta'_{B,R,b} a^{(\beta'_{B,R,b}-1)} e^{-\alpha'_{B,R,b} a^{\beta'_{B,R,b}}}$$

13 where $\alpha_{\bullet,\bullet}$ and $\alpha'_{\bullet,\bullet,b}$ (units & domain: a^{-1} & >0); and $\beta_{\bullet,\bullet}$ and $\beta'_{\bullet,\bullet,b}$ (unitless & >0) are

14 parameters of the random and correlated mortality processes for the four subscript combinations

15 N,R, N,C, B,R and B,C. When the shape parameters $\beta_{\bullet,\bullet}$ or $\beta'_{\bullet,\bullet,b}$ are set to their null value of

16 unity their effect on Eq. 3a or 3b is nullified. Values for the shape parameters that differ from

17 unity introduce age dependence to the survival rate. The parameters c_N and c_B define the

1   proportion of clutches and broods, respectively, vulnerable to a correlated mortality process at

2   age *a-I* and *a*, respectively, and which diminishes with age at rates f_N and f_B, respectively.

3   *Fig. 2 near here*

4   Note that the two scenarios of random (*R*) and correlated (*C*) mortalities are additive for

5   both clutches and broods (Fig. 2). Integration of Eqs. 3a&b yields the following survivorship

6   function for clutches or broods

7   [4a] $A_\bullet(a) = A_{\bullet,R}(a) + A_{\bullet,C}(a)$

8   where

9   [4b]
$$A_{N,R}(a) = \frac{\left(e^{-\alpha_{N,R}(a\text{-}I)^{\beta_{N,R}}} \left(1 - \frac{c_N \alpha_{N,R} e^{-f_N (a\text{-}I)^{\beta_{N,R}}}}{\alpha_{N,R} + f_N} \right) \right)}{\left(\frac{c_N f_N (\alpha_{N,C} - \alpha_{N,R})}{(\alpha_{N,C} + f_N)(\alpha_{N,R} + f_N)} + 1 \right)},$$

10   [4c]
$$A_{N,C}(a) = \frac{\left(\frac{c_N \alpha_{N,C} e^{-(\alpha_{N,C} + f_N)(a\text{-}I)^{\beta_{N,C}}}}{\alpha_{N,C} + f_N} \right)}{\left(\frac{c_N f_N (\alpha_{N,C} - \alpha_{N,R})}{(\alpha_{N,C} + f_N)(\alpha_{N,R} + f_N)} + 1 \right)},$$

1   [4d]
$$A_{B,R}(a) = \frac{\left(e^{-\alpha'_{B,R,b}a^{\beta'_{B,R,b}}} \left(1 - \frac{c_B \alpha'_{B,R,b} e^{-f_B a^{\beta'_{B,R,b}}}}{\alpha'_{B,R,b} + f_B} \right) \right)}{\left(\frac{c_B f_B (\alpha'_{B,C,b} - \alpha'_{B,R,b})}{(\alpha'_{B,C,b} + f_B)(\alpha'_{B,R,b} + f_B)} + 1 \right)} \, ,$$

2   and

3   [4e]
$$A_{B,C}(a) = \frac{\left(\frac{c_B \alpha'_{B,C,b} e^{-(\alpha'_{B,C,b} + f_B)a^{\beta'_{B,C,b}}}}{\alpha'_{B,C,b} + f_B} \right)}{\left(\frac{c_B f_B (\alpha'_{B,C,b} - \alpha'_{B,R,b})}{(\alpha'_{B,C,b} + f_B)(\alpha'_{B,R,b} + f_B)} + 1 \right)} \, .$$

4   The survivorship functions for both clutches and broods must be bounded in time. By

5   defining $a=0$ to correspond to the age that a clutch hatches, increasingly negative ages apply to

6   increasing younger clutches, while positive ages apply to broods. We therefore define a negative

7   number of days (I), corresponding to the age all clutches in the dataset are initiated. Likewise,

8   for broods we define a positive number of days corresponding the age (D) beyond which the

9   disappearance of a juvenile from a brood might be due to fledging rather than mortality.

10   Consequently, the age range for clutches is $a=I$ to 0 while that for broods is $a=0$ to D.

11   One goal of our model was to allow both the random and correlated survivorship profiles

12   for broods to be functions of external factors, our so-called brood covariates. We identified two

13   potential brood covariates directly associated with basic data collection; expected brood size on

14

1   hatch day ($E_{N,b}[a=0]$) and the day of the year that hatching occurred, t. We refer to these as

2   intrinsic brood covariates. Additionally, up to m adjunct brood covariates may have also been

3   measured. The functional relationships of the brood covariates to $\alpha_{B,\bullet}$ and $\beta_{B,\bullet}$ are defined by

4   [5a] $$\alpha'_{B,\bullet,b} = \alpha_{B,\bullet} e^{\zeta_{1,\bullet}E_{N,b}[0]+\zeta_{2,\bullet}t_b+\sum_{h=1}^{m}\zeta_{2+h,\bullet}K_{h,b}}$$

5   and

6   [5b] $$\beta'_{B,\bullet,b} = \beta_{B,\bullet} e^{\gamma_{1,\bullet}E_{N,b}[0]+\gamma_{2,\bullet}t_b+\sum_{h=1}^{m}\gamma_{2+h}K_{h,b}} ,$$

7   where b is an index for individual broods.

8   The deterministic survivorship model is now defined such that the conditional probability

9   of surviving a time period a to $a+i$, $\mu_{\bullet,\bullet}(a+i)$, can be predicted by

10   [6a] $$\mu_{\bullet,\bullet}(a+i) = \frac{A_{\bullet,\bullet}(a+i)}{A_{\bullet,\bullet}(a)}$$

11   for each of the four subscripted clutch or brood and random or correlated mortality scenarios

12   (*N,R*; *N,C*; *B,R*; *B,C*). The relationship between this prediction and a corresponding observed

13   outcome $s_\bullet(a+i)$ is

14   [6b] $$s_\bullet(a+i) = n_\bullet(a)\left(\frac{A_{\bullet,R}(a)}{A_\bullet(a)}\mu_{\bullet,R}(a+i)+\frac{A_{\bullet,C}(a)}{A_\bullet(a)}\mu_{\bullet,C}(a+i)\right)+\varepsilon_r$$

15   where ε_r is the model error for data record r.

1   *Model error*

2   A key model assumption is no, or more practically, negligible measurement error. That

3   is, we assume that counts of the number of eggs in a clutch or juveniles in a brood are accurate.

4   Therefore all data records (r, r=1 to $\Re$) for each clutch or brood must exhibit a steady or

5   declining number of individuals over time. As such, our model error structure presumes that

6   deviates from predicted survivals (ε_r) arise from actual stochastic outcomes. Further, we

7   consider the basic sampling or observational unit to be a clutch or brood followed through time,

8   with their eggs and juveniles, respectively, being considered elements of the sample.

9   Survivorship estimates are therefore inherently weighted by clutch or brood size. We also make

10   the point here that our implementation of the model treats individuals alive on hatch day as

11   juveniles in a brood.

12   When statistically evaluating the survivorship of $s_\bullet(a+i)$ individuals to age *a+i* from an

13   initial number $n_\bullet(a)$ alive at age *a*, the binomial probability mass function (pmf),

14    $BI[s_\bullet(a+i); n_\bullet(a), \mu_{\bullet \bullet \bullet}(a+i)]$, with

15   [7] $p_\bullet[s_\bullet(a+i)] = \begin{pmatrix} n_\bullet(a) \\ s_\bullet(a+i) \end{pmatrix} \mu_{\bullet \bullet \bullet}(a+i)^{s_\bullet(a+i)} \left(1 - \mu_{\bullet \bullet \bullet}(a+i)\right)^{n_\bullet(a) - s_\bullet(a+i)}$

16   has usually been the probability distribution of choice, where $p_\bullet[s_\bullet(a+i)]$ is the probability of

17   observing $s_\bullet(a+i)$ of $n_\bullet(a)$ individuals alive at time *a+i*, given a survival rate from *a* to *a+i* of

18    $\mu_{\bullet,\bullet}(a+i)$. However, we have often recognized in clutch and brood survivorship data that the

19   fundamental assumption that each mortality event is random and uncorrelated with other

20   mortality events fails. This is most apparent when we witness catastrophic mortalities due to, for

21   example, weather events. To address that deficiency of the binomial pmf we chose to employ the

1   beta-binomial probability pmf in our model. The advantage of the beta-binomial pmf,

2    $BB[s_\bullet(a+i); n_\bullet(a), \mu_{\bullet,\bullet}(a+i), \theta^2_{\bullet,\bullet}(a)]$, with

3   [8a] $p_\bullet[s_\bullet(a+i)] = \binom{n_\bullet(a)}{s_\bullet(a+i)} \frac{\Gamma(X+Y)}{\Gamma(X)\Gamma(Y)} \frac{\Gamma(s_\bullet(a+i)+X)\Gamma(n_\bullet(a)-s_\bullet(a+i)+Y)}{\Gamma(n_\bullet(a)+X+Y)}$;

4   where

5   [8b] $X = \mu_{\bullet,\bullet}(a+i)\left(\frac{(1-\theta^2_{\bullet,\bullet}(a))}{\theta^2_{\bullet,\bullet}(a)}\right)$,

6   [8c] $Y = \frac{X(1-\mu_{\bullet,\bullet}(a+i))}{\mu_{\bullet,\bullet}(a+i)}$,

7   and with variance

8   [9] $V_\bullet[a+i] = n_\bullet(a)\mu_{\bullet,\bullet}(a+i)(1-\mu_{\bullet,\bullet}(a+i)(1+\theta^2_{\bullet,\bullet}(a)(n_\bullet(a)-1))$,

9   is that its definition includes a third parameter, $\theta^2_{\bullet,\bullet}(a)$, that explicitly accommodates

10   overdispersed (i.e., correlated) outcomes when $\theta^2_{\bullet,\bullet}(a) > 0$. If $\theta^2_{\bullet,\bullet}(a) = 0$ there is no

11   overdispersion and the distribution limits to the binomial pmf. If, in the extreme, $\theta^2_{\bullet,\bullet}(a) = 1$ the

12   beta-binomial distribution is fully overdispersed such that the $n_\bullet(a)$ individuals in a clutch or

13   brood either all survive or none survive; by our definition a catastrophic outcome at a survival

14   rate of $\mu_{\bullet,\bullet}(a+i)$. Note that we have made $\theta^2_{\bullet,\bullet}(a)$ a function of age,

15   [10] $\theta^2_{\bullet,C}(a) = \theta^2_{\bullet,C}(0)e^{-v_\bullet a}$

16   to accommodate the plausible scenario that the degree of correlated mortality (C) is likely to

17   diminish ($v_\bullet \geq 0$) with age, especially for juveniles in a brood.

1   *Fig. 3 near here*

2   To illustrate our model error structure we draw attention to the graphic examples (Fig. 3)

3   of a binomial pmf of random outcomes (Fig. 3a), a beta-binomial pmf of correlated outcomes

4   with partial overdispersion (Fig. 3b), a fully overdispersed, catastrophic, beta-binomial pmf

5   (Fig. 3c), and a mixed distribution composed 70% of random mortalities and 30% of correlated

6   mortalities (Fig. 3d). The probability of an observed survivorship outcome for such a mixture is

7   defined by

8   [11] $$p_\bullet[s_\bullet(a+i)] = \sum_{j=R\&C} \frac{A_{\bullet,j}(a)}{A_\bullet(a)} \times BB[s_\bullet(a+i); n_\bullet(a), \mu_{\bullet,j}(a+i), \theta^2_{\bullet,j}(a)],$$

9   where we define $\theta^2_{\bullet,R}(a) = 0$ for all ages such that the error distribution for a random mortality

10   process (*R*) is always represented by the binomial distribution. Consequently, the expected

11   number of eggs surviving in a clutch, or juveniles surviving in a brood, $E_\bullet[a+i]$, is

12   [12a]
$$
\begin{aligned}
E_\bullet[a+i] &= \sum_{s_\bullet(a+i)=0}^{n(a)} s_\bullet(a+i) \sum_{j=R\&C} \frac{A_{\bullet,j}(a)}{A_\bullet(a)} p_j[s_\bullet(a+i)] \\
&= n_\bullet(a)\left(\frac{A_{\bullet,R}(a)}{A_\bullet(a)} \mu_{\bullet,R}(a+i) + \frac{A_{\bullet,C}(a)}{A_\bullet(a)} \mu_{\bullet,C}(a+i) \right)
\end{aligned}
$$

13   with variance

14   [12b] $$V_\bullet[a+i] = \sum_{s_\bullet(a+i)=0}^{n(a)} s_\bullet(a+i)^2 \sum_{j=R\&C} \frac{A_{\bullet,j}(a)}{A_\bullet(a)} p_j[s_\bullet(a+i)] - E_\bullet[a+i]^2.$$

15   The above formulae are sufficient to model a clutch from its initiation age (*a=I*) through

16   to hatch (*a=0*), or a brood from hatch until the fledging age (*a=D*). Thus this is a helpful model

17   only if an observer was able to record the number of juveniles present on hatch day. Recognizing

1   that even a determined observer is unlikely to witness many clutches hatching, we realized that

2   the utility of our model would rest with its ability to accept data records lacking observations of

3   the number of eggs or juveniles alive on hatch day. We therefore developed our model to

4   accommodate such data structures.

5   The calculation of the expected number of surviving juveniles in a brood when

6   individuals were last observed as eggs in a clutch is complicated by the reality that the

7   survivorship predictions for ages after hatch day result from a probabilistic mixture of four

8   processes. For example, one of those processes is eggs surviving a random mortality process

9   from age a to hatch ($a=0$), followed by the hatched juveniles surviving a random mortality

10   process to be observed at age $a+i$. Referring to that process as $R|R$ survivorship indexed by $j|k$,

11   expected survivorship potentially includes three other mortality processes $R|C$, $C|R$ and $C|C$.

12   Therefore

13   [13a] $$E_{N|B}[a+i] = \sum_{s_{N|B}(a+i)=0}^{n(a)} s_{N|B}(a+i) \sum_{j|k=R|R,R|C,C|R\&C|C} \frac{A_{N,j}(a)}{A_N(a)} \frac{A_{B,k}(a)}{A_B(a)} p_{j|k}[s_{N|B}(a+i)]$$

14   with variance

15   [13b] $$V_{N|B}[a+i] = \sum_{s_{N|B}(a+i)=0}^{n(a)} s_{N|B}(a+i)^2 \sum_{j|k=R|R,R|C,C|R\&C|C} \frac{A_{N,j}(a)}{A_N(a)} \frac{A_{B,k}(a)}{A_B(a)} p_{j|k}[s_{N|B}(a+i)] - E_{N|B}[a+i]^2$$

16   where

17   [14] $$p_{j|k}[s_B(a+i)] = \sum_{s_N(a+i)=0}^{n_N(a)} \sum_{s_B(a+i)=0}^{s_N(a+i)} \{BB[s_B(a+i); s_N(a+i), \mu_{B,k}(a+i), \theta_{B,k}(a)] \\ \times BB[s_N(a+i); n_N(a), \mu_{N,j}(a+i), \theta_{N,j}(a)]\}$$

1   Once the probabilities of observing any outcome $s_\bullet(a+i)$ have been defined, we can

2   calculate the negative ln-likelihood of each possible outcome for each data record r using

3   [15] $\lambda_{F_r[s_\bullet(a+i)]} = -2\ln\big[p_\bullet[s_\bullet(a+i)]\big]$

4   where $F_r[s_\bullet(a+i)]=1$ if the outcome $s_\bullet(a+i)$ for prediction $\mu_{\bullet,\bullet}(a+i)$ was observed, else

5    $F_r[s_\bullet(a+i)]=0$. We include the factor 2 to make Eq. 15 equivalent to the G-statistic for

6   evaluation using likelihood ratio tests (Burnham and Anderson 2002). The Pearson deviate

7   associated with Eq. 15, which has utility as a goodness-of-fit (GOF) statistic (Roff and Bentzen

8   1989), is

9   [16] $P_{F[s_\bullet(a+i)]=1} = \dfrac{1 - p_\bullet[s_\bullet(a+i)]}{p_\bullet[s_\bullet(a+i)]}$.

10   The model is now fully stated.

11   ***Hypotheses, data preparation, parameter estimation, and utile metrics***

12   Our purpose is to report on two hypotheses concerning survivorship to fledging of

13   Barrow's Goldeneye juveniles, primarily to illustrate our model. However, our results have

14   implications both for Barrow's Goldeneye conservation, and our understanding of the fitness

15   implications of the reproductive behaviors of clutch parasitism and brood amalgamation. Null

16   Hypothesis I proposes that there is no difference in the probability of surviving to fledge among

17   juveniles reared in broods of different sizes, as measured or inferred on the day the eggs hatched

18   (hatch day). Null Hypothesis II proposes that there is no difference in the probability of

19   surviving to fledge among juveniles reared on ponds with differing productivities, as measured

20   by estimates of invertebrate biomass (Evans 2003). Invertebrate biomass (mg/sample) was

1   estimated from benthic core samples and pelagic activity traps collected among 20 ponds in 1997

2   to 1999 *a priori* qualitatively judged to be of low, medium and high invertebrate productivity

3   (Evans 2003). An estimated interannual correlation of 93% among ponds supported that this

4   measure had merit as a reliable index of pond productivity. Invertebrate biomass varied by

5   roughly an order of magnitude among the ponds sampled, all of which were observed to support

6   Barrow's Goldeneye broods in at least one of the years sampled.

7   *Fig. 4 near here*

8   We had available for analysis a set of observations of the number of eggs in a clutch and

9   juveniles in a brood for individually followed families (Fig. 4). Offspring associated with an

10   adult tending hen, identified by her unique nasal disc pairing, allowed each egg or juvenile

11   observed to be assigned to a specific hen. However, clutches may have been parasitized, so we

12   generally did not know if a family was comprised of eggs from more than one hen. Typically

13   broods were observed and counted every two to five days, but sometimes more or less frequently.

14   Clutches were observed much less frequently than broods. The calendar date (t) of all

15   observations was recorded and used to calculate clutch and brood ages. If clutches were not

16   observed at, or just before, hatch, as was typically the case, calendar hatch date was usually

17   inferred from the observed stage of juvenile development when broods were first observed on a

18   pond (Gollop and Marshall 1954). Our analyzed dataset included egg counts only for dates on or

19   after the date the maximum number of eggs in a cavity was observed. Our data set did not

20   include broods that we knew underwent brood amalgamation or for which hatch date, and

21   therefore clutch and brood age, could not be confidently calculated. Further, observations of

22   clutches outside the age range $I \leq a$, $a+i \leq D$ were excluded from our dataset. Within the subset of

23   data that qualified for analysis (Fig. 4), a few families were first followed as clutches, while most

1   were not followed until they were first seen as broods on a pond. We chose I=-40 days and D=56

2   days for the analyses we present. We also clarify that for Barrow's Goldeneye I refers to the age

3   the tending hen began to incubate her full clutch in order to assure synchronous hatching. Egg

4   laying for any hen will have taken place over several days. Fewer data records qualified for our

5   challenge of Hypothesis II ($\Re$=659) than for Hypothesis I ($\Re = 1090$) since challenging

6   Hypothesis I could use data from families on ponds for which there was no estimate of pond

7   productivity.

8   *Table 1 near here*

9   Fitting the model to the data organized for this study required that values be estimated for

10   the parameters of the model introduced in the previous section (and see Table 1). Maximum

11   likelihood estimates for these parameters are those obtained when L (Eq. 17) is minimized

12   (L_{MIN}), where

13   [17] $$L(F_\bullet[s_\bullet(a+i)]|\alpha_{\bullet,\bullet},\beta_{\bullet,\bullet},\theta^2_{\bullet,\bullet},v_\bullet,c_\bullet,f_\bullet,\zeta_{\bullet,\bullet},\gamma_{\bullet,\bullet},I,D)=\sum_{r=1}^{\Re}\lambda_{F_r[s_\bullet(a+i)]}\times F_r[s_\bullet(a+i)]$$

14   We used with equal success either the derivative-based Marquardt's algorithm (Press

15   et al. 1986) or the direct search simplex method (Mittertreiner and Schnute 1985, Ebert 1999) of

16   function minimization to obtain L_{MIN}. L_{MIN} is sometimes referred to as model deviance since

17   theoretically L_{MIN}=0 when the model perfectly fits the data. A covariance matrix was calculated

18   by inverting the numerically calculated Hessian matrix of second partial derivatives of L with

19   respect to the parameter estimates at L_{MIN}. The quality of model fit (GOF) was liberally

20   diagnosed based on randomized Pearson deviates and randomized deviance (Roff and Bentzen

21   1989) using the L_{MIN} parameter estimates, and more conservatively diagnosed by parametric

1   bootstraps which also yielded confidence limits for parameter estimates and an *a posteriori*

2   estimate of overdispersion $\hat{C}$ (White and Burnham 1999). These diagnostics evaluate the

3   probability of the observed data given the model and parameter estimates. A satisfactory

4   diagnostic is a probability value that suggests the data are reasonably likely, given the model, i.e.,

5    $0.025<p<0.975$, where extremely small values for p suggest an underfitted model, and extremely

6   large values of p an overfitted model.

7   For an accepted model fit, we consider three metrics to be of special interest to many

8   analysts and are therefore reported in model output. One is the probability, at age a, that a

9   juvenile will fledge at age D, where for hatch day ($a=0$),

10   [18] $$p[Fledge(0,D)] = \sum_{j=R\&C} \frac{A_{B,j}(0)}{A_B(0)} \mu_{B,j}(D) .$$

11   This metric has particular utility for expressing the relative effect of model covariates on a

12   juvenile's propensity to fledge.

13   A second metric is expected brood size on hatch day, $E_{N,b}[0]$, from Eq. 12a, though here

14   we add the brood subscript (b) to emphasize that each brood has its own expectation. This

15   metric provides an estimate of the number of juveniles alive in brood b on hatch day when there

16   is at least one observation of the number of eggs alive prior to hatch. In this study we use $E_{N,b}[0]$

17   as an intrinsic covariate to challenge Null Hypothesis I. It has particular value in that it mitigates

18   an observer's inability to count the number of juveniles in a nest on hatch day. It worth noting

19   that for some interpretations $E_{N,b}[0]$ might be considered a better metric than an actual count of

20   juveniles on hatch day if the analyst's purpose is to infer a hen's intended initial brood size; i.e.,

1   analyses drawing fitness interpretations, however the two metrics will tend to be very highly

2   correlated.

3   Lastly, we present a measure of dispersion more intuitive than $\theta^2_{\bullet,\bullet}$, specifically,

4   [19] $EIU = 1 + \theta^2_{\bullet,\bullet}(a) \times (n_{\bullet}(a) - 1)$.

5   This metric calculates the '*effective independent unit*' (EIU), a statistical measure of the number

6   of individual eggs or juveniles that tend to associate as a single mortality event such that the

7   hypothetical outcomes of such mortality events would follow a binomial distribution. An EIU

8   value of, say 2.3, for juveniles might be interpreted that a predator tends to take on average 2.3

9   juveniles per mortality event interval. This metric has proven informative in other sampling

10   applications where individuals birds within a flock do not associate independently (Iverson et al.

11   2003). Conversely, when $\theta^2_{\bullet,\bullet} > 0$ the '*effective independent sample size*' (EISS) for a clutch or

12   brood observation is reduced from $n_{\bullet}(a)$ to

13   [20] $EISS = \dfrac{n_{\bullet}(a)}{1 + \theta^2_{\bullet,\bullet}(a) \times (n_{\bullet}(a) - 1)}$.

14   **RESULTS**

15   *Table 2 near here*

16   Competitive model trials to challenge Null Hypotheses I and II using our data from all

17   ponds produced a distinct ranking of models (Table 2). The highest ranked models for both

18   hypotheses narrowly passed parametrically bootstrapped goodness-of-fit diagnostics of model

19   adequacy ($p \pm 1$ SE=0.03±0.02 for Null Hypothesis I; $p \pm 1$ SE=0.06±0.02 for Null Hypothesis II).

20   More satisfying values for p could have been obtained had we chosen to remove a few outlier

1   data points that contributed disproportionately to model deviance (L_{MIN}). However, we had

2   confidence that our relatively large number of data records ($\Re$) effectively neutralized any bias

3   from these outliers. Our choice not to censor outliers resulted also in bootstrapped estimates of

4    $\hat{C}\pm1$ SE slightly greater than unity, at 1.08±0.04 and 1.06±0.05 for the best ranked models

5   (Model 1) for Null Hypotheses I and II, respectively.

6   Null Hypothesis I was poorly supported, with the second highest ranked model, Model 2

7   (ignoring Model 1 with function $\theta_{B,C}^{2}(a)$ for the moment), strongly supporting a parametrically

8   and statistically strong relationship between the probability, on hatch day, that a juvenile will

9   fledge at age D=56 days, $p[Fledge\,(0,D)]$, and expected brood size on hatch day, $E_{N,b}[0]$.

10   Model 2 is an ≈500 times more probable fit to our data that its direct competitor, Model 6 (Pair A

11   in Table 2, Fig. 5), lacking $E_{N,b}[0]$ as a covariate. A likelihood ratio test significantly favors

12   Model 2 (p[Model 2≡Model 6]=0.0004, ΔL_{MIN}=20.53, df=4). Model 2 also identifies strong

13   year-effects, with the effect of $E_{N,b}[0]$ varying among years to the extent that little effect is

14   evident in 1997, while in other years there is a distinct tendency for $p[Fledge\,(0,D)]$ to

15   increase as $E_{N,b}[0]$ increases. Model 2, with year-effects, is an ≈10^{4} times more probable fit to

16   our data that its competitor, Model 7, that lacks year-effects (Pair F in Table 2). A likelihood

17   ratio test significantly favors Model 2 (p[Model 2≡Model 7]<0.0001, ΔL_{MIN}=24.25, df=3).

18   *Figs. 5&6 near here*

19   Competitive model trials to challenge Null Hypothesis II using our data from those fewer

20   ponds for which we had covariate data on pond productivity also produced a distinct ranking of

21   models (Table 2). As for the original dataset used to challenge Null Hypothesis I, Model 3

1   challenging Null Hypothesis II also strongly supported a positive relationship between

2    $p[Fledge\,(0,D)]$ and $E_{N,b}[0]$, again with year-effects (Fig. 6a), though the statistical strength of

3   the relationship is weaker due to the smaller dataset. Indeed, Model 3 excluded pond

4   productivity as a covariate, indicating insufficient statistical support for the hypothesis that,

5   among the ponds sampled, $p[Fledge\,(0,D)]$ is influenced by pond productivity. The direct

6   competitor of Model 3, Model 5 (Pair B in Table 2), was approximately 5 times poorer at

7   explaining our data than was Model 3. Model 11, which included pond productivity, but not

8    $E_{N,b}[0]$, as a covariate, ranked poorly as a putative model to explain our data, though there is a

9   slight tendency for the $p[Fledge\,(0,D)]$ to increase with pond productivity in years other than

10   1997 (Fig. 6b). The weakness of this relationship is revealed in the random scatter of the

11   residuals $p[Fledge\,(0,D)]$ versus pond productivity from Model 1 (Fig. 6c). The influence of

12    $E_{N,b}[0]$ on brood survivorship is illustrated in Fig. 7 which portrays increasing shallower

13   survivorship profiles, $A_B(a)$, for increasing initial brood sizes. Fig. 7 also demonstrates that the

14   survival advantage conferred upon a juvenile by being in a larger brood is realized while it is

15   relatively young.

16   *Fig. 7 near here*

17   The best ranked models challenging Null Hypotheses I and II include the function

18    $\theta_{B,C}^2(a)$ (Eq. 10) with $v_B > 0$, indicating that the degree of correlated mortality among juveniles

19   (EIU) diminished with brood age. The models that included $v_B > 0$ were approximately 1300 and

20   14 times more probable than their competitors with $v_B = 0$, for Null Hypotheses I (Pair E in

21   Table 2) and II (Pair K in Table 2), respectively. Likelihood ratio tests affirmed the statistical

1   contribution of $v_B > 0$ to model fit (Null Hypothesis I: $p[v_B = 0] < 0.0001$, $\Delta L_{MIN} = 16.41$, df=1; Null

2   Hypothesis II: $p[v_B = 0] = 0.007$, $\Delta L_{MIN} = 7.30$, df=1). This was anticipated since juveniles would

3   be expected to behave more independently of their siblings as they aged, thereby lessening group

4   vulnerability to predation or weather threats. The inclusion of $\theta^2_{B,C}(a)$ in all competitive model

5   pairs significantly improved the fit of these models but did not change the relative ranking of

6   models based on the covariates of age, year, $E_{N,b}[0]$, or pond productivity.

7   *Fig. 8 near here*

8   For neither Null Hypotheses I nor II was there statistical evidence of an age-effect on

9   juvenile survivorship independent of any putative covariates. That is, there was no evidence to

10   support either $\beta_{B,R} \neq 1$ or $\beta_{B,C} \neq 1$. This implies a constant survivorship rate during the brood

11   rearing period, though there is clear evidence that this rate varies among years and is affected by

12   $E_{N,b}[0]$. Nevertheless, our highest ranked models for both hypotheses (Model 1) included the

13   intrinsic brood-effect parameters $\gamma_{1,R}$ and $\gamma_{1,C}$ operating on $\beta_{B,R}$ and $\beta_{B,C}$, respectively (Eq. 5b),

14   such that $\beta'_{B,R,\bullet} \neq 1$ and $\beta'_{B,R,\bullet} \neq 1$. Thus an effect of $E_{N,b}[0]$ was to change daily survivorship

15   with age among broods. Figure 8 illustrates that the correlated mortality process was more

16   strongly affected by $E_{N,b}[0]$ than was the random mortality process, the former process showing

17   a greater range of daily survivorships among broods at a young age. The tendency was for young

18   broods with higher values for $E_{N,b}[0]$ to experience higher survivorships early in life (Fig. 9),

19   which eventually resulted in a higher overall $p[Fledge\,(0,D)]$ for those broods. When

20   interpreting Fig. 9, recall that the proportion of broods vulnerable to the correlated mortality

1   process portrayed there diminishes with brood age (Fig. 10a), as does the degree of correlation

2   among juveniles in a brood as measured by the EIU (Fig. 10b).

3   *Figs. 9&10 near here*

4   Finally, the more precise estimates of the $E_{N,b}[0]$ provided by Model 1 challenging Null

5   Hypothesis I afforded an opportunity to look for a relationship between $E_{N,b}[0]$ and pond

6   productivity for those clutches and broods for which we had adjunct data on pond productivity.

7   No significant statistical relationship was detected (Fig. 11) thereby providing no evidence that

8   that the $E_{N,b}[0]$ for Barrow's Goldeneye hens using those ponds may be determined in part by the

9   pond's productivity.

10   *Fig. 11 near here*

11   **DISCUSSION**

12   Our results have demonstrated the utility of our clutch and brood survivorship model for

13   addressing two key hypotheses concerning the breeding success of Barrow's Goldeneye in

14   British Columbia. More importantly, we think this demonstration of our model introduces

15   researchers to a robust analytical tool for investigating environmental effects (e.g., pesticides,

16   predation, habitat alterations, weather, etc.) on the reproductive success of birds, or for providing

17   high quality parameter estimates and a measure of their uncertainty for inclusion in population

18   viability (PVA) or similar analyses. With respect to similar analyses, we have used our model

19   successfully on previously published dataset of our colleagues (Gill et al. 2000, 2003) to

20   challenge the null hypothesis that pesticides do not affect the reproductive success of American

21   Robins (*Turdus migratorius*) nesting in fruit orchards of the Okanagan Valley, British Columbia.

22   As we expected, we found no detectable effect of pesticides on reproductive success in

1   accordance with the authors' original interpretations using the Mayfield method (Mayfield 1961,

2   1975) and Program MARK's Nest Survival module (White and Burnham 1999). The reason for

3   our expectation arises from our recognition that overdispersion in a dataset acts to reduce the

4   effective independent sample size (*EISS*, Eq. 20) and thus appropriately decreases the power to

5   falsely detect a significant effect. That is, our model reduces the probability of making a Type II

6   error (Walpole et al. 1998) when survivorship outcomes are not independent. A corollary to this

7   benefit of our model is that analyses that do not explicitly account for overdispersion run a higher

8   risk of falsely detecting statistical correlations which can ultimately lead to fictitious

9   interpretations of cause and effect.

10   Readers may have perceived that our model is not limited in application to demographic

11   analyses of bird reproduction, but can be applied to any species where an interpretation of its

12   reproductive life history is analogous to that of birds, e.g., egg-laying reptiles. Indeed, when

13   there is no need to model the clutch to brood transition, our model can be applied to any species

14   where an integer number of offspring in a brood can be accurately counted over time, there is a

15   desire to explicitly account for overdispersion, and the model's caveats and assumptions stated in

16   the *Introduction* are acceptable to the analyst.

17   As you have read, we illustrated our model using data on Barrow's Goldeneye clutch and

18   brood survivorship to challenge two null hypothesis. (Incidentally, in preliminary analyses we

19   found no support for the null hypothesis that juvenile survivorship was not influenced by hatch

20   day of the year, *t*). Rejection of Null Hypothesis I clearly supported that a juvenile's probability

21   of surviving to fledge at 56 days increased with its expected brood size on hatch day ($E_{N,b}[0]$).

22   This finding supports the life history argument that conspecific clutch parasitism has a fitness

23   advantage for the juveniles (Eadie and Lyon 1998, Eadie at al. 1998, Lyon and Eadie 2000) with

1   perhaps an ultimate fitness for the recipient hen (Eadie and Lumsden 1985, Eadie et al. 1988).

2   The juveniles of both the tending hen, and the hen that deposited her eggs in that tending hen's

3   nest, are conferred a survivorship advantage by having their offspring as members of larger

4   broods. However, this interpretation must be tempered by the realization that the tending hen is

5   probably not indifferent to the parentage of the brood she is tending. There is evidence in

6   common eiders (*Somateria mollissima*) that a tending hen, or her ducklings, may act to

7   preferentially increase their fitness over that of the other ducklings in amalgamated broods (Öst

8   and Bäck 2003), a so-called "selfish herd" behavior (Hamilton 1971, Eadie at al. 1988). We

9   point out that we did not have information on which, if any, of the broods in our analysis were

10 formed through clutch parasitism, but this seems certain to be true for the largest of broods (i.e.,

11 those with brood sizes on hatch day of 20-25 juveniles; J.-P. Savard, *personal communication*,

12 Evans et al. 2002). Likewise, we did not follow the survivorship of broods which were observed

13 to increase in size by brood amalgamation. However, our interpretations of a higher probability

14 of surviving to fledge in larger broods endorses the fitness value of brood amalgamation (Savard

15 1987).

16   A conservation interpretation of our rejection of Null Hypothesis I is that increasing the

17 size of broods in a region, such as the Riske Creek region of our study, appears a conservation

18 option if survival to fledge is considered to limit population growth. Thus our results add

19 another question to conservation planning. That is, what is the trade-off between providing nest

20 boxes to increase the number of Barrow's Goldeneye nesting opportunities in underutilized

21 ponds, versus increasing the survivorship of offspring in currently used ponds? The answer is

22 inconspicuous with our current knowledge. However, Barrow's Goldeneye have invested in the

23 life history fitness option of relinquishing offspring to the care of another, perhaps more

1 established or closely related (Andersson and Åhlund 2000, Lyon and Eadie 2000) hen. This

2 suggests that this option might be preferable to a hen raising her own offspring in a more risky

3 habitat, perhaps despite nesting opportunities provided by artificial nest boxes. Though the use

4 of nest boxes has been proven to have successful outcomes, large (e.g., bears) and small (e.g.,

5 squirrels) mammal predation can defeat their efficacy (Evans et al. 2002), perhaps more so in less

6 preferred habitat. However, our study supplements the findings of Evans et al. (2002) which

7 demonstrate a significantly increased clutch size for nest boxes over natural cavities.

8 Notwithstanding unconsidered factors, our results imply that such increases in clutch size can

9 disproportionately increase the expected number of juveniles fledged.

10 Had our data supported a positive relationship between pond productivity and the

11 probability of juveniles surviving to fledge (i.e., a rejection of Null Hypothesis II), we would

12 have been able to provide guidance as to which ponds would have the highest priority for nest

13 boxes. Unfortunately we found no such relationship, possibly because there was insufficient

14 contrast in pond productivity, with no pond's productivity below a critical threshold affecting

15 juvenile survival. Supporting this interpretation of adequate productivity, we also found no

16 relationship between expected brood size on hatch day and pond productivity, given that it has

17 recently been established that Barrow's Goldeneye hens from the Riske Creek region acquire the

18 vast majority of their nutrition for egg development locally (Hobson et al. submitted). Our

19 failure to detect such a relationship must be interpreted with the understanding that only ponds

20 that supported at least one brood were included for consideration in this analysis. Clearly ponds

21 depauperate of prey biomass would be poor choices for brood rearing. More positively, there

22 appears to be a considerable range of pond productivities that support successful rearing of

23 Barrow's Goldeneye broods.

1   We conclude by emphasizing the key contributions of our model for advancing our

2   understanding of the dynamics of reproduction in birds and perhaps other egg-laying species.

3   Principally, we provide a method and model application for measuring and statistically

4   evaluating survivorship during the critical life history phase of egg-laying to fledging. We

5   particularly want to emphasize two elements of our modeling approach. First, we demonstrate

6   the utility of our model for statistically discriminating between random and correlated mortality

7   events. We think this is a key advance that reinforces the need for demographic models,

8   including population viability models, to strive for realism concerning survivorship dynamics.

9   Second, our emphasis on overdispersion (correlated mortality) reinforces that mortality events

10   are unlikely to be random events, particularly in young broods, and indeed may be fully

11   correlated, i.e., catastrophic. We implore investigators to recognize this potential feature of

12   brood survivorship when they draw statistical inferences from their similar data. To that end we

13   have also introduced the concept of the effective independent sample size (*EISS*, Eq. 20), which

14   we trust will motivate readers to take heed of the potential for non-independence of individual

15   mortalities.

16   Finally, despite the benefits of our statistical modeling approach to the hypotheses

17   challenged here, there potentially remain with our model the same subtle suite of biases that also

18   can plague studies that have relied on the more traditional Mayfield (Mayfield 1961, 1975) and

19   Kaplan-Meier (Kaplan and Meier 1958), or the more contemporary Program MARK (White and

20   Burnham 1999) methodologies. Since we can only draw statistical interpretations from the data

21   we collected, clutches or broods that failed before they were witnessed by an observer introduce

22   interpretive biases to which a researcher must be astute. We consider such biases in our

23   particular study to be minimal because of the dutiful nature of data collection and the easily

1 observed brood rearing by Barrow's Goldeneye hens. Our most overt bias is our compulsory

2 selection only of ponds supporting broods for challenging Null Hypothesis II. So as with all

3 modeling interpretations, our ultimate conclusions are conditional upon the constraints that

4 determined what data were collected and the circumstances under which they were collected.

13   **LITERATURE CITED**

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1   **TABLES**

2

Table 1: Definitions and symbols for model variables.			
Symbol	Units	Character	Definition
a	days	data	Clutch or brood age relative to hatch day ($a=0$)
t	days	data	Sequential day of the year (1 to 365)
I	days	data	Age at which all eggs in all clutches are laid
D	days	data	Age at which all juveniles in all broods fledge
i	days	data	age increment
b	integer	index	Index for individual broods
r	integer	index	Index for each qualified data record*.
$\Re$	integer	index	Number of qualified data records
N	-	subscript	Subscript for a mortality process occurring entirely within a clutch (nest)
B	-	subscript	Subscript for a mortality process occurring entirely within a brood
R	-	subscript	Subscript for a random mortality process
C	-	subscript	Subscript for a correlated mortality process
j	-	subscript	Index for R or C
k	-	subscript	Index for R or C
j|k	-	subscript	Subscript notation for mortality processes originating in a clutch and progressing to a brood
$P_{F[s_\bullet(a+i)]\dashv}$	unitless	calculation	Pearson deviate associated with having observed

			$s_\bullet(a+i)$ of $n_\bullet(a)$ individuals to have survived the age increment i.
$\mu_{\bullet\bullet}(a+i)$	probability	calculation	Probability an individual egg in a clutch (N) or juvenile in a brood (B) survives the age increment i when subjected to either a random (R) or correlated (C) mortality process
$\omega_\bullet(a)$	pdf	calculation	Probability density function (pdf) at age a for the mortality of eggs in a clutch (N) and juveniles in a brood (B) when either may be subjected to a mixture of random (R) and correlated (C) mortality processes
$A_{\bullet\bullet}(a)$	probability	calculation	Probability of surviving to age a for the mortality of eggs in a clutch (N) and juveniles in a brood (B) when either may be subjected to a mixture of random (R) and correlated (C) mortality processes
$F_r[s_\bullet(a+i)]$	frequency	data	A Bernoulli frequency of observation of the possible survivorship outcomes $s_\bullet(a+i)$; i.e., $F_r[s_\bullet(a+i)]=1$ if observed, else 0.
$\lambda_{F_r[s_\bullet(a+i)]=1}$	unitless	calculation	Negative ln-likelihood associated with having observed $s_\bullet(a+i)$ of $n_\bullet(a)$ individuals to have survived age increment i.
$n_\bullet(a)$	integer	data	Number of eggs in a clutch (N) or juveniles in brood (B) vulnerable to mortality at age a
$s_\bullet(a+i)$	integer	data	Number of surviving eggs in a clutch (N) or juveniles

			in brood (B) at age $a+i$. Note that $s_\bullet(a+i)$ is undefined when $n_\bullet(a)=0$ or is unknown; and when $a<I$ or $a+i>D$.
$E_\bullet[a+i]$	individuals	calculation	Expected number of surviving eggs in a clutch (N) or juveniles in brood (B) at age $a+i$
$V_\bullet[a+i]$	individuals^2	calculation	Variance of the number of surviving eggs in a clutch (N) or juveniles in brood (B) at age $a+i$
$p[\bullet]$	probability	calculation	Probability of the event represented by $\bullet$.
$c_\bullet$	a^{-1}	parameter	Instantaneous rate of mortality due to a correlated (C) mortality process for clutches (N) or broods (B) at $a=0$
$f_\bullet$	a^{-1}	parameter	Instantaneous attenuation rate of $c_\bullet$ with age a
$\theta^2_{\bullet,\bullet}(a)$	scalar	parameter	Overdispersion parameter ($0 \leq \theta^2_{\bullet,\bullet}(a) \leq 1$) of the beta-binomial probability mass function (pmf)
$v_\bullet$	a^{-1}	parameter	Instantaneous attenuation rate of $\theta_{\bullet,\bullet}(a)$ with age a
$\alpha_{\bullet,\bullet}$	a^{-1}	parameter	Weibull mortality pdf function scaling coefficient
$\beta_{\bullet,\bullet}$	scalar	parameter	Weibull mortality pdf function shape coefficient
$\alpha'_{B,\bullet,b}$	a^{-1}	calculation	$\alpha_{\bullet,\bullet}$, as modified by Eq. 5a for brood b
$\beta'_{B,\bullet,b}$	scalar	calculation	$\beta_{\bullet,\bullet}$, as modified by Eq. 5b for brood b
$\zeta_{1,\bullet}$	individuals^{-1}	parameter	Instantaneous effect of the expected number of juveniles in a brood on hatch day ($a=0$), $E_{N,b}[0]$, on $\alpha_{\bullet,\bullet}$
$\zeta_{2,\bullet}$	t^{-1}	parameter	Instantaneous effect of hatch day of the year (t) on $\alpha_{\bullet,\bullet}$

h	integer	data	Index for adjunct brood covariates
m	integer	data	Maximum number of adjunct brood covariates
$\zeta_{2+h,\bullet}$	$K_{h,b}^{-1}$	parameter	Instantaneous effect of $K_{h,b}$ on $\alpha_{\bullet,\bullet}$
$\gamma_{1,\bullet}$	individuals^{-1}	parameter	Instantaneous effect of the expected number of juveniles in a brood on hatch day (a=0), $E_{N,b}[0]$, on $\beta_{\bullet,\bullet}$
$\gamma_{2,\bullet}$	t^{-1}	parameter	Instantaneous effect of hatch day of the year (t) on $\beta_{\bullet,\bullet}$
$\gamma_{h+2,\bullet}$	$K_{h,b}^{-1}$	parameter	Instantaneous effect of $K_{h,b}$ on $\beta_{\bullet,\bullet}$
$K_{h,b}$	Covariate unit^{-1}	data	Adjunct covariate h associated with all observations in any brood b.

* A data record qualifies for a statistical evaluation of an observation $s_{\bullet}(a+i)$ with respect to a prediction $p_{\bullet}[s_{\bullet}(a+i)]$ only when an observer recorded the date, identified the family, exactly counted the number of eggs or juveniles alive within the family, and recorded the age of the eggs or juveniles. The age of the eggs may have been determined retroactively once hatching was witnessed. A data record may qualify for an analysis of mortality as a function of time, not age, if only parameters independent of time are included in the analysis. Data records can qualify only if $n_{\bullet}(a)>0$, $I\leq a$, and $a+i\leq D$.

1

1

Table 2: Model rankings and associated statistics for Null Hypotheses I and II. For both

hypotheses 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

statistically identifies also 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 differs with expected brood size on hatch day; PP: juvenile

survivorship differs among ponds with different invertebrate productivities. The symbol $\theta^2_{B,C}(a)$

indicates that the degree of correlated mortality among juveniles can diminish with brood age.

The heading 'Pair' identifies, using shared characters, paired rank comparisons for the effect of

$E_{N,b}[0]_{RC}$ for Hypothesis I, the effect of PP_R for Hypothesis II, and other comparisons referred to

in the text. The heading # represents the number of estimated parameters, *W* the AIC$_C$ weights.

Null Hypothesis I: There is no difference in the probability of surviving to fledge among

juveniles reared in broods of different sizes as measured or inferred on their hatch day.

Rank	Pair	Model description	ΔAIC_C	#	W	Deviance (L_{MIN})
1	E,H	NULL+YEAR$_R$+$E_{N,b}[0]_{RC}$+$\theta^2_{B,C}(a)$	0.00	14	0.99	1522.67
2	A,E,F	NULL+YEAR$_R$+$E_{N,b}[0]_{RC}$	14.40	13	0.01	1539.09
3	B	NULL+YEAR$_R$+AGE$_R$+$E_N[0]_{RC}$	16.26	14	0.00	1538.93
4	G,H	NULL+YEAR$_R$+$\theta^2_{B,C}(a)$	21.02	10	0.00	1551.72
5	B	NULL+YEAR$_R$+AGE$_R$	24.10	10	0.00	1554.80

6	A,G	NULL+YEAR$_R$	26.91	9	0.00	1559.62
7	C,F	NULL+ $E_{N,b}[0]_{RC}$	32.64	10	0.00	1563.34
8	D	NULL+AGE$_R$+ $E_{N,b}[0]_{RC}$	34.29	11	0.00	1562.99
9	D	NULL+AGE$_R$	36.86	7	0.00	1573.57
10	C	NULL (E$_C$,J$_{RC}$)	42.30	6	0.00	1581.02

Null 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. The best model (AIC$_C$=1550.73) passed the parametric bootstrap diagnostic for goodness-of-fit.

Null Hypothesis II: There is no difference 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.

Rank	Pair	Model description	ΔAIC$_C$	#	W	Deviance (L_{MIN})
1	A,K	NULL+YEAR$_R$+ $E_{N,b}[0]_{RC}$ + $\theta^2_{B,C}(a)$	0.00	14	0.77	849.05
2	A	NULL+YEAR$_R$+PP$_R$+ $E_{N,b}[0]_{RC}$ + $\theta^2_{B,C}(a)$	3.50	16	0.13	848.53
3	B,K	NULL+YEAR$_R$+ $E_{N,b}[0]_{RC}$	5.29	13	0.06	856.35
4	C	NULL+YEAR$_R$+AGE$_R$+ $E_{N,b}[0]_{RC}$	7.13	14	0.02	856.18
5	B	NULL+YEAR$_R$+PP$_R$+ $E_{N,b}[0]_{RC}$	8.52	15	0.01	855.56
6	C	NULL+YEAR$_R$+AGE$_R$+PP$_R$+ $E_{N,b}[0]_{RC}$	10.49	16	0.04	855.52

7	D	NULL+AGE_R+$E_{N,b}[0]_{RC}$	19.09	11	0.00	874.17
8	E	NULL+$E_{N,b}[0]_{RC}$	19.20	10	0.00	876.30
9	D	NULL+AGE_R+PP_R+$E_{N,b}[0]_{RC}$	20.19	13	0.00	871.26
10	F,J	NULL+$YEAR_R$+PP_R	20.87	11	0.00	875.95
11	J	NULL+$YEAR_R$+PP_R+$\theta^2_{B,C}(a)$	21.40	12	0.00	874.47
12	E	NULL+PP_R+$E_{N,b}[0]_{RC}$	21.62	12	0.00	874.70
13	F	NULL+$YEAR_R$	21.66	9	0.00	880.76
14	G	NULL+$YEAR_R$+AGE_R	22.74	10	0.00	879.83
15	H	NULL+AGE_R	23.07	7	0.00	886.19
16	G	NULL+$YEAR_R$+AGE_R+PP_R	23.69	12	0.00	876.76
17	H	NULL+AGE_R+PP_R	24.09	9	0.00	883.20
18	I	NULL (E_C,J_{RC})	24.47	6	0.00	889.59
19	I	NULL+PP_R	34.86	8	0.00	895.97

Null 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 $\hat{C}\pm1$ SE for the null and best models are 1.05±0.05 and 1.06±0.05, respectively. The best model (AIC$_C$=877.14) passed the parametric bootstrap diagnostic for goodness-of-fit.

1

1 **FIGURES**

2 Fig. 1. Map indicating the approximate location of Riske Creek, and portraying landscape

3 characteristics of the Chilcotin-Cariboo region of British Columbia (B.C.), Canada.

4 Fig. 2. Example plots of (a) probability density functions and their associated (b) survivorship

5 attenuation functions for random (R) and correlated (C) mortality processes and both additively

6 combined ($R\&C$). The functions for $R\&C$ in plot (a) and (b) portray a situation with an initial

7 period where young juveniles experience a high rate of correlated mortality (perhaps catastrophic

8 losses of broods) which diminishes with time as the rate of random mortality increases then

9 diminishes with age. The parameter values for this example are: $\alpha_{B,R}=0.001$, $\beta_{B,R}=2.5$,

10 $\alpha_{B,C}=0.1$, $\beta_{B,C}=0.9$, $c_B=0.7$ and $f_B=0.05$.

11 Fig. 3. Examples of plausible probability mass distributions of survivorship outcomes,

12 $p_\bullet[s_\bullet(a+i)]$, for $n_\bullet(a)=10$, $\mu_{\bullet,\bullet}(a)=0.6$, and $v_\bullet=0$. Plot (a), no overdispersion, $\theta^2_{\bullet,\bullet}(a)=0$,

13 generates a binomial distribution of survivorship outcomes; (b) partial overdispersion,

14 $\theta^2_{\bullet,\bullet}(a)=0.2$, generates a greater spread of possible survivorship outcomes according to a beta-

15 binomial distribution; while (c) full overdispersion, $\theta^2_{\bullet,\bullet}(a)=1.0$, generates a beta-binomial

16 distribution with only two possible outcomes, either all $n_\bullet(a)$ individuals survive or die. Plot (d)

17 portrays an example where 70% of the mortalities follow a random mortality process (C), while

18 30% of mortalities ($c_\bullet=0.3; f_\bullet=0$) are correlated ($C$) and fully overdispersed as per plot (c).

19 Fig. 4. Typical (a) observed, (b) predicted, and (c) simulated profiles of the observed number of

20 eggs (brood ages <0) in a clutch and juveniles (brood ages ≥0) in a brood. Clutches and broods

21 for each tending hen are connected by faded lines. The observed data (a) are those for the years

1   1995 and 1997 to 1999. These data were analyzed to challenge Null Hypothesis I ($\Re = 1090$). It

2   is evident that many more broods were observed than clutches. Note that the observed data are

3   truncated at a brood age of 56 days corresponding to the analyst's choice of *D*=56 for age at

4   fledging. The model predictions (b) are those provided by Model 1 of Table 2. Likewise, the

5   simulated data (c) are one realization using the maximum likelihood estimated parameters of

6   Model 1 of Table 2.

7   Fig. 5. The probability, on hatch day, that a juvenile Barrow's Goldeneye will fledge at *D*=56

8   days, $p[Fledge\,(0,D)]$, as a function of expected brood size on hatch day, $E_{N,b}[0]$. The values

9   portrayed are those reported by the highest ranked model (Model 1) of those used to challenge

10   Null Hypothesis I (Table 1). Year-effects are clearly evident. There is no evidence that

11    $p[Fledge\,(0,D)]$ is influenced by $E_{N,b}[0]$ in 1997, while in other years there is a clear tendency

12   for juveniles hatched into larger broods have an increased $p[Fledge\,(0,D)]$.

13   Fig. 6. (a) The probability, on hatch day, that a juvenile Barrow's Goldeneye will fledge at *D*=56

14   days, $p[Fledge\,(0,D)]$, as a function of expected brood size on hatch day, $E_{N,b}[0]$. The values

15   portrayed are those reported by the highest ranked model (Model 2) of those models used to

16   challenge Null Hypothesis II that include pond productivity as a covariate (Table 1). This result

17   is similar to that portrayed in Fig. 5 which is based on a larger sample size. (b) The

18    $p[Fledge\,(0,D)]$ as a function of standard deviates of pond productivity measured as mean

19   invertebrate biomass per pond-year (mg/sample). The values portrayed are those reported by

20   Model 11 of those used to challenge Null Hypothesis II. The results indicate both a

21   parametrically and statistically weak tendency for the $p[Fledge\,(0,D)]$ to be higher on the more

22   productive ponds. The inadequacy of this relationship is emphasized by the very low rank (11th)

1   of this model when compared to models including $E_{N,b}[0]$ as a covariate. (c) Illustrating this

2   point, the $p[Fledge\,(0,D)]$ as a function of the standard deviates of pond productivity for the

3   highest ranked model (Model 1), which includes the covariate $E_{N,b}[0]$, but excludes pond

4   productivity, shows no residual relationship between $p[Fledge\,(0,D)]$ and pond productivity.

5   Fig. 7. The influence of $E_{N,b}[0]$ on brood survivorship in years 1995 and 1997 to 1999 is

6   illustrated by the increasing shallower survivorship profiles, ($A_B(a)$, solid lines), for three

7   deliberately chosen increasing initial brood sizes (5, 15 and 25 juveniles hatched). These profiles

8   correspond to Model 1 challenging Null Hypothesis I. Associated with each survivorship profile

9   are three simulated brood outcomes (faded lines with symbols) illustrating the degree of

10   variability in brood survivorship that can be realized in a sampled dataset.

11   Fig. 8. Daily survivorship profiles for juveniles from hatch day (a=0) to fledge day (a=D), and

12   according to year, with lines connecting juveniles within a brood. Daily survivorship for the

13   random (R) and correlated (C) mortality processes combined (solid circles, solid lines) results

14   from the weighted addition of the random mortality process (open circles, faded lines) and

15   correlated mortality process (open diamonds, faded lines). The correlated mortality process

16   diminishes with brood age when $f_B>0$ as in this result for Model 1 challenging Null Hypothesis

17   I (see Fig. 10a). Individual broods portray different survivorship profiles due to differences

18   among broods in their expected brood size on hatch day, $E_{N,b}[0]$. The tendency is for larger

19   values of $E_{N,b}[0]$ to be associated with higher survivorships (see Fig. 9).

20   Fig. 9. Daily survivorship for the first day after hatch, and according to year, for juveniles versus

21   expected brood size on hatch day, $E_{N,b}[0]$, for Model 1 challenging Null Hypothesis I.

1   Fig. 10. (a) The proportion of juveniles alive at the plotted brood age that are vulnerable to a

2   correlated mortality process. This proportion will diminish with brood age when $f_B > 0$ as in this

3   result for Model 1 challenging Null Hypothesis I.   (b) The effective independent unit (EIU)

4   versus brood age. EIU will diminish with $n_B(a)$ as well as with brood age when $v_B > 0$ as in this

5   result for Model 1 challenging Null Hypothesis I. The scatter within and among years for both

6   (a) and (b) arises from differences among broods in their expected brood size on hatch day,

7    $E_{N,b}[0]$, and for (b) also from differences the number of juveniles alive at brood age a, $n_B(a)$.

8   Fig. 11. The expected brood size on hatch day, $E_{N,b}[0]$, as a function of the standard deviate of

9   pond productivity measured as mean invertebrate biomass per pond-year (mg/sample). The

10   values portrayed for $E_{N,b}[0]$ are those reported by Model 1 of those used to challenge Null

11   Hypothesis I.

Figure 1

Figure 2

a)

b)

Figure 3

a) No overdispersion

b) Partial overdispersion

c) Full overdispersion

d) Mixture of b & c

5

Figure 4

a) Observed

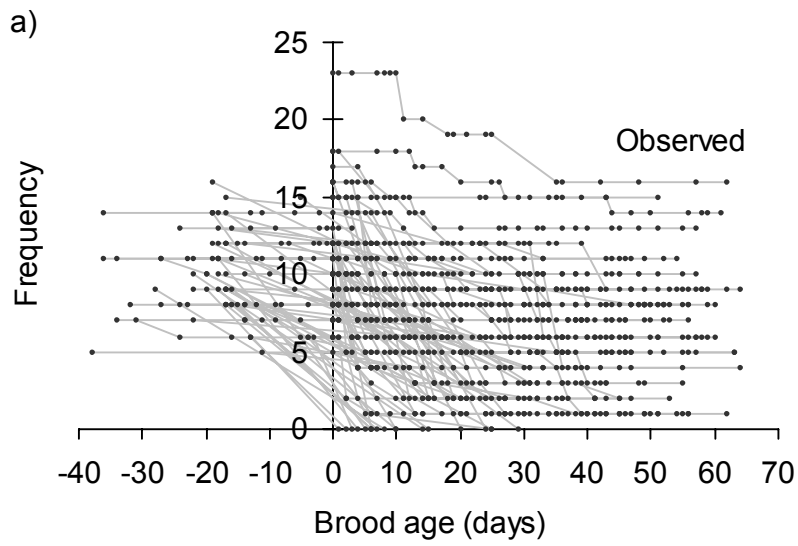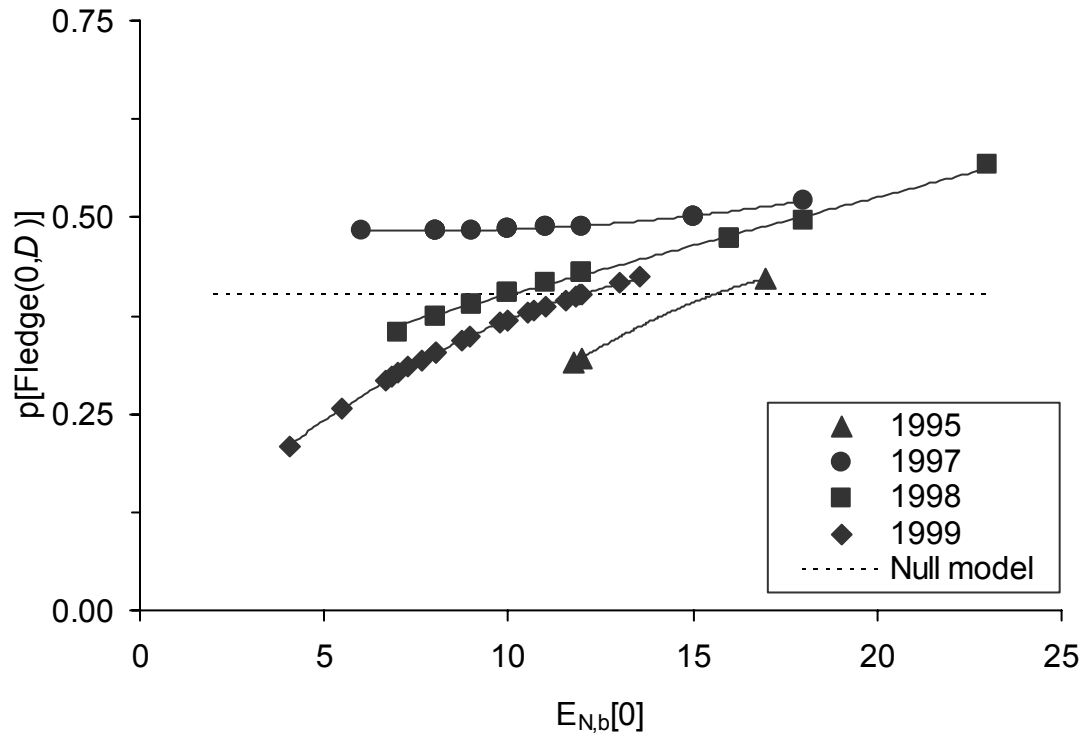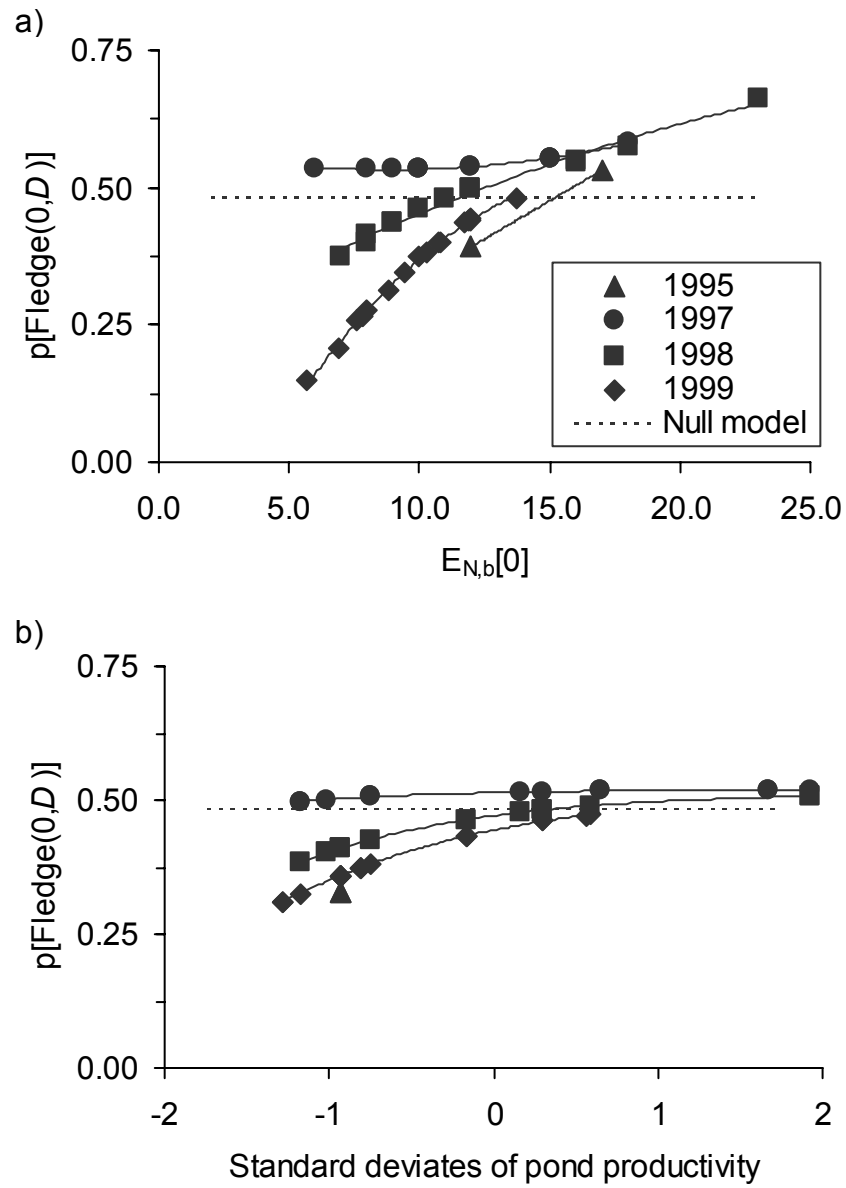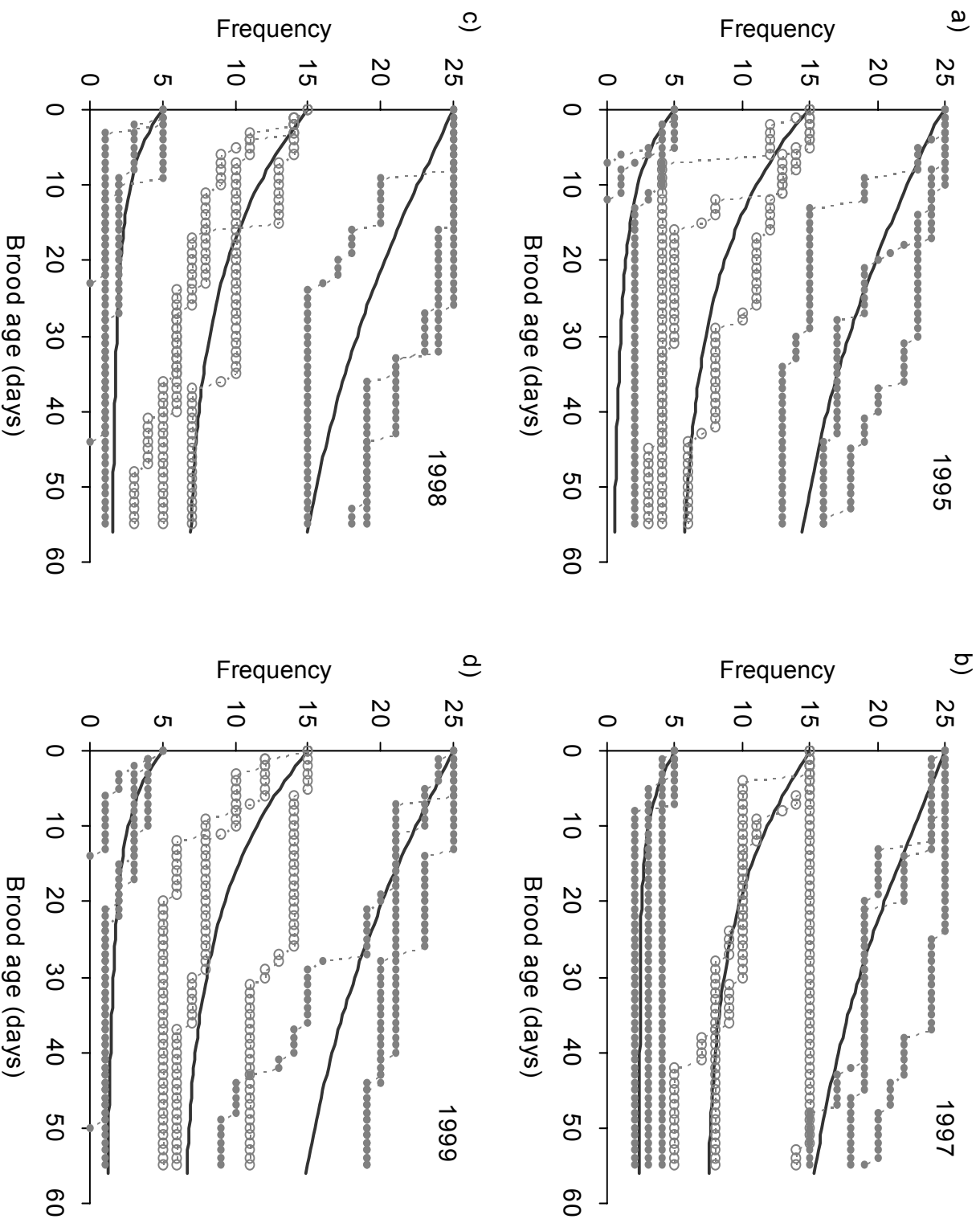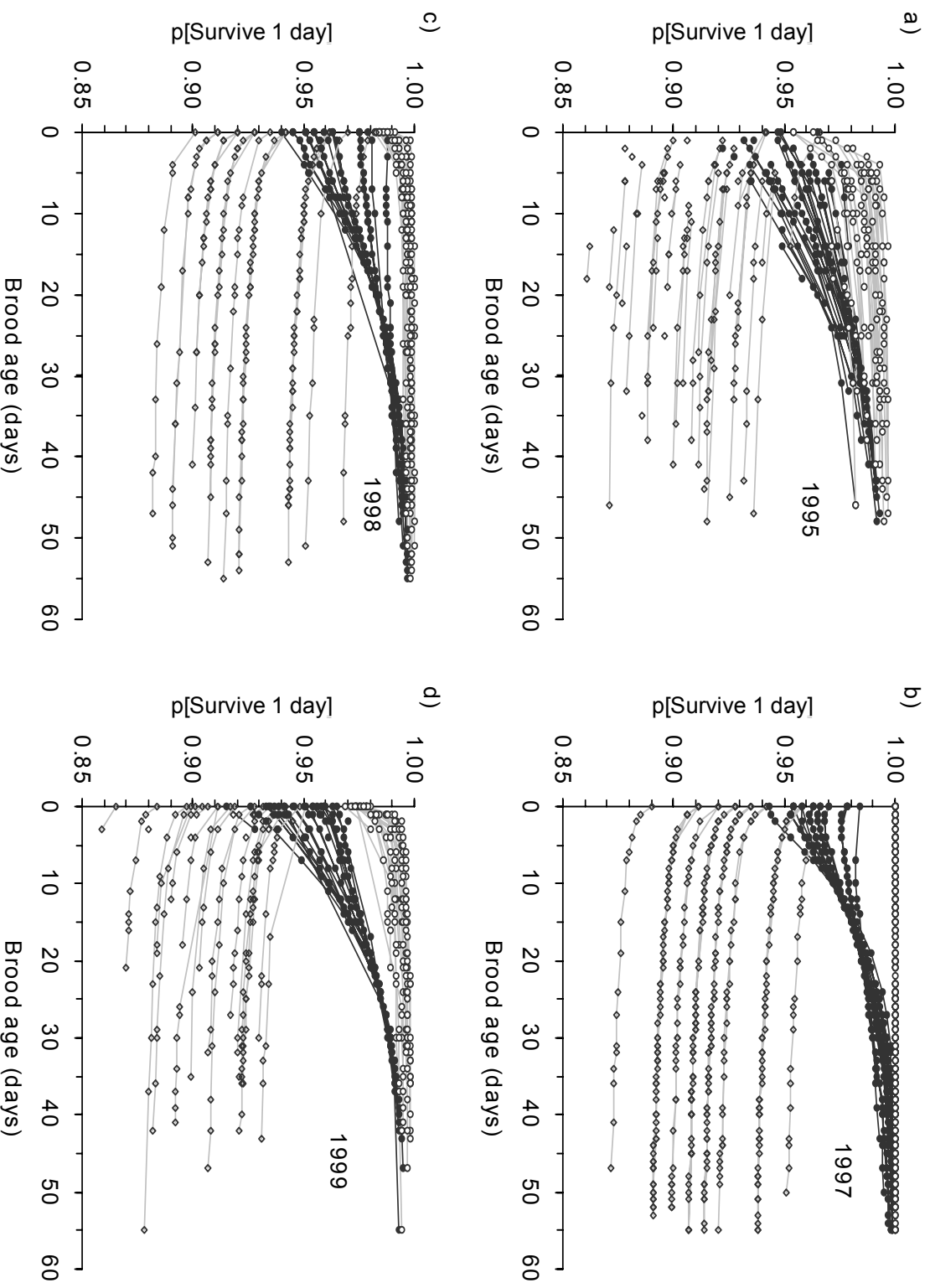b) Predicted

c) Simulated

Figure 5
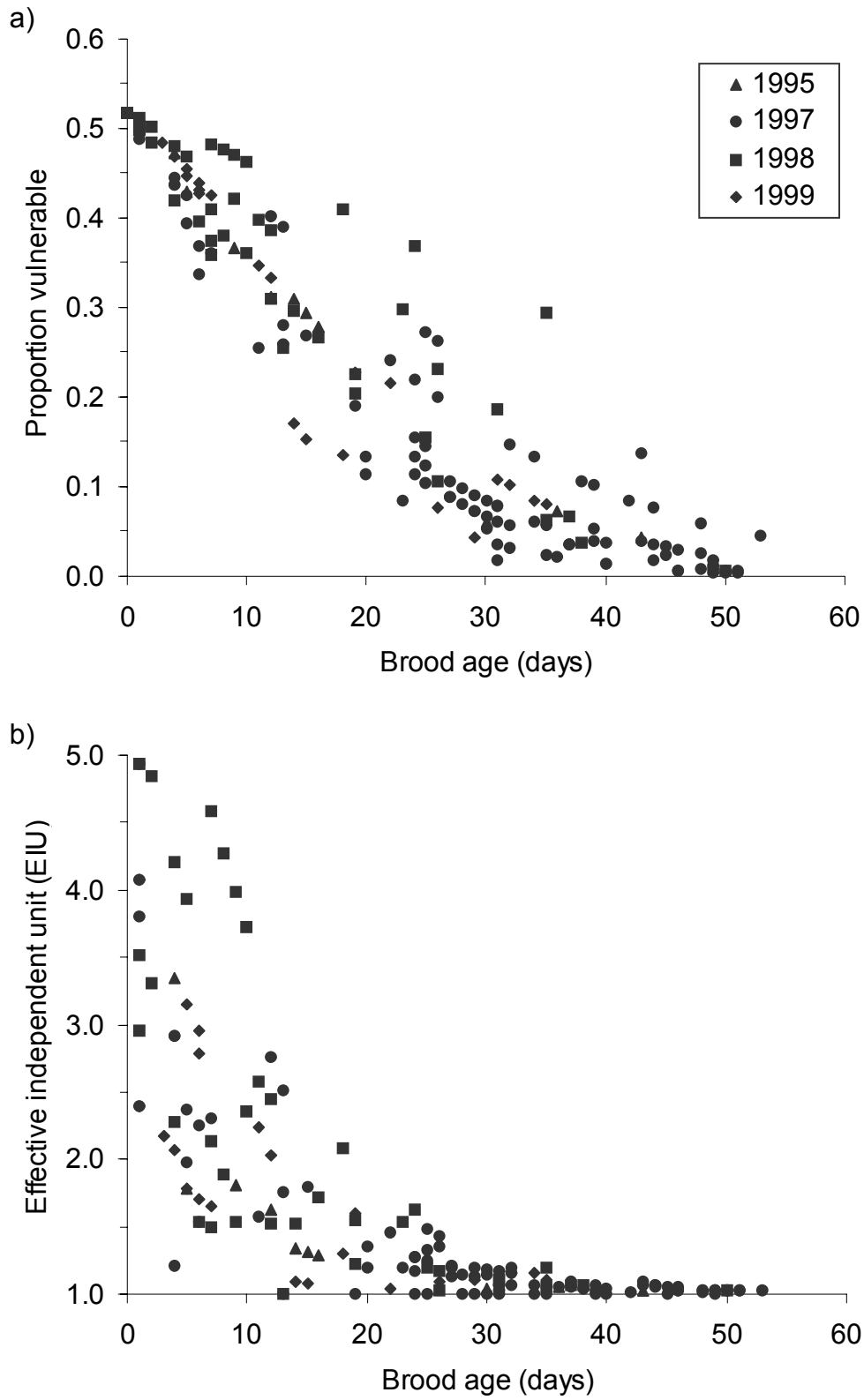
Figure 6

Smith et al.: Clutch & brood survivorship
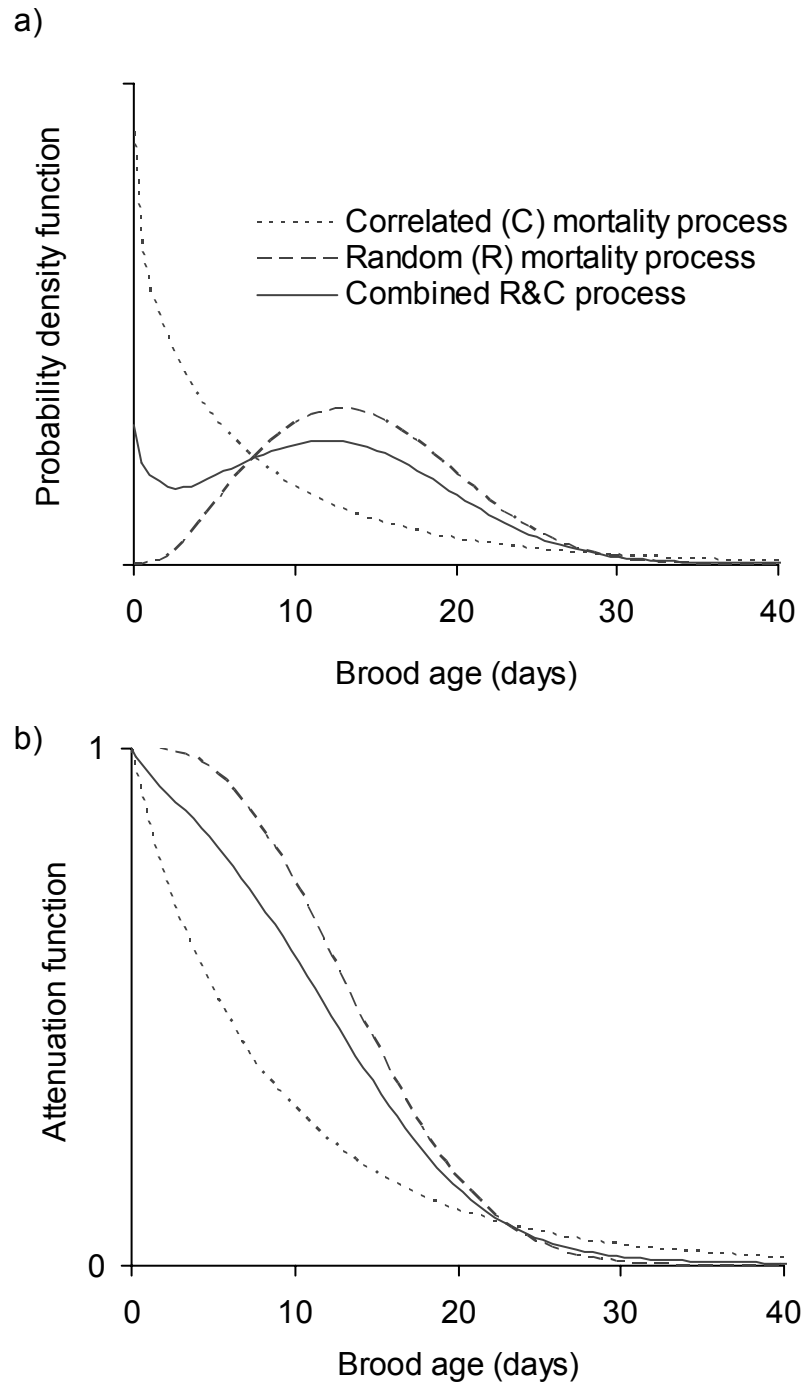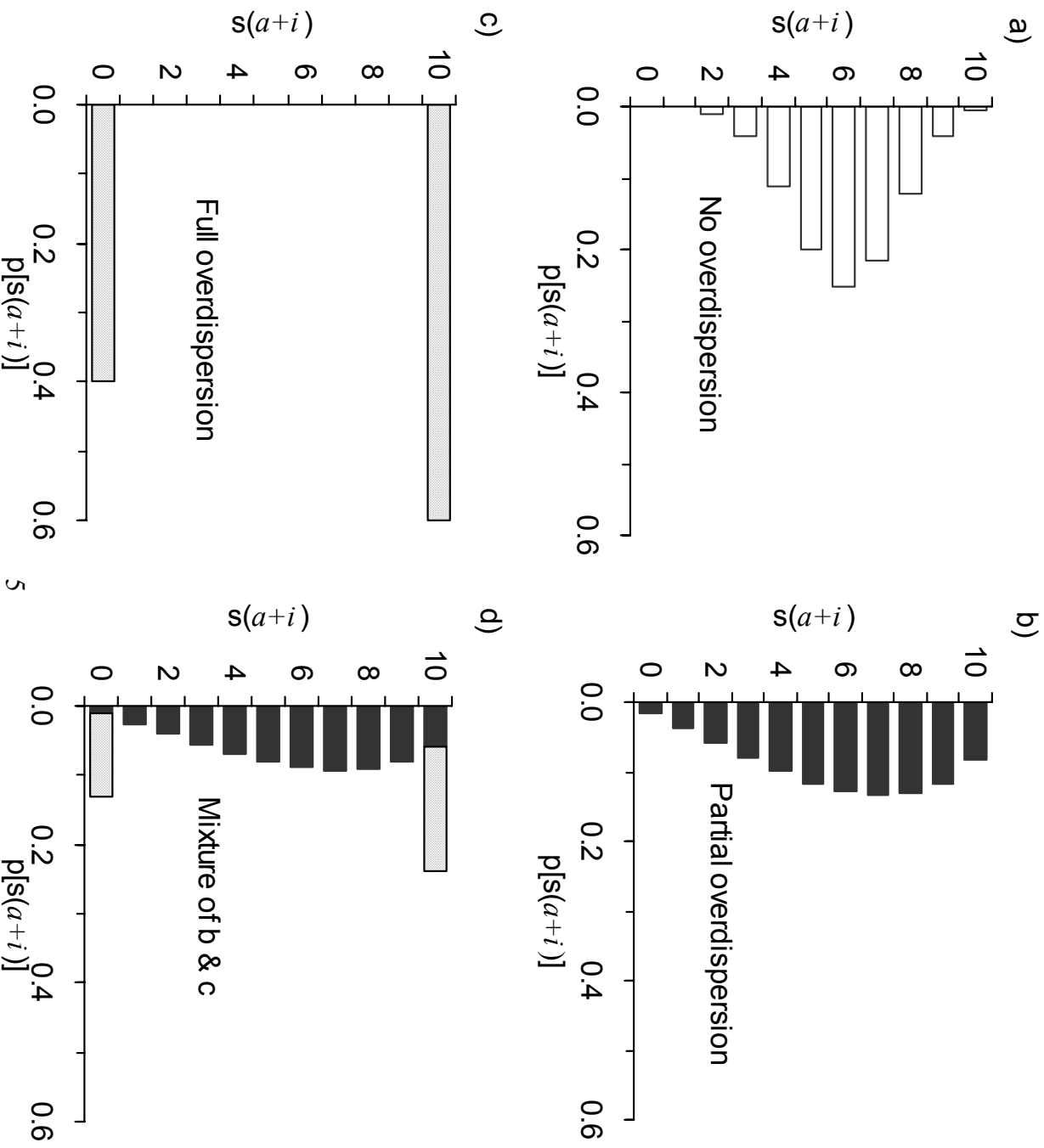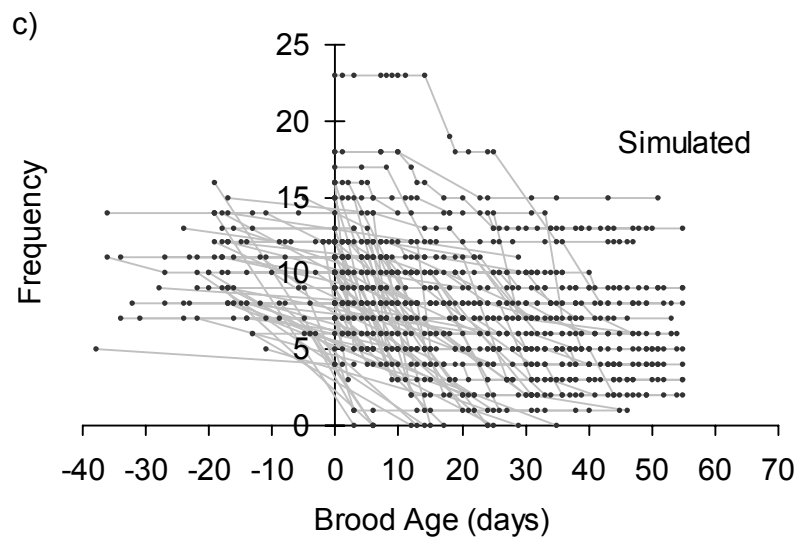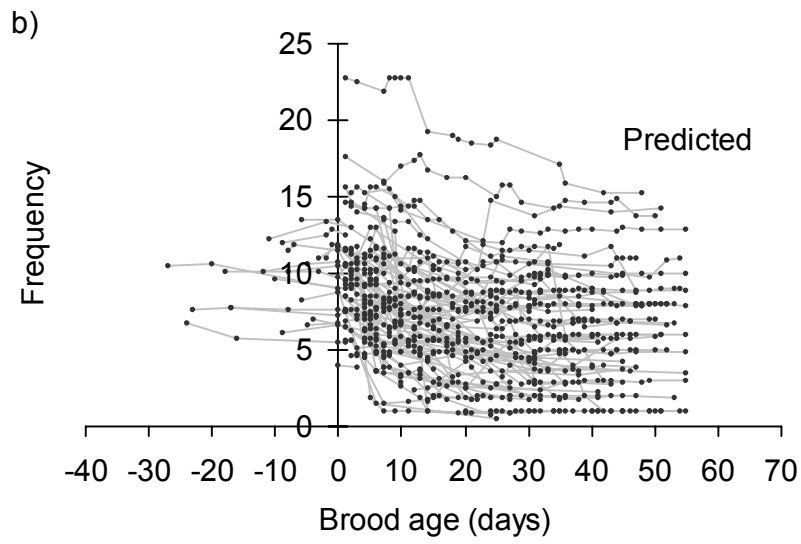
Figure 7

Figure 8

Figure 9

Figure 10

a)

b)

Figure 11