

# Long-term research and hierarchical models reveal consistent fitness costs of being the last egg in a clutch

Cheyenne R. Acevedo<sup>1</sup>  | Thomas V. Riecke<sup>1,2</sup>  | Alan G. Leach<sup>1,2</sup>  |  
 Madeleine G. Lohman<sup>1</sup>  | Perry J. Williams<sup>1</sup>  | James S. Sedinger<sup>1</sup>

<sup>1</sup>Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV, USA

<sup>2</sup>Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, NV, USA

## Correspondence

Cheyenne R. Acevedo  
 Email: cheyenne.acevedo13@gmail.com

## Funding information

Migratory Bird Management Region 7, U. S. Fish and Wildlife Service; Ducks Unlimited; Morro Bay Brant Group; Institute for Wetland and Waterfowl Research, Ducks Unlimited Canada; Alaska Science Center, US Geological Survey; Phil Jebbia (in memory of Marnie Shepherd); National Science Foundation, Grant/Award Number: DEB 0743152, DEB 1252656, DEB 9815383, OPP 0196406, OPP 9214971 and OPP 9985931

Handling Editor: David Koons

## Abstract

1. Maintenance of phenotypic heterogeneity in the face of strong selection is an important component of evolutionary ecology, as are the consequences of such heterogeneity. Organisms may experience diminishing returns of increased reproductive allocation as clutch or litter size increases, affecting current and residual reproductive success. Given existing uncertainty regarding trade-offs between the quantity and quality of offspring, we sought to examine the potential for diminishing returns on increased reproductive allocation in a long-lived species of goose, with a particular emphasis on the effect of position in the laying sequence on offspring quality.
2. To better understand the effects of maternal allocation on offspring survival and growth, we estimated the effects of egg size, timing of breeding, inter- and intra-annual variation, and position in the laying sequence on gosling survival and growth rates of black brant *Branta bernicla nigricans* breeding in western Alaska from 1987 to 2007.
3. We found that gosling growth rates and survival decreased with position in the laying sequence, regardless of clutch size. Mean egg volume of the clutch a gosling originated from had a positive effect on gosling survival ( $\beta = 0.095$ , 95% CRI: 0.024, 0.165) and gosling growth rates ( $\beta = 0.626$ , 95% CRI: 0.469, 0.738). Gosling survival ( $\beta = -0.146$ , 95% CRI:  $-0.214$ ,  $-0.079$ ) and growth rates ( $\beta = -1.286$ , 95% CRI:  $-1.435$ ,  $-1.132$ ) were negatively related to hatching date.
4. These findings indicate substantial heterogeneity in offspring quality associated with their position in the laying sequence. They also potentially suggest a trade-off mechanism for females whose total reproductive investment is governed by pre-breeding state.

## KEYWORDS

black brant, *Branta bernicla nigricans*, fitness, growth, lack clutch, life-history evolution, reproductive allocation, survival

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2020 The Authors. *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society

## 1 | INTRODUCTION

The maintenance of individual heterogeneity in natural populations in the face of strong directional selection remains an issue of fundamental importance (McDonald & Yeaman, 2018). The principal hypotheses explaining such heterogeneity include (a) genetic covariance between traits under directional selection (Assis, Patton, Hubbe, & Marroig, 2016; Penna, Melo, Bernardi, Oyarzabal, & Marroig, 2017); (b) dispersal into habitats with novel selection gradients (Hargreaves & Eckert, 2014; Pontarp et al., 2019); (c) temporal variation in the direction of selection gradients (Clegg, Frentiu, Kikkawa, Tavecchia, & Owens, 2008); (d) trade-offs between offspring number and quality (Smith, Kallander, & Nilsson, 1989) and (e) maternal or environmental influence on phenotype (Galloway, 1995; Hoffmann & Merilä, 1999; Larsson, 1993; Rossiter, 1996). Differential allocation of resources to offspring based on birth order or position in the laying sequence represents one manifestation of the last hypothesis (Gilby, Sorato, & Griffith, 2012). Many avian species also exhibit variation in egg size within the laying sequence (Arnold, 1991), where egg size declines marginally as the position in the laying sequence increases (Flint & Sedinger, 1992; Williams, Lank, & Cooke, 1993). The decline in egg size with laying position may contribute to synchronized hatching within clutches (Nicolai, Sedinger, & Wege, 2004). This is due to variation in yolk and albumen content within clutches (Alisauskas, 1986; Williams, 1994), where embryos that are laid later in the clutch have higher metabolic rates (Nicolai et al., 2004), require less incubation (Flint, Lindberg, Maccluckie, & Sedinger, 1994) and have reduced yolk reserves at hatch (Boonstra, Clarke, & Reed, 2010; Nicolai et al., 2004). Alternatively, decreased allocation of resources to later laid eggs may also be an adaptive response to the reduced recruitment probability of these eggs (Williams, Lank, & Cooke, 1993). Such variation may also reflect a mechanism to provide advantages to the first-born young in altricial birds (Faurie, Russell, & Lummaa, 2009; Gilby et al., 2012; Magrath, Brouwer, & Komdeur, 2003; Martínez-Padilla, Vergara, & Fargallo, 2017).

Life-history theory suggests individual organisms attempt to optimize their residual reproductive value and the fitness of their offspring in the presence of trade-offs, for example, between offspring size and number (Stearns, 1992). Lack (1947) proposed trade-offs among offspring quantity and quality, where birds with altricial young modify their allocation in the clutch based on resource availability and their ability to provision and ultimately fledge their young (Lack, 1954). Lack expanded his hypotheses to include species with precocial young but hypothesized trade-offs occurred at the egg production stage because precocial species do not provision their young (Lack, 1967). He suggested that the inverse relationship between clutch size and egg size among species of waterfowl (Order Anseriformes) provided evidence to support his hypothesis that nutrient constraints at the time of laying regulated clutch size in species with precocial young (Lack, 1967). While clutch size–egg size trade-offs are apparent among species, they rarely hold up within species (Arnold & Rohwer, 1991; Charnov & Ernest, 2006; Rohwer, 1988), perhaps because variation in individual abilities to acquire resources

may partially mask such trade-offs (Van Noordwijk & de Jong, 1986). In particular, variation in pre-breeding condition can create a positive association between condition and total investment in eggs (Ankney, 1984; Ankney & MacInnes, 1978; Raveling, 1979) that masks the negative association between egg size and clutch size expected under a trade-off between the two (Flint, Grand, & Sedinger, 1996).

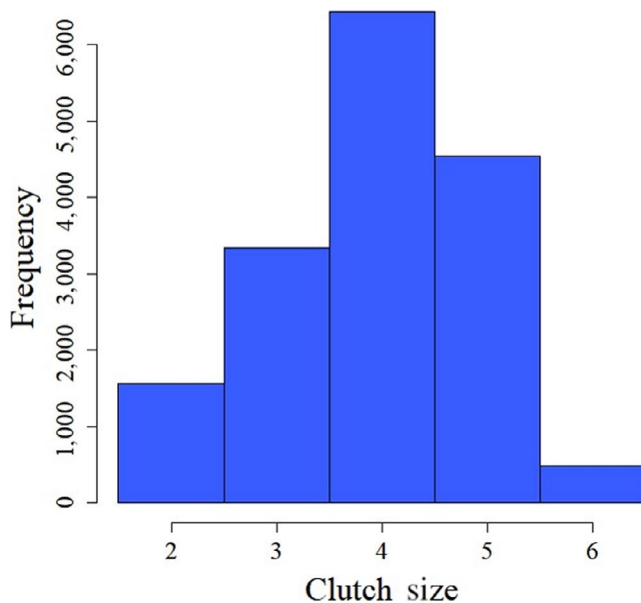
Drent and Daan (1980) expanded upon Lack's ideas, and formalized these relationships, proposing that individuals optimized the combination of reproductive allocation and breeding date, conditional on their pre-breeding state (Daan, Dijkstra, & Tinbergen, 1990). However, research examining these relationships in precocial species remains limited (but see, Descamps, Bêty, Love, & Gilchrist, 2011; Leach, Dellen, Riecke, & Sedinger, 2017; Rosenheim & Rosen, 1991; Sedinger, Dellen, Leach, & Riecke, 2017; Warren, Cutting, & Koons, 2013; Williams, Lank, Cooke, & Rockwell, 1993). Females in poor condition can delay breeding to increase their nutritional status but delayed breeding within a season is negatively associated with per capita recruitment of offspring (Dawson & Clark, 2000). Therefore, the clutch size-timing of breeding optimization hypothesis is that females optimize their fitness through trade-offs between clutch size and timing of breeding (Daan et al., 1990; Drent & Daan, 1980).

Clutch initiation dates often vary substantially among breeding seasons (Dickey, Gauthier, & Cadieux, 2008; Lindberg, Sedinger, & Flint, 1997). Phenological mismatches between the timing of reproduction and optimal foraging conditions contribute substantially to variation in reproductive success among years (Dickey et al., 2008; Ross, Alisauskas, Douglas, & Kellett, 2017). While short-distance migrants and residents can adjust the timing of breeding as a response to varying spring conditions (Clark, Pöysä, Runko, & Paasivaara, 2014), long-distance migrants are less plastic in their response to environmental conditions on the breeding grounds (Arzel, Elmer, & Guillemain, 2006; Both & Visser, 2001). Critically, inter- and intra-annual variation in the timing of breeding (Lindberg et al., 1997) have strong effects on long-distance migrants and could represent one source of individual heterogeneity in these species. Additionally, there are unique strengths in utilizing long-term studies, compared to short-term experiments, to examine inter- and intra-annual variation when addressing individual variability (Clutton-Brock & Sheldon, 2010).

Arctic-nesting geese provide excellent model systems to examine variation in reproductive strategies, because they experience short reproductive seasons, selecting for rapid growth and development, potentially magnifying trade-offs and individual heterogeneity. Additionally, well-established phenological mismatches between delayed reproductive attempts and forage quality make timing of breeding critically important (Cooch, Lank, Rockwell, & Cooke, 1992; Dawson & Clark, 2000; Ross et al., 2017; Sedinger & Raveling, 1986), strengthening selection for optimization of clutch size and timing of breeding (Rowe, Ludwig, & Schluter, 1994). Additionally, geese display both within- and among-female variation in egg size (Larsson & Forslund, 1992) that could contribute to the maintenance of heterogeneity and trade-offs between clutch size and egg size. Black brant *Branta bernicla nigricans* (hereafter brant) are small, arctic-nesting geese, breeding in coastal tundra in the Nearctic, and wintering

primarily in coastal estuaries and wetlands along the Pacific coast of North America (Lewis, Ward, Sedinger, Reed, & Derksen, 2013). Brant and other arctic-nesting geese are capital breeders; they must acquire and store lipid and protein reserves for egg production and incubation (Ankney, 1984; Dawson & Clark, 1996; Sedinger, Flint, & Lindberg, 1995), before their arrival on the breeding grounds (Ross et al., 2017). Moreover, brant exhibit substantial heterogeneity in the size of laid clutches, where inexperienced 2-year-old females often lay two egg clutches (Flint & Sedinger, 1992), and natural clutches of six eggs have been documented (Leach et al., 2017), albeit rarely (Figure 1). Previous work has demonstrated trade-offs may exist among clutch size, egg success and pre-fledging survival (Leach et al., 2017; Sedinger et al., 2017). Reproductive success and offspring quality are also related to the timing of breeding in brant (Cooke, Findlay, & Rockwell, 1984; Sedinger, Flint, et al., 1995) and other waterfowl (Christians, 2002; Clark et al., 2014). Egg size and position in the laying sequence influence offspring survival in other precocial species, but have not yet been revealed in black brant (Leblanc, 1987; Pelayo & Clark, 2003; Williams, 1994; Williams, Lank, & Cooke, 1993).

Our purpose was to examine how within- and among-clutch variation in egg size and position in the laying sequence contributed to the maintenance of heterogeneity in offspring quality and survival. To do so, we examined how position in the laying sequence affected pre-fledging survival and growth, and how the effect of position might vary among clutches of different sizes. Additionally, we accounted for the effects of timing of breeding, within and among years. To the extent that heterogeneity in offspring fitness is inherent in the production of a clutch, our findings also contribute to understanding ultimate regulation in clutch size.



**FIGURE 1** The frequency of clutch sizes in black brant from 16,349 clutches observed at the Tutakoke River Brant Colony, Alaska, USA, 1987–2007. One and seven egg clutches were excluded, as they represent <0.01 of observed clutches, and are typically a result of unobserved partial predation or intraspecific nest parasitism

## 2 | MATERIALS AND METHODS

### 2.1 | Data collection

This study was conducted at the Tutakoke River Brant Colony (hereafter, TRC; 61°N 165°W), where between 25% and 40% of breeding adults have been marked with uniquely engraved 2.5-cm high plastic bands and U. S. Geological Survey steel leg bands (Sedinger, Lindberg, Rexstad, Chelgren, & Ward, 1997). Brant arrive and initiate their nests on the breeding colony in May (Lindberg et al., 1997). Following the beginning of nest initiation, observers monitored nests by searching forty-nine 50-m radius circular plots approximately every 4 days during the laying period. We monitored all brant nests within each plot, and also opportunistically located nests of marked brant outside the plots (Sedinger, Herzog, & Ward, 2004). Each nest was recorded on an aerial photographic map, assigned a unique number and each egg present was assigned a position in the laying sequence and identified with a permanent marker. When more than one new egg was present, we determined the laying order of each egg using shell staining (Flint & Sedinger, 1992). We estimated the nest initiation date by backdating and assuming that one egg was laid per day with a day skipped between eggs four and five (Flint & Sedinger, 1992). The long and short axes of the egg were measured with dial calipers (Sedinger & Flint, 1991), and egg volume ( $\text{cm}^3$ ) was estimated using a previously developed equation (Flint & Sedinger, 1992). The mean egg volume of a clutch was determined by summing the individual volumes of all eggs and dividing by the number of eggs in the clutch. Residual egg volume was the difference between each individual egg's volume and the mean egg volume for the clutch. Incubation duration varies with clutch size with most nests requiring 24–27 days to hatch (Eichholz & Sedinger, 1998; Leach et al., 2017). Nests associated with marked adults were visited on their hatch days to attach web tags to goslings and goslings emerging from eggs (Alliston, 1975; Sedinger et al., 2004). We included web-tagged goslings in this paper only if goslings were clearly associated with specific eggs. Approximately 30 days post-hatch, we recaptured adult and juvenile brant (Sedinger et al., 2004) by driving broods and molting adult brant into corral traps (Sedinger et al., 1997). See Sedinger et al. (1997) and Sedinger et al. (2001) for more comprehensive data collection methods. Captured goslings with web tags were weighed, measured and given a unique plastic colour band and a metal U.S.G.S. band (Sedinger, Flint, et al., 1995; Sedinger et al., 2004). While brant goslings are robust to capture and handling (Sedinger et al., 1997), we do not recapture individuals within a season in an attempt to minimize handling stress. Therefore, we do not have data typical of capture–mark–recapture studies, where researchers can directly estimate detection conditioned on presence (e.g. Sedinger et al., 2001) because we did not have a third capture occasion within each breeding season (Lebreton, Burnham, Clobert, & Anderson, 1992).

## 2.2 | Gosling survival analysis

Direct recapture rates of goslings within summers are valuable as an index of pre-fledging survival for geese (Williams, Lank, Cooke, & Rockwell, 1993). However, direct recapture rates are also a product of biological processes and an observation process, in this instance, survival and recapture rates. Fortunately, direct recapture rates of brant goslings provide two sources of information that allow us to separate these processes when assessing variation in survival within broods. First, the detection of goslings within a brood is dependent, where we typically capture either all of the surviving goslings and their parents or fail to encounter the entire family group. Second, broods that are encountered provide valuable information about the effects of biological covariates on survival rates specific to each individual or covariates shared among individuals within broods, and variation in survival probabilities among broods. This is a reasonable assumption because banding operations are targeted at family groups.

To separate the biological and observation processes, we developed a novel Bayesian hierarchical model (Supporting Information: Methods). This model allowed us to examine the effects of a suite of covariates related to maternal allocation. We modelled the encounter data ( $Y$ ) for each gosling ( $i$ ) in each brood ( $j$ ) as a function of the probability of a marker being noticed, and recorded ( $\rho = 1$ ) the latent state of each brood ( $\pi$ ) and each gosling's latent state ( $Z$ ),

$$Y_{ij} \sim \begin{cases} \text{Bernoulli}(\rho), & Z_{i,j}\pi_j = 1 \\ 0, & Z_{i,j}\pi_j = 0 \end{cases}.$$

We modelled the latent state of each gosling ( $z_{i,j}$ ) as a function of each gosling's individual survival probability,

$$z_{ij} \sim \text{Bernoulli}(\varphi_i).$$

We modelled individual gosling survival probability as a function of shared temporal variation and individual and brood-specific covariates. First, we modelled random annual variation in survival probability of goslings ( $\varepsilon_{t,\varphi}$ ) around a time-varying mean ( $\mu_{t,\varphi}$ ) with variance ( $\sigma_\varphi^2$ ), where the mean survival rates for each year were a function of the relative mean hatching date of that year (PHENOLOGY) compared to the other years in the study as an index of phenological mismatch (Ross et al., 2017), and a long-term linear trend (TREND) as an index of forage availability (Table S1). Recent work has shown long-term declines in the availability of *Carex subspathacea* (Hoppner's sedge; Lohman et al., 2019; Uher-Koch et al., 2019), which governs the growth rates of brant goslings (Hupp et al., 2017; Sedinger et al., 2001). Thus, we modelled mean annual pre-fledging survival as:

$$\mu_{t,\varphi} = \alpha_\varphi + \beta_{\text{PHENOLOGY},\varphi} \times \text{PHENOLOGY}_t + \beta_{\text{TREND},\varphi} \times \text{TREND},$$

$$\varepsilon_{t,\varphi} \sim N(\mu_{t,\varphi}, \sigma_\varphi^2).$$

After controlling for annual variation in survival and capture probability, we modelled variation in the survival probability of each individual gosling as a function of the mean egg volume in the clutch

(MEAN), its residual egg volume (RES), its hatching date within the season (HATCH) and its position in the laying sequence (PILS), which we modelled as an additional random intercept with variance ( $\sigma_{\text{PILS},\varphi}^2$ ). We modelled both mean egg volume of each clutch, and the residual of each egg from the mean egg volume of each clutch, to decouple position in the laying sequence from egg size, as these covariates can be correlated (Nicolai et al., 2004).

$$\varepsilon_{\text{PILS},\varphi} \sim N(0, \sigma_{\text{PILS},\varphi}^2),$$

$$\begin{aligned} \text{logit}(\varphi_i) = & \varepsilon_{t,\varphi} + \varepsilon_{\text{PILS},\varphi} + \beta_{\text{MEAN},\varphi} \times \text{MEAN}_b \\ & + \beta_{\text{RES},\varphi} \times \text{RES}_i + \beta_{\text{HATCH},\varphi} \times \text{HATCH}_b. \end{aligned}$$

Finally, we modelled the latent state of each brood as a function of whether any brood members had survived to capture, and time-varying annual detection probability ( $p_t$ )

$$\pi_j \sim \begin{cases} \text{Bernoulli}(p_t), & \sum_{k=1}^{k=n_j} z_{ij} > 1 \\ 0, & \sum_{k=1}^{k=n_j} z_{ij} = 0 \end{cases},$$

$$\text{logit}(p_t) \sim N(\mu_p, \sigma_p^2),$$

$$\mu_p \sim N(0, 2.25),$$

$$\sigma_p \sim \text{Uniform}(0, 3).$$

To ensure the validity of this novel approach for estimating survival from direct recaptures of juveniles within a family group, we simulated data and recovered our simulated parameter estimates using analytical techniques identical to those used in this manuscript (Supporting Information R Script).

## 2.3 | Gosling growth rate analysis

We used common covariates for models of both survival and growth. To examine temporal and individual variation in gosling growth rates, we first modelled variation in mean growth rates for each year ( $\varepsilon_{t,g}$ ) as a normal distribution around a time-varying mean ( $\mu_{t,g}$ ). We specified the mean growth rates for each year as a function of the relative mean hatching date of that year (PHENOLOGY) compared to the other years in the study, and a long-term linear trend (TREND).

$$\mu_{t,g} = \alpha_g + \beta_{\text{PHENOLOGY},g} \times \text{PHENOLOGY} + \beta_{\text{TREND},g} \times \text{TREND},$$

$$\varepsilon_{t,g} \sim N(\mu_{t,g}, \sigma_g^2).$$

We then modelled individual daily growth rates (in grams) as a function of the mean egg volume of the clutch (MEAN), the residual of each egg's volume in the clutch (RESIDUAL), the hatching date, z-standardized within each year (HATCH) and its position in the laying

sequence ( $\epsilon_{PILS,g}$ ). When continuous covariates were unknown, we assigned individuals a value of 0, when the position in the laying sequence was unknown, we assigned the mean of the distribution of positions across all clutches.

$$\epsilon_{PILS,g} \sim N(0, \sigma_{PILS,g}^2),$$

$$\beta_i = \epsilon_{t,g} + \epsilon_{PILS,g} + \beta_{MEAN,g} \times MEAN_b + \beta_{RES,g} \times RES_i + \beta_{HATCH,g} \times HATCH_b.$$

Thus, we modelled the effects of position in the laying sequence independently across clutch sizes in both the gosling survival and growth models. This allowed us to account for the interactive effects of clutch size and position in the laying sequence. We assumed a common mean starting mass of 43.6 g (Palmer, 1976), and a linear relationship between gosling age and growth rate (Lindholm, Gauthier, & Desrochers, 1994; Sedinger, Eichholz, & Flint, 1995), where the mass of each gosling at capture was a function of its age in days, and year and individual-specific covariates, with a common variance ( $\sigma_{mass}^2$ ).

$$\mu_i = 43.6 + \beta_i \times \text{age}_i,$$

$$\text{mass}_i \sim N(\mu_i, \sigma_{mass}^2).$$

## 2.4 | Computational details

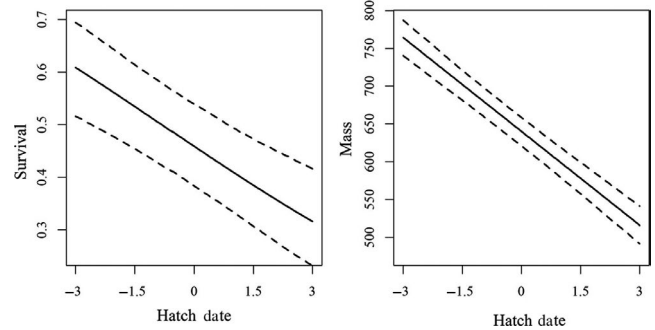
We specified the previously described mixed-effects regression models in JAGS (Plummer, 2003) using the R (R Core Team, 2018) packages `RJAGS` (Plummer, 2013) and `JAGSUI` (Kellner, 2015). We specified a burn-in of 200,000, a thinning rate of 5 and 500,000 total iterations for three chains for both models. We present posterior means, 95% credible intervals in the figures, and proportion of the posterior on the same side of 0 as the mean of the posterior ( $f$ ) in the text.

## 3 | RESULTS

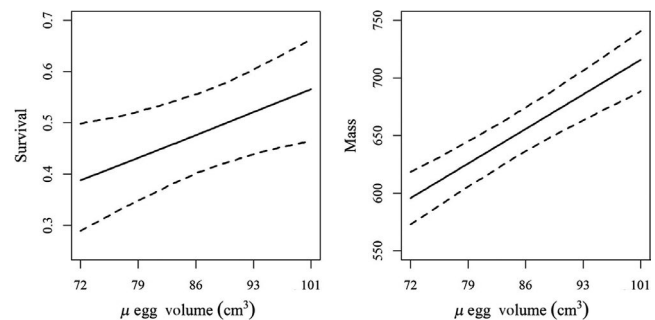
We web-tagged 22,201 goslings at the nest from 1987 through 2007. We re-encountered 2,922 uniquely marked goslings during banding in the same year they were web-tagged and we use data from 2,685 goslings captured at banding to inform gosling growth models, as some recaptured goslings were not measured due to time constraints in animal handling. MCMC chains for all estimated parameters in both models converged ( $\hat{R} < 1.01$ ).

### 3.1 | Survival

Gosling survival was negatively affected by relative hatching date within years ( $\beta = -0.147$ , 95% CRI:  $-0.208, -0.085$ , Figure 2). Annual phenology did not explain significant variation in gosling survival ( $\beta = -0.017$ , 95% CRI:  $-0.436, 0.340$ ). Mean egg volume of each clutch ( $\beta = 0.079$ , 95% CRI:  $0.016, 0.146$ , Figure 3) and residual



**FIGURE 2** Estimated effects of z-standardized hatching date on black brant gosling survival ( $\beta = -0.146$ , 95% CRI:  $-0.214, -0.079$ ), and predicted gosling mass at 30 days of age ( $\beta = -1.29$ , 95% CRI:  $-1.44, -1.14$ ) for goslings uniquely marked and released at the Tutakoke River Brant Colony, Alaska, USA, 1987–2007



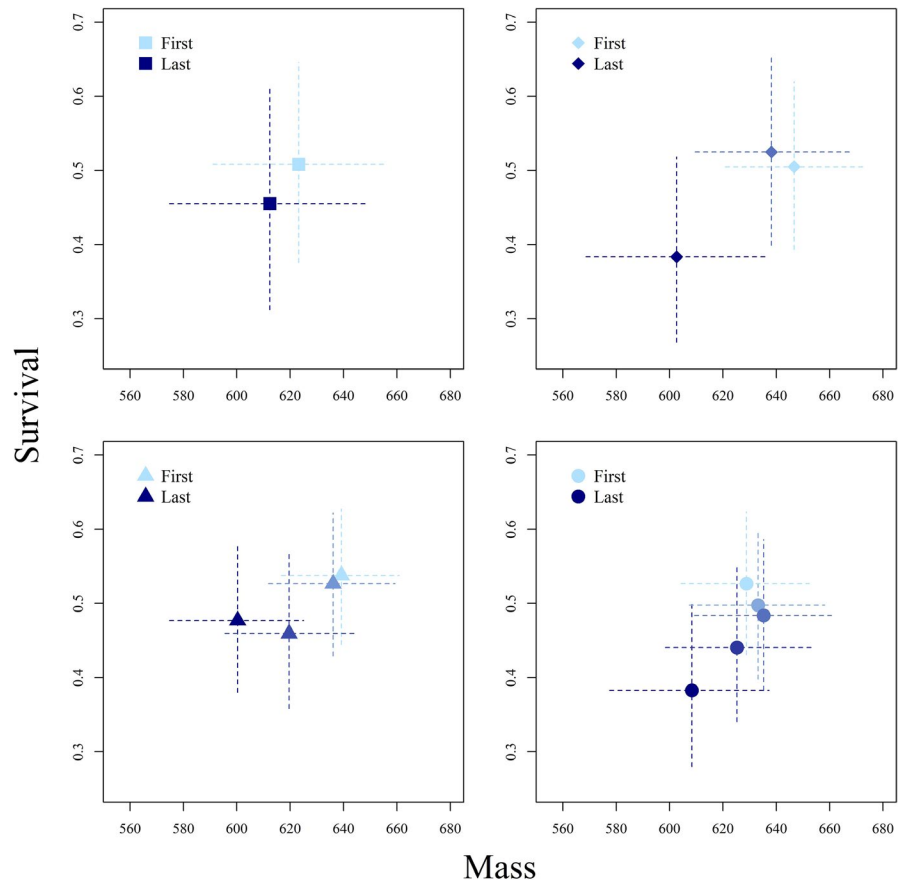
**FIGURE 3** Estimated effects of mean egg volume in each clutch on black brant gosling survival ( $\beta = 0.095$ , 95% CRI:  $0.024, 0.165$ ), and predicted gosling mass at 30 days of age ( $\beta = 0.625$ , 95% CRI:  $0.467, 0.778$ ) for goslings uniquely marked and released at the Tutakoke River Brant Colony, Alaska, USA, 1987–2007

egg volume ( $\beta = 0.055$ , 95% CRI:  $-0.014, 0.125$ ,  $f = 0.933$ ) both explained substantial variation in gosling survival. The third egg in a three-egg clutch had a lower survival probability than an average egg ( $\beta = -0.413$ , 95% CRI:  $-0.858, 0.0257$ ,  $f = 0.968$ ), and the fourth ( $\beta = -0.177$ , 95% CRI:  $-0.512, 0.150$ ,  $f = 0.862$ ) and fifth ( $\beta = -0.419$ , 95% CRI:  $-0.789, -0.061$ ,  $f = 0.989$ ) eggs in a five-egg clutch had a lower survival probability than an average egg. Goslings from the first ( $\beta = 0.214$ , 95% CRI:  $-0.021, 0.439$ ,  $f = 0.964$ ) and second ( $\beta = 0.165$ , 95% CRI:  $-0.102, 0.429$ ,  $f = 0.889$ ) eggs from a four-egg clutch had a higher survival probability than the average egg. Finally, goslings from the first ( $\beta = 0.167$ , 95% CRI:  $-0.096, 0.425$ ,  $f = 0.904$ ) egg from a five-egg clutch had a higher survival probability than the average egg (Figure 4; Table S2).

### 3.2 | Growth

Gosling growth rate was negatively affected by later relative hatching date ( $\beta = -1.289$ , 95% CRI:  $-1.341, -1.136$ ,  $f = 1.000$ , Figure 2), but we did not detect inter-annual variation in the effect of hatching date on growth rates ( $\beta = -0.362$ , 95% CRI:  $-0.710, 0.695$ ,

**FIGURE 4** Means and 95% Bayesian credible intervals of survival (y-axis) and predicted mass at 30 days (x-axis), in relation to position in the laying sequence for goslings from two- (top left), three- (top right), four- (bottom left) and five- (bottom right) egg clutches laid at the Tutakoke River Brant Colony, Alaska, USA (1987–2007)



$f = 0.755$ ). Gosling growth rate was positively affected by mean egg volume ( $\beta = 0.625$ , 95% CRI: 0.572, 0.778,  $f = 1.000$ , Figure 3) and residual egg volume ( $\beta = 0.377$ , 95% CRI: 0.330, 0.517,  $f = 1.000$ ). Goslings from the third egg in a three-egg clutch were significantly smaller than goslings from an average egg ( $\beta = -1.451$ , 95% CRI:  $-2.437$ ,  $-0.450$ ,  $f = 0.997$ ; Figure 4), goslings from the fourth egg in a four-egg clutch were smaller than goslings from an average egg ( $\beta = -1.532$ , 95% CRI:  $-2.113$ ,  $-0.934$ ,  $f = 1.000$ ) and goslings from the fifth egg in a five-egg clutch were also smaller than goslings from an average egg ( $\beta = -1.282$ , 95% CRI:  $-2.035$ ,  $-0.518$ ,  $f = 0.999$ , Figures 4 and 5; Table S3). Finally, variation in survival and growth was strongly positively correlated across positions in the laying sequence (Figure 4).

## 4 | DISCUSSION

### 4.1 | Heterogeneity associated with egg size, position in the laying sequence and hatch date

Gosling survival and growth rates were positively correlated with the mean egg volume of the clutch (Figure 3), as well as the residual volume of each egg relative to the mean egg volume of the clutch. This is consistent with relationships observed in snow geese *Chen caerulescens* (Ankney, 1980; Cooch, Lank, Rockwell, & Cooke, 1991; Williams, Lank, & Cooke, 1993), ruddy ducks *Oxyura jamaicensis*

(Pelayo & Clark, 2003), American kestrels *Falco sparverius* (Wiebe & Bortolotti, 1995) and other species (Dawson & Clark, 1996; Krist, 2011). We attribute this relationship to increased nutrient reserves at hatch, where goslings from larger eggs hatch at larger masses with larger yolk reserves (Ankney, 1980). Yolk reserves and developmental state both affect the ability of precocial young to walk long distances to brood-rearing habitats (Lack, 1967), where some broods travel up to 40 km to reach the brood-rearing areas on the YKD (Lindberg & Sedinger, 1998).

After controlling for variation in egg volume within the laying sequence, position within the sequence remained an important predictor of gosling growth and apparent detection. Eggs laid later in the sequence have fewer days to develop (Boonstra et al., 2010; Nicolai et al., 2004), likely causing them to hatch in a less developed state. Reduced development time can also have a direct impact on immunocompetence (Brommer, 2004; Ricklefs, 1992), as well as adult body size (Nunney, 1996) in other organisms. Irrespective of the precise mechanism, individuals originating from eggs laid later in the sequence grow more slowly and survive at lower rates than those from eggs earlier in the sequence (Figure 4). These impacts on the early life phenotype have repercussion later in life because gosling size at 30 days of age is positively related to first-year survival probability (Sedinger & Chelgren, 2007), adult size and fecundity (Sedinger, Flint, et al., 1995), and breeding probability as an adult (Riecke, Leach, Gibson, & Sedinger, 2018; Rosenheim & Rosen, 1991; Sedinger et al., 2004).

Similar to other studies (Flint & Sedinger, 1992; Rowe et al., 1994; Sedinger & Flint, 1991), we found that gosling growth and survival decreased with hatching date (Figure 2). Offspring born earlier in the season often have access to more nutritious foods, because their food sources begin declining in quality around the time of hatch (Aubry et al., 2012; Brook, Leafloor, Abraham, & Douglas, 2015; Lepage, Gauthier, & Reed, 1998; Ross et al., 2017; Sedinger & Raveling, 1986; van der Jeugd et al., 2009) or birth (Plard et al., 2014). Eggs that are laid earlier in the season have a higher recruitment probability (Clark et al., 2014; Descamps et al., 2011; Sedinger, Flint, et al., 1995) associated with both higher growth rates and greater post-fledging survival, and higher pre-fledging survival that we demonstrate here. Overall, our results combined with earlier work (Sedinger, Eichholz, et al., 1995) show that variation in egg size, position in the laying sequence and hatch date all contribute to the maintenance of individual heterogeneity in the brant population which has strong fitness consequences.

## 4.2 | Heterogeneity and the evolution of clutch size

Progressive declines in growth and pre-fledging survival of goslings originating from eggs laid later in clutches have the effect of reducing the marginal value of the last goslings produced in each clutch. A multivariate suite of variables ultimately selects for a particular upper limit to clutch size in populations. These include the ability to incubate a clutch (Leach et al., 2017) and rear a brood (Lessells, 1986; Sedinger et al., 2017). Additionally, body size and the ability of females to store sufficient nutrients to produce a particular volume of eggs (e.g. Ankney & MacInnes, 1978) potentially interact with egg size in species that rely on stored nutrients for breeding, like waterfowl (Lack, 1967; Rohwer, 1988) to influence the distribution of clutch sizes. There are also carry-over costs associated with clutches both larger and smaller than the modal clutch in brant (Leach et al., 2019) and potentially in other species. The declining marginal value of young originating from eggs later in the sequence acts with these other factors to influence fitness at the upper limit of the observed clutch size distribution and may explain why clutches >5 eggs are rare.

## ACKNOWLEDGEMENTS

The authors thank over 200 field technicians and volunteers who have contributed to the Tutakoke River brant dataset during this study. Field work at the Tutakoke River Colony was funded by the Alaska Science Center, U. S. Geological Survey, Migratory Bird Management Region 7, U. S. Fish and Wildlife Service, Ducks Unlimited, the Morro Bay Brant Group, Phil Jebbia (in memory of Marnie Shepherd) and the National Science Foundation (OPP 9214971, DEB 9815383, OPP 9985931, OPP 0196406, DEB 0743152, DEB 1252656). T.V.R. was also supported by the Bonnycastle Fellowship in Wetland and Waterfowl Biology from the Institute for Wetland and Waterfowl Research, Ducks Unlimited Canada. Data were collected on the Yukon Delta National Wildlife Refuge. The authors have no conflict of interest to declare. We would also like to thank David Koons and three

anonymous reviewers for providing positive contributions to the manuscript.

## AUTHORS' CONTRIBUTIONS

J.S.S. led long-term data collection efforts; C.R.A., T.V.R. and A.G.L. conceived the study; C.R.A. led the writing of the manuscript; C.R.A., P.J.W. and T.V.R. developed the analyses; J.S.S., A.G.L. and T.V.R. collected data. All the authors contributed critically to manuscript development, analytical work and gave their approval for manuscript submission.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.fttdz08pp> (Acevedo et al., 2020).

## ORCID

Cheyenne R. Acevedo  <https://orcid.org/0000-0002-0965-3791>

Thomas V. Riecke  <https://orcid.org/0000-0001-7998-5233>

Alan G. Leach  <https://orcid.org/0000-0002-7645-8312>

Madeleine G. Lohman  <https://orcid.org/0000-0001-7213-8293>

Perry J. Williams  <https://orcid.org/0000-0002-8439-1859>

## REFERENCES

- Acevedo, C. R., Riecke, T. V., Leach, A. G., Lohman, M. G., Williams, P. J., & Sedinger, J. S. (2020). Data from: Long-term research and hierarchical models reveal consistent fitness costs of being the last egg in a clutch. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.fttdz08pp>
- Alisauskas, R. T. (1986). Variation in the composition of the eggs and chicks of American coots. *The Condor*, *88*, 84–90.
- Alliston, W. G. (1975). Web-tagging ducklings in pipped eggs. *Journal of Wildlife Management*, *45*, 625–628.
- Ankney, C. D. (1980). Egg weight, survival, and growth of lesser snow goose goslings. *The Journal of Wildlife Management*, *44*, 174–182.
- Ankney, C. D. (1984). Nutrient reserve dynamics of breeding and molting brant. *The Auk*, *101*, 361–370. <https://doi.org/10.1093/auk/101.2.361>
- Ankney, C. D., & MacInnes, C. D. (1978). Nutrient reserves and reproductive performance of female lesser snow geese. *The Auk*, *95*, 459–471.
- Arnold, T. W. (1991). Intraclutch variation in egg size of American coots. *The Condor*, *93*, 19–27. <https://doi.org/10.2307/1368601>
- Arnold, T. W., & Rohwer, F. C. (1991). Do egg formation costs limit clutch size in waterfowl? A skeptical view. *The Condor*, *93*, 1032–1038. <https://doi.org/10.2307/3247744>
- Arzel, C., Elmer, J., & Guillemain, M. (2006). Ecology of spring-migrating Anatidae: A review. *Journal of Ornithology*, *147*, 167–184. <https://doi.org/10.1007/s10336-006-0054-8>
- Assis, A. P. A., Patton, J. L., Hubbe, A., & Marroig, G. (2016). Directional selection effects on patterns of phenotypic (co) variation in wild populations. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843), 20161615. <https://doi.org/10.1098/rspb.2016.1615>
- Aubry, L. M., Rockwell, R. F., Cooch, E. G., Brook, R. W., Mulder, C. P. H., & Koons, D. N. (2012). Climate change, phenology, and habitat degradation: Drivers of gosling body condition and juvenile survival in lesser snow geese. *Global Change Biology*, *19*, 149–160. <https://doi.org/10.1111/gcb.12013>
- Boonstra, T. A., Clarke, M. E., & Reed, W. L. (2010). Position in the sequence of laying, embryonic metabolic rate, and consequences for hatching synchrony and offspring survival in Canada geese. *The Condor*, *112*, 304–313. <https://doi.org/10.1525/cond.2010.090043>

- Both, C., & Visser, M. E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, *411*, 296–298. <https://doi.org/10.1038/35077063>
- Brommer, J. E. (2004). Immunocompetence and its costs during development: An experimental study in blue tit nestlings. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(Suppl\_3), S110–S113. <https://doi.org/10.1098/rsbl.2003.0103>
- Brook, R. W., Leafloor, J. O., Abraham, K. F., & Douglas, D. C. (2015). Density dependence and phenological mismatch: Consequences for growth and survival of sub-arctic nesting Canada geese. *Avian Conservation and Ecology*, *10*, 1. <https://doi.org/10.5751/ace-00708-100101>
- Charnov, E. L., & Ernest, S. M. (2006). The offspring-size/clutch-size trade-off in mammals. *The American Naturalist*, *167*, 578–582. <https://doi.org/10.1086/501141>
- Christians, J. K. (2002). Avian egg size: Variation within species and inflexibility within individuals. *Biological Reviews*, *77*(1), 1–26. <https://doi.org/10.1017/s1464793101005784>
- Clark, R. G., Pöysä, H., Runko, P., & Paasivaara, A. (2014). Spring phenology and timing of breeding in short-distance migrant birds: Phenotypic response and offspring recruitment patterns in common goldeneyes. *Journal of Avian Biology*, *45*, 457–465. <https://doi.org/10.1111/jav.00290>
- Clegg, S. M., Frentiu, F. D., Kikkawa, J., Tavecchia, G., & Owens, I. P. (2008). 4000 years of phenotypic change in an island bird: Heterogeneity of selection over three microevolutionary timescales. *Evolution: International Journal of Organic Evolution*, *62*(9), 2393–2410. <https://doi.org/10.1111/j.1558-5646.2008.00437.x>
- Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*, *25*(10), 562–573. <https://doi.org/10.1016/j.tree.2010.08.002>
- Cooch, E. G., Lank, D. B., Rockwell, R. F., & Cooke, F. (1991). Long-term decline in body size in a snow goose population: Evidence of environmental degradation? *Journal of Animal Ecology*, *60*, 483–496. <https://doi.org/10.2307/5293>
- Cooch, E. G., Lank, D. B., Rockwell, R. F., & Cooke, F. (1992). Is there a positive relationship between body size and fecundity in lesser snow geese? *The Auk*, *109*, 667–673.
- Cooke, F., Findlay, C. S., & Rockwell, R. F. (1984). Recruitment and the timing of reproduction in Lesser Snow Geese (*Chen caerulescens caerulescens*). *The Auk*, *101*, 451–458. <https://doi.org/10.1093/auk/101.3.451>
- Daan, S., Dijkstra, C., & Tinbergen, J. M. (1990). Family planning in the kestrel (*Falco tinnunculus*): The ultimate control of covariation of laying date and clutch size. *Behaviour*, *114*, 83–116. <https://doi.org/10.1163/156853990x00068>
- Dawson, R. D., & Clark, R. G. (1996). Effects of variation in egg size and hatching date on survival of Lesser Scaup *Aythya affinis* ducklings. *Ibis*, *138*, 693–699.
- Dawson, R. D., & Clark, R. G. (2000). Effects of hatching date and egg size on growth, recruitment, and adult size of lesser scaup. *The Condor*, *102*, 930–935. <https://doi.org/10.1093/condor/102.4.930>
- Descamps, S., Bêty, J., Love, O. P., & Gilchrist, H. G. (2011). Individual optimization of reproduction in a long-lived migratory bird: A test of the condition-dependent model of laying date and clutch size. *Functional Ecology*, *25*, 671–681. <https://doi.org/10.1111/j.1365-2435.2010.01824.x>
- Dickey, M. H., Gauthier, G., & Cadieux, M. C. (2008). Climatic effect of the breeding phenology and reproductive success of an arctic-nesting goose species. *Global Change Biology*, *14*, 1973–1985. <https://doi.org/10.1111/j.1365-2486.2008.01622.x>
- Drent, R., & Daan, S. (1980). The prudent parent: Energetic adjustments in avian breeding. *Ardea*, *68*, 225–252.
- Eichholz, M. W., & Sedinger, J. S. (1998). Factors affecting length of the incubation period in black brant. *Condor*, *100*, 164–168. <https://doi.org/10.2307/1369910>
- Faurie, C., Russell, A. F., & Lummaa, V. (2009). Middleborns disadvantaged? Testing birth-order effects on fitness in pre-industrial Finns. *PLoS ONE*, *4*(5), e5680. <https://doi.org/10.1371/journal.pone.0005680>
- Flint, P. L., Grand, J. B., & Sedinger, J. S. (1996). Allocation of limited resources to a clutch: A model explaining the lack of a relationship between clutch size and egg size. *The Auk*, *113*, 939–942. <https://doi.org/10.2307/4088875>
- Flint, P. L., Lindberg, M. S., Maccluckie, M. C., & Sedinger, J. S. (1994). The adaptive significance of hatching synchrony of waterfowl eggs. *Waterfowl*, *45*, 248–254.
- Flint, P. L., & Sedinger, J. S. (1992). Reproductive implications of egg-size variation in the black brant. *The Auk*, *109*, 896–903. <https://doi.org/10.2307/4088164>
- Galloway, L. F. (1995). Response to natural environmental heterogeneity: Maternal effects and selection on life-history characters and plasticities in *Mimulus guttatus*. *Evolution*, *49*(6), 1095–1107. <https://doi.org/10.2307/2410434>
- Gilby, A. J., Sorato, E., & Griffith, S. C. (2012). Maternal effects on begging behaviour: An experimental demonstration of the effects of laying sequence, hatch order, nestling sex and brood size. *Behavioral Ecology and Sociobiology*, *66*(11), 1519–1529. <https://doi.org/10.1007/s00265-012-1407-3>
- Hargreaves, A. L., & Eckert, C. G. (2014). Evolution of dispersal and mating systems along geographic gradients: Implications for shifting ranges. *Functional Ecology*, *28*(1), 5–21. <https://doi.org/10.1111/1365-2435.12170>
- Hoffmann, A. A., & Merilä, J. (1999). Heritable variation and evolution under favourable and unfavourable conditions. *Trends in Ecology & Evolution*, *14*(3), 96–101. [https://doi.org/10.1016/s0169-5347\(99\)01595-5](https://doi.org/10.1016/s0169-5347(99)01595-5)
- Hupp, J. W., Ward, D. H., Hogrefe, K. R., Sedinger, J. S., Martin, P. D., Stickney, A. A., & Obritschkewitsch, T. (2017). Growth of black brant and lesser snow goose goslings in northern Alaska. *The Journal of Wildlife Management*, *81*(5), 846–857. <https://doi.org/10.1002/jwmg.21246>
- Kellner, K. (2015). *jagsUI: A wrapper around rjags to streamline JAGS analyses*.
- Krist, M. (2011). Egg size and offspring quality: A meta-analysis in birds. *Biological Reviews*, *86*, 692–716. <https://doi.org/10.1111/j.1469-185x.2010.00166.x>
- Lack, D. (1947). The significance of clutch-size. *Ibis*, *89*, 302–352.
- Lack, D. (1954). *Natural regulation of animal numbers*. Oxford, UK: Oxford University Press.
- Lack, D. (1967). The significance of clutch size in waterfowl. *Wildfowl*, *19*, 125–128.
- Larsson, K. (1993). Inheritance of body size in the barnacle goose under different environmental conditions. *Journal of Evolutionary Biology*, *6*(2), 195–208. <https://doi.org/10.1046/j.1420-9101.1993.6020195.x>
- Larsson, K., & Forslund, P. (1992). Genetic and social inheritance of body and egg size in the barnacle goose (*Branta leucopsis*). *Evolution*, *46*(1), 235–244. <https://doi.org/10.1111/j.1558-5646.1992.tb01998.x>
- Leach, A. G., Sedinger, J. S., Riecke, T. V., Van Dellen, A. W., Ward, D. H., & Boyd, W. S. (2019). Brood size affects future reproduction in a long-lived bird with precocial young. *The American Naturalist*, *193*(3), 458–471. <https://doi.org/10.1086/701783>
- Leach, A. G., Van Dellen, A. W., Riecke, T. V., & Sedinger, J. S. (2017). Incubation capacity contributes to constraints on maximal clutch size in brent geese, *Branta bernicla nigricans*. *Ibis*, *159*, 588–599. <https://doi.org/10.1111/ibi.12480>
- Leblanc, Y. (1987). Intraclutch variation in egg size of Canada geese. *Canadian Journal of Zoology*, *65*, 3044–3047. <https://doi.org/10.1139/z87-461>
- Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, *62*(1), 67–118. <https://doi.org/10.2307/2937171>



- Lepage, D., Gauthier, G., & Reed, A. (1998). Seasonal variation in growth of greater snow goose goslings: The role of food supply. *Oecologia*, 114, 226–235. <https://doi.org/10.1007/s004420050440>
- Lessells, C. M. (1986). Brood size in Canada geese: A manipulation experiment. *Journal of Animal Ecology*, 55, 669–689. <https://doi.org/10.2307/4747>
- Lewis, T. L., Ward, D. H., Sedinger, J. S., Reed, A., & Derksen, D. V. (2013). Brant (*Branta bernicla*). In P. G. Rodewald (Ed.), *The birds of North America online*. Ithaca, NY: Cornell Lab of Ornithology.
- Lindberg, M. S., & Sedinger, J. S. (1998). Ecological significance of brood site fidelity in Black Brant: Spatial, annual, and age-related variation. *The Auk*, 115, 436–446. <https://doi.org/10.2307/4089202>
- Lindberg, M. S., Sedinger, J. S., & Flint, P. L. (1997). Effects of spring environment on nesting phenology and clutch size of black brant. *The Condor*, 99, 381–388. <https://doi.org/10.2307/1369944>
- Lindholm, A., Gauthier, G., & Desrochers, A. (1994). Effects of hatching date and food supply on gosling growth in arctic-nesting greater snow geese. *The Condor*, 96, 898–908. <https://doi.org/10.2307/1369100>
- Lohman, M. G., Riecke, T. V., Acevedo, C. R., Person, B. T., Uher-Koch, B. D., Schmutz, J. A., & Sedinger, J. S. (2019). Linking resource availability, behavior, and demography in a long-lived specialist. *Ecology and Evolution*, 9, 5281–5291.
- Magrath, M. J., Brouwer, L., & Komdeur, J. (2003). Egg size and laying order in relation to offspring sex in the extreme sexually size dimorphic brown songlark, *Cinclorhamphus cruralis*. *Behavioral Ecology and Sociobiology*, 54(3), 240–248. <https://doi.org/10.1007/s00265-003-0627-y>
- Martínez-Padilla, J., Vergara, P., & Fargallo, J. A. (2017). Increased lifetime reproductive success of first-hatched siblings in Common Kestrels *Falco tinnunculus*. *Ibis*, 159(4), 803–811. <https://doi.org/10.1111/ibi.12494>
- McDonald, T. K., & Yeaman, S. (2018). Effect of migration and environmental heterogeneity on the maintenance of quantitative genetic variation: A simulation study. *Journal of Evolutionary Biology*, 31(9), 1386–1399. <https://doi.org/10.1111/jeb.13341>
- Nicolai, C. A., Sedinger, J. S., & Wege, M. L. (2004). Regulation of development time and hatch synchronization in black brant (*Branta bernicla nigricans*). *Functional Ecology*, 18, 475–482. <https://doi.org/10.1111/j.0269-8463.2004.00860.x>
- Nunney, L. (1996). The response to selection for fast larval development in *Drosophila melanogaster* and its effect on adult weight: An example of a fitness trade-off. *Evolution*, 50, 1193–1204. <https://doi.org/10.1111/j.1558-5646.1996.tb02360.x>
- Palmer, R. S. (1976). *Handbook of North American birds* (Vol. 2: Waterfowl. Part 1). New Haven, CT: Yale University Press.
- Pelayo, J. T., & Clark, R. G. (2003). Consequences of egg size for offspring survival: A cross-fostering experiment in ruddy ducks (*Oxyura jamaicensis*). *The Auk*, 120, 384–393. [https://doi.org/10.1642/0004-8038\(2003\)120\[0384:coesofj\]2.0.co;2](https://doi.org/10.1642/0004-8038(2003)120[0384:coesofj]2.0.co;2)
- Penna, A., Melo, D., Bernardi, S., Oyarzabal, M. I., & Marroig, G. (2017). The evolution of phenotypic integration: How directional selection reshapes covariation in mice. *Evolution*, 71(10), 2370–2380. <https://doi.org/10.1111/evo.13304>
- Plard, F., Gaillard, J. M., Coulson, T., Hewison, A. M., Delorme, D., Warnant, C., & Bonenfant, C. (2014). Mismatch between birth date and vegetation phenology slows the demography of roe deer. *PLoS Biology*, 12, e1001828. <https://doi.org/10.1371/journal.pbio.1001828>
- Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*. Vienna, Austria, p. 125.
- Plummer, M. (2013). rjags: Bayesian graphical models using MCMC. R package version 3-10. Retrieved from <http://CRAN.R-project.org/package=rjags>
- Pontarp, M., Bunnefeld, L., Cabral, J. S., Etienne, R. S., Fritz, S. A., Gillespie, R., ... Hurlbert, A. H. (2019). The latitudinal diversity gradient: Novel understanding through mechanistic eco-evolutionary models. *Trends in Ecology & Evolution*, 34(3), 211–223. <https://doi.org/10.1016/j.tree.2018.11.009>
- R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Raveling, D. G. (1979). The annual cycle of body composition of Canada Geese with special reference to control of reproduction. *The Auk*, 96(2), 234–252. <https://doi.org/10.1093/auk/96.2.234>
- Ricklefs, R. E. (1992). Embryonic development period and the prevalence of avian blood parasites. *Proceedings of the National Academy of Sciences of the United States of America*, 89, 4722–4725. <https://doi.org/10.1073/pnas.89.10.4722>
- Riecke, T. V., Leach, A. G., Gibson, D., & Sedinger, J. S. (2018). Parameterizing the robust design in the BUGS language. Lifetime carryover effects of environmental conditions during growth on a long-lived bird. *Methods in Ecology and Evolution*, 9, 2294–2305. <https://doi.org/10.1111/2041-210x.13065>
- Rohwer, F. C. (1988). Inter- and intraspecific relationships between egg size and clutch size in waterfowl. *The Auk*, 105, 161–176. <https://doi.org/10.1093/auk/105.1.161>
- Rosenheim, J. A., & Rosen, D. (1991). Foraging and oviposition decisions in the parasitoid *Aphytis lingnanensis*: Distinguishing the influences of egg load and experience. *The Journal of Animal Ecology*, 60, 873–893. <https://doi.org/10.2307/5419>
- Ross, M. V., Alisauskas, R. T., Douglas, D. C., & Kellett, D. K. (2017). Decadal declines in avian herbivore reproduction: Density-dependent nutrition and phenological mismatch in the Arctic. *Ecology*, 98, 1869–1883. <https://doi.org/10.1002/ecy.1856>
- Rossiter, M. (1996). Incidence and consequences of inherited environmental effects. *Annual Review of Ecology and Systematics*, 27(1), 451–476. <https://doi.org/10.1146/annurev.ecolsys.27.1.451>
- Rowe, L., Ludwig, D., & Schluter, D. (1994). Time, condition, and the seasonal decline of avian clutch size. *The American Naturalist*, 143, 698–722. <https://doi.org/10.1086/285627>
- Sedinger, J. S., & Chelgren, N. D. (2007). Survival and breeding advantages of larger black brant (*Branta bernicla nigricans*) goslings: Within- and among-cohort variation. *The Auk*, 124, 1281–1293. <https://doi.org/10.1093/auk/124.4.1281>
- Sedinger, J. S., Eichholz, M. W., & Flint, P. L. (1995). Variation in brood behavior of black brant. *The Condor*, 97, 107–115. <https://doi.org/10.2307/1368988>
- Sedinger, J. S., & Flint, P. L. (1991). Growth rate is negatively correlated with hatching date in black brant. *Ecology*, 72, 496–502. <https://doi.org/10.2307/2937190>
- Sedinger, J. S., Flint, P. L., & Lindberg, M. S. (1995). Environmental influence on life-history traits: Growth, survival, and fecundity in black brant (*Branta bernicla*). *Ecology*, 76, 2404–2414. <https://doi.org/10.2307/2265816>
- Sedinger, J. S., Herzog, M. P., Person, B. T., Kirk, M. T., Obritchkewitch, T., Martin, P. P., ... Bosque, C. (2001). Large-scale variation in growth of Black Brant goslings related to food availability. *The Auk*, 118, 1088–1095. <https://doi.org/10.1093/auk/118.4.1088>
- Sedinger, J. S., Herzog, M. P., & Ward, D. H. (2004). Early environment and recruitment of black brant (*Branta bernicla nigricans*) into the breeding population. *The Auk*, 121, 68–73. [https://doi.org/10.1642/0004-8038\(2004\)121\[0068:earob\]2.0.co;2](https://doi.org/10.1642/0004-8038(2004)121[0068:earob]2.0.co;2)
- Sedinger, J. S., Lindberg, M. S., Rexstad, E. A., Chelgren, N. D., & Ward, D. H. (1997). Testing for handling bias in survival estimation for black brant. *The Journal of Wildlife Management*, 61, 782–791. <https://doi.org/10.2307/3802185>
- Sedinger, J. S., & Raveling, D. G. (1986). Timing of nesting by Canada geese in relation to the phenology and availability of their food plants. *The Journal of Animal Ecology*, 55, 1083. <https://doi.org/10.2307/4435>

- Sedinger, J. S., Van Dellen, A. W., Leach, A. G., & Riecke, T. V. (2017). Ultimate regulation of fecundity in species with precocial young: Declining marginal value of offspring with increasing brood size does not explain maximal clutch size in black brent geese. *Oecologia*, 183, 431–440. <https://doi.org/10.1007/s00442-016-3772-5>
- Smith, H. G., Kallander, H., & Nilsson, J. A. (1989). The trade-off between offspring number and quality in the great tit *Parus major*. *The Journal of Animal Ecology*, 383–401. <https://doi.org/10.2307/3565309>
- Stearns, S. C. (1992). *The evolution of life histories*. London, UK: Oxford University Press.
- Uher-Koch, B. D., Schmutz, J. A., Wilson, H. M., Anthony, R. M., Day, T. L., Fondell, T. F., ... Sedinger, J. S. (2019). Ecosystem-scale loss of grazing habitat impacted by abundance of dominant herbivores. *Ecosphere*, 10(6), e02767. <https://doi.org/10.1002/ecs2.2767>
- van der Jeugd, H. P., Eichorn, G., Litvin, K. E., Stahl, J., Larsson, K., van der Graaf, A. J., & Drent, R. H. (2009). Keeping up with early springs: Rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Global Change Biology*, 15, 1057–1071. <https://doi.org/10.1111/j.1365-2486.2008.01804.x>
- Van Noordwijk, A. J., & de Jong, G. (1986). Acquisition and allocation of resources: Their influence on variation in life history tactics. *The American Naturalist*, 128, 137–142. <https://doi.org/10.1086/284547>
- Warren, J. M., Cutting, K. A., & Koons, D. N. (2013). Body condition dynamics and the cost-of-delay hypothesis in a temperate-breeding duck. *Journal of Avian Biology*, 44, 575–582.
- Wiebe, K. L., & Bortolotti, G. R. (1995). Egg size and clutch size in the reproductive investment of American Kestrels. *Journal of Zoology*, 237, 285–301. <https://doi.org/10.1111/j.1469-7998.1995.tb02763.x>
- Williams, T. D. (1994). Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. *Biological Reviews*, 69, 35–59. <https://doi.org/10.1111/j.1469-185x.1994.tb01485.x>
- Williams, T. D., Lank, D. B., & Cooke, F. (1993). Is intraclutch egg-size variation adaptive in the lesser snow goose? *Oikos*, 67, 250–256. <https://doi.org/10.2307/3545469>
- Williams, T. D., Lank, D. B., Cooke, F., & Rockwell, R. F. (1993). Fitness consequences of egg-size variation in the lesser snow goose. *Oecologia*, 96, 331–338. <https://doi.org/10.1007/bf00317502>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Acevedo CR, Riecke TV, Leach AG, Lohman MG, Williams PJ, Sedinger JS. Long-term research and hierarchical models reveal consistent fitness costs of being the last egg in a clutch. *J Anim Ecol*. 2020;89:1978–1987. <https://doi.org/10.1111/1365-2656.13232>