*Individual heterogeneity in Fitness in a long-lived herbivore*

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**ABSTRACT**

Heterogeneity in the intrinsic quality and nutritional condition of individuals affects reproductive success and consequently fitness. Understanding differences in energy allocation towards survival and reproduction within and among years might help explain variability in individual fitness. Black brant (*Branta bernicla nigricans*) are long-lived, migratory, specialist herbivores. Long migratory pathways and short summer breeding seasons constrain the time and energy available for reproduction, thus magnifying life-history trade-offs. These constraints, combined with long lifespans and trade-offs between current and future reproductive value, provide a model system to examine the role of individual heterogeneity in driving life-history strategies and individual heterogeneity in fitness. We used hierarchical Bayesian models to examine reproductive trade-offs, modeling the relationships between within-year measures of reproductive energy allocation and among-year demographic rates of individual females breeding on the Yukon-Kuskokwim Delta, Alaska using capture-recapture and reproductive data from 1988 to 2014. We provide evidence for relationships between breeding probability and clutch size (posterior mean of *β* = 0.45, 95% CRI = 0.33 – 0.57, SD = 0.06), breeding probability and nest initiation date (posterior mean of *β* = -0.12, 95% CRI = -0.2 ­– -0.04, SD = 0.04), and an interaction between clutch size and initiation date (posterior mean of *β* = -0.12, 95% CRI = -0.2 – -0.04, SD = 0.04). Average lifetime clutch size also had a weak positive relationship with survival probability (posterior mean of *β* = 0.03, 95% CRI = -0.01 – 0.7, SD = 0.02). Our results support the use of demographic buffering strategies for black brant; reductions in reproductive energy allocation preserve high adult survival rates during years with poor environmental conditions, maximizing future reproductive value. We also indirectly show links among environmental conditions during growth, fitness, and energy allocation, highlighting the effects of early growth conditions on individual heterogeneity, and subsequently, reproductive investment.

*Keywords:* black brant, breeding probability, fitness, life-history, reproduction, survival, trade-offs

**COVER LETTER**

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Ecology and Evolution, Editorial Board:

We ask you to consider our submission of *Individual heterogeneity in fitness in a long-lived herbivore*, the attached manuscript, for publication in Ecology and Evolution. This manuscript connects within- and among-year reproductive trade-offs in a long-lived species and shows the important contributions of individual heterogeneity to fitness.

Using long-term (1988–2014) capture-mark-recapture and reproductive data of adult female Pacific black brent (*Branta bernicla nigricans*), we link individual clutch sizes and initiation dates with yearly survival and breeding probabilities. Our results support the demographic buffering hypothesis and illustrate the role of individual heterogeneity in regulating reproductive output and lifetime fitness. Further, we indirectly show how early growth conditions may affect individual heterogeneity, and thus reproductive investment, for long-lived organisms by connecting environmental conditions during growth, fitness, and energy allocation. Ultimately, understanding the dynamics of reproductive trade-offs, individual heterogeneity, and early growth conditions can help create better demographic predictions for brent and other long-lived organisms.

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     We thank you for your consideration of this manuscript and look forward to your correspondence.  
  
Sincerely,  
Madeleine Lohman (Corresponding Author)

# INTRODUCTION

Expression of life-history traits may be conditional on the current physiological state or environmental conditions experienced by individuals because such flexibility maximizes fitness (McNamara and Houston 1996). The negative association between clutch size and laying date, which is ubiquitous in birds (Klomp 1970), is an important example of physiological state-dependent life-histories. Covariation between clutch size and laying date is driven by a trade-off between the quantity of offspring individuals in a particular state can produce on a given breeding date against the declining quality of those offspring as laying date progresses (Drent and Daan 1980, Daan et al. 1990, Rowe et al. 1994). This covariation is at least partially under genetic control (Sheldon et al. 2003) and mediated by physiological processes that translate environmental cues into the expression of life-history traits (Meijer et al. 1990, Sinervo and Svensson 1998). Parallel patterns of clutch size and laying date occur in long-distance migrants, driven by variation in nutritional status before and during spring migration (Bêty et al. 2003, Prop & de Vries 1993). In these species, nutritional status influences the timing of migration and arrival on breeding areas. Individuals with smaller nutrient reserves tend to arrive on breeding areas later and nest later (Bêty et al. 2003, Prop et al. 2003), although they do not delay long enough to acquire sufficient nutrients to produce the largest clutches, resulting in a decline in clutch size (Hamann and Cooke 1989, Dalhaug et al. 1996, Bêty et al. 2003). The “individual optimization” or “prudent parent” strategy, as this strategy is known, does not equalize yearly reproductive fitness advantages for individuals in inferior and superior states before the breeding season; individuals in superior states still produce more and higher quality offspring than those in inferior states before breeding (Prop et al. 2003, Bêty et al. 2003).

Reproductive strategies also derive from trade-offs between current and future reproductive fitness or the quantity and quality of offspring in the current reproductive event (Stearns 1992). Such trade-offs are well established by potentially hundreds of experimental studies for species with altricial young, beginning with Lack’s revolutionary studies (e.g., Lack 1948, 1950) and continuing to the present (Leach et al. 2019). A larger number of studies have detected trade-offs between quantity and quality of offspring (Klomp 1970) than between current and future reproduction (Santos and Nakagawa 2012), possibly because of the difficulty of detecting the latter.

Species with precocial young do not feed their offspring, which has led investigators to assume that clutch size must be limited by the proximal constraint of nutrients available to females before or during egg laying (Lack 1967, Ankney and MacInnes 1978, Alisauskas and Ankney 1992). Recently, experimental manipulations of clutch and brood size in black brant (*Branta bernicla nigricans*, hereafter brant) demonstrated diminishing fitness returns as brood size increased (Sedinger et al. 2017) and costs to future reproduction of producing broods larger than the most common brood size of four (Leach et al. 2019). Additionally, egg size has a positive association with the size of goslings at fledging (Acevedo et al. 2020), which strongly influences first-year survival (Sedinger and Chelgren 2007) and recruitment into the breeding population (Sedinger et al. 2004, Riecke et al. 2018). Because nutrients stored before breeding regulate investment in clutches (Ankney 1984, Schmutz et al. 2006), trade-offs occur between clutch size and egg size among females (Flint and Sedinger 1992) but may be obscured by variation in pre-breeding nutrient reserves among females (Flint et al. 1996). When pre-breeding nutrient reserves exceed those needed to produce the maximum clutch and egg size, trade-offs may not manifest (Drent and Daan 1980, van Noordwijk and de Jong 1986). However, when nutrient reserves are limited, variation in egg size among females (Flint and Sedinger 1992, Lemons et al. 2011) produces a trade-off among females between the quantity and quality of offspring produced.

Positive covariance in fitness traits within individuals may diminish the ability of researchers to assess trade-offs at the population level (van Noordwijk and de Jong 1986). For example, offspring quality and quantity might be positively correlated in a study with unmanipulated broods because “higher quality” parents produce both more and higher quality offspring. Thus, the ability to assess trade-offs between fitness traits will depend on whether there is sufficient residual variance remaining after accounting for the relationship between the main effects of the traits of interest. We note that substantial residual variability remains in clutch size after accounting for laying date in above paragraph. Sedinger et al. (1995*a*) reported positive correlations among multiple traits associated with fitness, including the probability of breeding. Because researchers could link these traits to growth conditions experienced by individuals, Sedinger et al. (1995*a)* attributed much of the variation in fitness to variation in the breeding ground environment. Given these relationships and the importance of understanding life-history trade-offs, our objective was to assess the potential for relationships between reproductive traits associated with yearly fitness and longer-term life-history traits. In this manuscript, we model the effects of clutch size and nest initiation date and their interaction on annual survival and breeding probabilities. We discuss the direct and indirect effects of these relationships on fitness and population dynamics.

# MATERIALS AND METHODS

# We collected data at the Tutakoke River Colony (TRC; Sedinger et al. 1993) (61.25◦N, 165.61◦W) and related brood rearing areas on the YKD near the mouth of the Kashunuk River from 1988-2014 (Sedinger et al. 1995; Lindberg and Sedinger 1998). We divided the breeding season into three secondary occasions. First (May - June), nests were monitored in forty-nine 50m radius random plots every four days throughout nest initiation, and again before and during hatch. Observers recorded clutch sizes and initiation dates of nests during this time. Incubation time is generally 23-29 days, varying with laying date and clutch size. Thus, we back-calculated initiation dates for hatched nests using mean incubation period (~26 days; Eichholz and Sedinger 1998, Leach et al. 2017*a*). We also monitored nests of marked individuals outside of plots during this time. Second (June - early July), following hatch, observers entered observation towers to observe marked adults and broods (Sedinger et al. 2001). Third (mid-late July), adult and juvenile brant were herded into pens and marked with a unique U.S. Geological Survey metal band and an alpha-numerically coded plastic band during the adult wing-molt (Sedinger et al. 1997). We included data for all marked females (*n* = 7*,* 845) to estimate mean survival and breeding probability and temporal variation in those parameters. However, only those individuals with within-year reproductive data were used to estimate relationships between within-year measures of reproduction, clutch size (*n* = 6*,*256; *µ* = 3*.*83; SD= 1*.*12) and initiation date (*n* = 5*,*207; *µ* = 146*.*49 (Julian Day); SD= 5*.*59), and among-year demographic rates (survival and breeding probability).

**Data Analysis**

**Estimating detection, breeding and survival probabilities.** We estimated survival and breeding probability using robust design models with both primary and secondary occasions (Kendall and Nichols 1995, Riecke et al. 2018). Primary occasions were the time period in which individuals could be encountered, which we defined as the entiresummer breeding season from May to July. Secondary occasions were distinct periods within the primary occasion, consisting of the nesting period, a period of three weeks following hatch, and the adult remigial molt, described above. Secondary occasion encounter data were represented by *yi,t,k*, where *i* = 1*, ..., n* indicated the individual, *t* = 1*, ..., T* indicated the primary occasion, and *k* = 1*,* 2*,* 3 indicated the secondary occasion. We assumed the data arose from a Bernoulli distribution with the probability of success equal to the encounter probability of the secondary occasion (*pt,k*) and conditional on the individual’s sampling availability (*πi,t*) and latent state (alive or dead, *zi,t*)

We defined an individual’s sampling availability as a Bernoulli random variable, conditional on the individual’s latent state and breeding probability (*γi,t*),

We modeled an individual’s latent state using a Bernoulli distribution and the individual’s survival probability (*φi,t*), conditional on the individual’s previous latent state

**Relationships between clutch size and initiation date, and survival and breeding probability.** We estimated the effects of clutch size (*κi*) and initiation date (*δi*) on survival (*φi,t*) and breeding probability (*γi,t*) using the lifetime means of observed individual clutch sizes and initiation dates. We z-standardized clutch size and initiation date within years, and then took the mean across years for each individual to produce a value representing average within-year reproductive energy allocation. These measures essentially placed individuals on a ‘quality’ gradient, where individuals laying larger and earlier clutches were considered higher ‘quality’, as on average they were better able to acquire nutrients for annual reproductive allocation (Figure 1). Our analyses did not assess the potential for trade-offs between annual survival or breeding probability and reproduction in a particular year, as this has been considered elsewhere (Leach et al. 2019). We assessed the relationships between within-year reproduction (clutch size and initiation date) and the demographic rates survival and breeding probability) using a generalized linear model, with a logit link function. Temporal variability was also included in candidate models (*εt*) for each year

The interaction between clutch size and laying date assessed the effect on survival or breeding probability of deviating from the mean relationship between clutch size and laying date. Such deviations (e.g., clutches that are larger than predicted for a particular laying date) allowed us to assess the potential for trade-offs between investments in eggs and survival or breeding probability, after controlling for laying date. That is, did individuals suffer a reduction in survival or breeding probability if they produced larger clutches than predicted by the clutch size laying date trend?

We performed analyses in JAGS (Plummer 2003) using the R (R Core Team 2018) package *jagsUI* (Kellner 2018). We sampled two chains for 15,000 iterations, with a burn-in of 10,000, and a thinning rate of 2. We report the posterior medians, 95% credible intervals, and *ξ* (the proportion of the posterior distribution on the same side of 0 as the mean, Plummer 2003).

# RESULTS

Annual survival was not correlated with initiation date (*β*2 = -0.003; 95% CRI = -0.04 — 0.03; SD = 0.02; *ξ* = 0.56). However, model estimates did provide evidence for a modest positive relationship between survival and clutch size (*β*1 = 0.03; 95% CRI = -0.01 — 0.07; SD = 0.02; *ξ =* 0.92). The resulting survival surface (Figure 2A) was relatively flat in the region where most clutch-size-laying date data lay, indicating only modest survival selection against either larger or smaller clutches than the mean for a particular laying date. Breeding probability was strongly related to both clutch size and laying date (Table 3). Breeding probability was positively related to clutch size (*α*1 = 0.45; 95% CRI = 0.33 — 0.57; SD = 0.06; *ξ* = 1.00) and negatively related to initiation date (*α*2 = -0.12; 95% CRI = -0.2 — -0.04; SD = 0.04; *ξ* = 1). Overall, relationships between survival and breeding probability with clutch size were consistent with the hypothesis that fitness traits covary along an axis of individual quality, where individuals that laid larger, earlier clutches were also more likely to breed

Annual survival had a weak negative relationship with the interaction between clutch size and laying date suggesting a modest survival cost to individuals laying larger clutches than the mean for their laying date (*β*3 = 0.03; 95% CRI = -0.07 — 0.08; SD = 0.02; ξ = 0.894). Breeding probability was strongly negatively related to the interaction between clutch size and initiation date (*α*3 = -0.11; 95% CRI = -0.21 — -0.01; SD = 0.05; *ξ* = 0.99; Figure 2B, D). The resulting surface was relatively flat for clutch sizes larger than the mean for a particular laying date. In contrast females producing clutches smaller than the mean suffered a substantial reduction in breeding probability the next year. For example, mothers with clutch sizes two standard deviations below the mean had a breeding probability of 0.6 (~2 eggs; 95% CRI = 0.54 — 0.73), about 30% less than mothers with clutch sizes two standard deviations above the mean (~5 eggs; *µ* = 0.91; 95% CRI = 0.87 — 0.94). Overall, the negative correlations between survival and breeding probability and the interaction between clutch size and laying date suggest a cost to future reproduction for individuals laying larger clutches than the mean for the population for a given initiation date, but also a substantial cost (acting through reduced breeding probability) for females producing clutches smaller than the population mean for a particular initiation date.

Mean survival was 0.82 (95% CRI: 0.81 — 0.84) and mean breeding probability 0.81 (95% CRI: 0.75 — 0.87 across all years and individuals.

# DISCUSSION

Our results identify an axis of positive relationships among traits positively related to fitness in brant. Individuals producing the earliest (below the 10th percentile), and largest clutches (above the 90th percentile), which maximize current reproductive fitness, had a 19% higher probability of breeding the next year than females producing the latest (above the 90th percentile) and smallest clutches (below the 10th percentile) (Fig. 1B). Thus, females that experience the greatest reproductive fitness in one year are more likely to do so in subsequent years because they have a greater probability of breeding. The interaction term revealed additional structures in the relationship among clutch size, laying date, and breeding probability. Females producing clutches smaller and earlier clutches than the mean suffered reduced probability of breeding (Fig. 1B).

The relationship between clutch size and subsequent breeding probability is consistent with results from experimental reduction of clutches in brant (Leach et al. 2019) and observations of higher probabilities of breeding in the year after a successful breeding attempt (Sedinger et al. 2011). The likely mechanism for these patterns is the well-known association between family size and social status in winter flocks of geese (Raveling 1970, Black et al. 1992), including brant (Poisbleau et al. 2006). These carry-over effects of reduced breeding probability following the production of a small clutch have a larger effect on fitness than just reduced breeding probability the next year. Once an individual has skipped breeding, their probability of returning to the breeding population is about half of that for a female that did nest (Sedinger et al. 2008).

The surface relating annual survival to clutch size and laying date was flatter than that for breeding probability with annual survival ranging from 0.78 to 0.85 across the range of clutch size-laying date combinations (Fig. 1A). As with breeding probability, there was a general trend for individuals producing larger clutches to survive at higher rates. That said, the shape of the surface induced by the interaction between clutch size and laying date suggested weak destabilizing selection away from the mean clutch size-laying date line; females producing large late clutches and small early clutches tended to survive at slightly higher rates than females producing large early clutches or small late clutches, respectively. We urge caution in interpreting this result because evidence for the interaction was modest and the overall surface was relatively flat.

The patterns we report here are consistent with the hypothesis that early environment and maternal effects have an important influence on adult fitness in brant. These effects (Sedinger et al. 1995*a*, 2004, Cooch et al. 1991, Larsson and Forslund 1991) help drive adult body size and reproductive fitness in several goose species. Hatch date plays a prominent role in such variation because early hatching goslings grow more rapidly (Cooch et al. 1991, Sedinger and Flint 1991, Lindholm et al. 1994), resulting in larger adult body sizes (Larsson and Forslund 1991). Further, the size of eggs produced by female geese explains some variation in gosling size at fledging (Acevedo et al. 2020). While much of the relevant variation appears heritable (Larsson and Forslund 1992), the general lack of response to apparently strong selection for larger body sizes and associated reproductive variables suggests that either such heritability does not have a substantial additive genetic basis, or there are unknown associated negative genetic covariances (Larsson 1993, Hoffmann and Merilä 1999). We generally found that fitness-related life-history traits were positively correlated, consistent with a primarily non-additive genetic explanation for this variation, though our analysis was not exhaustive.

Over the past three decades, clutch size for brant has remained relatively constant, indicating that clutch size has not responded to selection (Figure 3). This lack of response suggests that differences in environmental conditions during growth largely determine heterogeneity in individual quality which exists within (Sedinger and Chelgren 2007, Riecke et al. 2018) and among (Lohman et al. 2019) cohorts. Previous work has shown the importance of environmental conditions during growth; nutrient availability during the breeding season can affect first-year survival (Sedinger and Chelgren 2007), recruitment of young into the breeding population (Lindström 1999, Sedinger et al. 2004), and their fitness as an adult (Sedinger et al. 1995*b*). Thus, variation in growth conditions produces variation in gosling size at fledging (Cooch et al. 1991, Sedinger et al. 2004) and adult size and life-history traits (Sedinger et al. 1995*a*, Douhard et al. 2014). Foraging conditions for brant goslings have declined through time (Sedinger et al. 2016, Lohman et al. 2019) resulting in a general decline in gosling size at fledging (Lohman et al. 2019). A strong positive association between gosling size and first-year survival (Sedinger and Chelgren 2007), however, implies that a declining mean in gosling size has resulted in increasingly strong selection acting on brant cohorts through time. In fact, Leach et al. (2017*b*) reported that first-year survival declined by >50% from the early 1990s to the early 2010s. This pattern of selection against small individuals after their first summer has resulted in only relatively small declines in adult body size (Riecke 2020) and no clear trend in clutch size (Figure 3), consistent with the idea that much of the variation results from environmental or maternal origins. Nevertheless, we cannot rule out negative pleiotropy (Sinervo and Svensson 1998) to explain the relatively weak response to selection.

Our findings are consistent with the demographic buffering hypothesis for long-lived, iteroparous organisms. This hypothesis states that because population dynamics and individual fitness are more sensitive to survival than reproduction (Schmutz et al. 1997, Gaillard et al. 1998, Rotella et al. 2012), selection has tended to canalize adult survival, resulting in reduced variance in survival relative to other demographic traits. For example, the nearly seven-fold greater range of variation in breeding probability compared to apparent annual survival of adult female brant (Figure 2A, B) complies with expectations under demographic buffering. Moreover, the relatively flat selection gradient on clutch size, owing to variation in survival (Table 2, Figure 2A), would follow from a considerable lack of variation in innate survival from the brant population (Gaillard et al. 1998, Sæther and Bakke 2000).

Understanding links between within- and among-year reproductive trade-offs could help better predict population trends moving forward for brant and other long-lived organisms. Our results provide further evidence for the demographic buffering hypothesis and demonstrate substantial individual heterogeneity in fitness. This heterogeneity is reflected both in the general positive covariation among several components of fitness and in carry-over effects of reproductive tactics from one breeding season to the next. This work, in conjunction with earlier research (Sedinger et al. 2004, Monaghan 2007, Douhard et al. 2014), indirectly provides support for the importance of early growth conditions as regulators of individual fitness and population growth rates.

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**AUTHOR CONTRIBUTIONS**

JSS conceived the long-term monitoring program and has led data collection efforts through the course of the project. MGL and TVR conceived and led the analysis, with important contributions from PJW. MGL led the writing of the manuscript, with important contribution from all co-authors.

**COMPETING INTERESTS**

There are no competing interests to declare.

**DATA ACCESSIBILITY**

Data are available on the Dryad Digital Repository (XXX). Data will be archived upon manuscript acceptance.

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**TABLES**

**Table 1.** Prior distributions used in Bayesian robust-design models to estimate the effects of mean lifetime clutch size and nest initiation date on survival and breeding propensity of adult female black brant, marked and re-encountered at the Tutakoke River Colony, Alaska (1988 — 2014). Priors were chosen following Sedinger and Chelgren (2007), Kéry and Schaub (2011), Williams (2016), Riecke et al. (2018).

|  |  |
| --- | --- |
| **Parameter** | **Distribution** |
| *β*0 | *∼* Beta(8.5, 1.5) |
| *α*0 | *∼* Beta(7.2, 2.8) |
| ***β*** | *∼* Normal(**0**, 100**I**) |
| ***α*** | *∼* Normal(**0**, 100**I**) |
| *p* | *∼* Uniform(0,1) |
| *ε* | *∼* Normal(0, *σ*) |
| *σ* | *∼* Uniform(0, 5) |

**Table 2.** Estimates of *β* parameters for the relationships between average lifetime clutch size, nest initiation date, and their interaction on survival. Estimates come from hierarchical Bayesian robust design models that used reproductive and capture-recapture data collected from female black brant breeding on the Yukon-Kuskokwim Delta, Alaska (1988 — 2014). Parameters include the mean (*µ*), standard deviation (*σ*), 95% credible intervals (CRI), and the proportion of the posterior distribution on the same side of 0 as the mean (*ξ*).

|  |  |  |
| --- | --- | --- |
|  | **Parameter** | **Estimate** |
| Clutch Size | *µ* | 0.03 |
| *σ* | 0.02 |
| 2.5% CRI | -0.01 |
| 97.5% CRI | 0.07 |
| *ξ* | 0.92 |
| Initiation Date | *µ* | -0.003 |
| *σ* | 0.02 |
| 2.5% CRI | -0.04 |
| 97.5% CRI | 0.03 |
| *ξ* | 0.56 |
| Interaction | *µ* | 0.03 |
| *σ* | 0.02 |
| 2.5% CRI | -0.07 |
| 97.5% CRI | 0.08 |
| *ξ* | 0.89 |

**Table 3.** Estimates of *β* parameters for the relationships between average lifetime clutch size, nest initiation date, and their interaction on breeding probability. Estimates come from hierarchical Bayesian robust design models that used reproductive and capture-recapture data collected from female black brant breeding on the Yukon-Kuskokwim Delta, Alaska (1988 — 2014). Parameters include the mean (*µ*), standard deviation (*σ*), 95% credible intervals (CRI), and the proportion of the posterior distribution on the same side of 0 as the mean (*ξ*).

|  |  |  |
| --- | --- | --- |
|  | **Estimate** | **Values** |
| Clutch Size | *µ* | 0.45 |
| *σ* | 0.06 |
| 2.5% CRI | 0.33 |
| 97.5% CRI | 0.57 |
| *ξ* | 1.00 |
| Initiation Date | *µ* | -0.12 |
| *σ* | 0.04 |
| 2.5% CRI | -0.12 |
| 97.5% CRI | -0.04 |
| *ξ* | 1 |
| Interaction | *µ* | -0.11 |
| *σ* | 0.05 |
| 2.5% CRI | -0.21 |
| 97.5% CRI | -0.01 |
| *ξ* | 0.99 |

# FIGURE LEGENDS

**Figure 1.** Theoretical gradients of survival (**A**) and breeding probability (**B**). Under the demographic buffering hypothesis, long lived species should have little within population variation in survival across gradients of individual quality. Breeding probability, however, should show substantial variation, with high quality having much higher breeding probabilities than low quality individuals.

Fi**gure 2.** Predicted survival (**A**) and breeding probability (**B**), and *σ* values of predicted survival (**C**) and breeding probability (**D**), using clutch size, initiation date, and clutch size/initiation date interaction for female black brant breeding on the Yukon-Kuskokwim River Delta, Alaska (1988-2014). Surfaces were predicted from linear models lining survival and breeding probability and associated parameter estimates described in the Methods and Results.

**Figure 3.** Frequency of recorded clutch sizes of female black brant breeding on the YKD in Alaska from 1988 — 2014.