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Fitness Consequences of Clutch Size Decisions and Mate Change in Black Brant

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By

Alan Gregory Leach

Dr. James S. Sedinger/Dissertation Advisor

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We recommend that the dissertation prepared under our supervision by

ALAN G. LEACH

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DOCTOR OF PHILOSOPHY

James S. Sedinger, Ph.D, Advisor

Marjorie Matocq, Ph.D, Committee Member

Anne Leonard, Ph.D, Committee Member

Matt Forister, Ph.D, Committee Member

Aleksey Telyakovskiy, Ph.D, Graduate School Representative

David W. Zeh, Ph. D., Dean, Graduate School

December, 2015
ABSTRACT: For long-lived species with perennial, socially monogamous pair bonds and bi-parental brood care, decisions concerning how much to invest in reproduction and whether to remain with a partner could substantially affect lifetime fitness. I studied the fitness consequences of reproductive effort (Chapter 2) and mate change (Chapters 3-5) in black brant geese (*Branta bernicla nigricans*, hereafter brant), an Arctic nesting goose species with precocial young. I used a 25 year (1990–2014) dataset collected at the Tutakoke River brant colony (TRC), in southwestern Alaska, USA to investigate these questions. Brant provide an ideal study species because researchers are able monitor large numbers of individuals and obtain unbiased estimates of fitness components throughout their life cycle.

In my second chapter, I used experimental manipulations of clutch and broods sizes (i.e., the number of goslings leaving the nest) to understand if the maximal clutch size laid by brant (i.e., 5 eggs) is under ultimate control as a result of tradeoffs between reproduction and residual reproductive value of females. I used the Barker robust design mark-recapture model to estimate two components of female fitness: (1) true survival and (2) breeding probability in \( t+1 \). I found no evidence that incubated clutch size affects future fitness of female brant. However, breeding probability in \( t+1 \) (0.82 ± 0.10 [95% CI]) was maximized for females tending 4–5 goslings and declined for females with smaller or larger brood sizes. Thus, the brood sizes that maximized the residual reproductive value of adult females matched the most common clutch sizes laid by brant. The unexpected result that females tending smaller broods had lower future fitness may result from their smaller family size during winter which may decrease their social status in wintering flocks and result in reduced foraging profitability which may carryover to affect reproduction. My findings support the hypothesis that the maximal clutch size in brant is under ultimate regulation because of tradeoffs with adult residual reproductive value.
In Chapter 3, I investigated whether or not mate change influenced reproductive success of female brant. I hypothesized that changing mates could affect reproductive success because (1) new pairs are unfamiliar with each other and (2) females may repair with a male that is an inexperienced breeder (i.e., fewer than two previous breeding attempts at TRC). I investigated the reproductive consequences of mate change using generalized linear models to estimate relative initiation date, clutch size, and the number of goslings leaving the nest and a Cormack-Jolly-Seber mark-recapture analysis to estimate prefledging survival. I found that females breeding with an unfamiliar, but otherwise experienced male fledged at least as many goslings as females breeding with an experienced, familiar mate. However, females who had switched to an inexperienced mate initiated their nests 0.48 (± 0.26 [95% CI]) days later and incubated clutches that were 0.17 (± 0.10 [95% CI]) eggs smaller than females breeding with a familiar mate. More importantly, goslings attended by a mother who was breeding with an experienced, familiar mate had greater prefledging survival ($\phi = 0.30 \pm 0.04$ [95% CI]) than those whose mother had changed mates in year $t$ and paired with an inexperienced male ($\phi = 0.19 \pm 0.04$ [95% CI]). These results support the hypothesis that there can be reproductive costs of changing mates for female brant, but male experience rather than familiarity of partners determines these costs.

In Chapter 4, I estimated rates of mate retention and investigated if there were long-term fitness benefits of mate retention. This analysis included 3021 and 3039 mature female and male brant who bred at TRC from 1990–2014. From 1990–2010, I recorded 748 and 196 breeding attempts after mate change for female and male brant, respectively. I estimated mate fidelity in $t+1$ of brant that were breeding with a familiar or unfamiliar mate in year $t$ using a multi-strata robust design capture-mark-recapture analysis. I investigated whether breeding with a new mate reduced true survival or breeding probability in $t+1$ using the Barker robust design capture-
mark-recapture framework. I found that mate retention in year $t+1$ for brant breeding with a familiar mate in year $t$ was high for females ($0.881 \pm 0.017 \text{ [95\% CI]}$) and males ($0.952 \pm 0.013 \text{ [95\% CI]}$). However, for individuals who had switched mates in year $t$ the probability of mate fidelity was greatly reduced for females ($0.277 \pm 0.163 \text{ [95\% CI]}$) and males ($0.343 \pm 0.246 \text{ [95\% CI]}$). There was also long-term fitness costs associated with mate change. Such that individuals who nested with a new mate had true survival rates which were lower ($S_{\text{females}} = 0.85 \pm 0.009 \text{ [95\% CI]}$; $S_{\text{males}} = 0.80 \pm 0.017 \text{ [95\% CI]}$) than those breeding with a familiar mate in year $t$ ($S_{\text{females}} = 0.90 \pm 0.006 \text{ [95\% CI]}$; $S_{\text{males}} = 0.89 \pm 0.011 \text{ [95\% CI]}$). Additionally, individuals nesting with a new mate had a lower probability of breeding in year $t+1$ (females = $0.80 \pm 0.035 \text{ [95\% CI]}$; males = $0.44 \pm 0.090 \text{ [95\% CI]}$) than those breeding with a familiar mate in year $t$ (females = $0.96 \pm 0.008 \text{ [95\% CI]}$; males = $0.98 \pm 0.006 \text{ [95\% CI]}$). I hypothesize that the demographic costs of mate change are partially related to the relatively low rates of mate retention among newly formed pairs. As a result, individuals breeding with a new mate are more likely to be single for part of the next winter which likely reduces their social status in wintering flocks and results in additional energy expenditure while they attempt to repair. To my knowledge, these results represent the first strong evidence of a link between breeding with a familiar mate and adult demographics in a long-lived bird, with perennial, socially monogamous pair bonds.

In my fifth chapter, I investigated factors influencing mate retention and the proportion of female brant that pair with an inexperienced mate after mate change. I predicted that female brant that had undergone a mate change in year $t$ and had paired with an inexperienced breeder or who failed to produce at least one gosling would have low rates of mate retention. I also suspected that brant would pair in a positive assortative manner by body size, previous breeding
experience, and age because of the potential fitness benefits of breeding with larger, older and more experienced mates. Contrary to a priori predictions I found that females who had repaired with an inexperienced male were 39% more likely to retain their mate than those who repaired with an experienced male. I found no evidence that successfully producing at least one gosling influenced future mate retention. I recorded 273 cases where experienced female brant switched mates and the new mate was previously marked. In these cases the age of each mate was more strongly correlated (r = 0.26, P < 0.001) than the previous number of breeding attempts by each partner (r = 0.16, P = 0.007). There were weak, but statistically significant correlations between tarsus (r = 0.07, P = 0.012) and culmen (r = 0.07, P = 0.016) lengths of partners (i.e., proxies for structural size). However, body mass during brood-rearing was more strongly correlated among pair members than structural measurements (r = 0.28, P < 0.001). I estimated that about 90% of females who change mates acquire a male who is likely an inexperienced TRC breeder. It is unclear why females who pair with experienced partners have lower rates of mate retention, but it could result from experienced males being in short supply, thereby, enabling them to increase their choosiness in mates. It is clear that most females who change mates will suffer short term reductions in reproductive success, because they will likely acquire partners who are inexperienced breeders.

When taken together, the results of chapters 3-5 suggest that there are short and long-term fitness benefits for brant that remained paired with an experienced, familiar partner. These benefits of mate retention may at least partially explain why brant have a perennial, socially monogamous mating system.
ACKNOWLEDGMENTS: It is relatively unique for a researcher project of this size to continue for more than 30 years and this has required a diversity of funding agencies and folks willing to collect the data. Studies at the Tutakoke River brant colony have been funded by a variety of individuals and organizations over the years including: 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 Jeppia; and the National Science Foundation (OPP 9214970, DEB 9815383, OPP 9985931, OPP 0196406, DEB 0743152, DEB 1252656). I received additional stipend and travel support from the U.S. Geological Survey, the Dennis Raveling scholarship, the UNR Ecology, Evolution, and Conservation Biology program, the UNR graduate student association, the California Waterfowl Association and the UNR college of Agriculture, Biotechnology, and Natural Resources. I thank David Ward (Alaska Science Center, USGS) and Sean Boyd (Environment Canada) for sharing their live resight datasets from Baja California and British Columbia, respectively.

Obviously, considering that data collection at the Tutakoke River colony began when I was 2 years old, I have been fortunate to utilize the amazing dataset collected by former graduate students and more than a hundred research technicians. Thanks to all of you for your efforts. Specifically, I would like to thank Brandie Cheatham, Andrew Clark, Cody Deane, Andy Ganick, Eric Huskinson, Heather Johnson, Maureen McClintock, Howie Singer, Stephanie Walden, Everett Willey, and Nathan Yeldell who were technicians while I was a graduate student working at Tutakoke from 2010–2013. Matt Irinaga of CH2M Hill Polar Services provided valuable logistical field support during camp setup the years I worked at Tutakoke. Thanks Matt for your help training each new crew, conveying valuable knowledge about how to safely and effectively carry out logistics in a remote setting, and for your friendship. The staff of
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I am sincerely grateful to my major advisor, Jim Sedinger, thank you for having the foresight and endurance to keep the Tutakoke River project running for all these years. Overseeing the logistics and data collection at Tutakoke requires a great deal of responsibility from Jim’s graduate students, but I can honestly say I grew much during the time and had some of the greatest experiences of my life on the delta. Jim, I also appreciate your willingness to let me pursue my interests and discuss quantitative methods and possible ways forward with my dissertation at each juncture. The rest of my committee including: Matt Forister, Anne Leonard, Marjorie Matocq, Anna Panorska, and Aleksey Telyakovskiy helped me refine the ideas in my dissertation and made me a more broadly trained ecologist; I thank them for their support and assistance. Given the amount of logistical preparation, hiring, and travel involved in the Tutakoke River project I would not have been able to navigate the UNR bureaucracy without the NRES and CABNR staff, thanks to Diana Arrendale, Lindsey Barnes, Vicky Boyles, Heidi McConnell, Kerrie Medeiros, and Ron Rocky. All of the students in the EECB program have created a great atmosphere for thought and critical examination of ones ideas. I specifically want to thank Erik Blomberg, Dan Gibson, Josh Jahner, Levi Jaster, Abby Lawson, Sabrina Morano, Thomas Riecke, Ben Sedinger, Phillip Street, and Mandy Van Dellen for assistance with everything from statistics, fieldwork logistics, and teaching to generally enjoying my time in Reno.
Last but not least I want to thank my family for their support over the years. When I started down this career path some 15 years ago I didn’t know where it would lead and never expected it to include spending four summers of my life in a remote field camp in Alaska and a Ph.D at the University of Nevada-Reno. I have to especially thank my parents for their support during this time of exploration and discovery. I am not sure that all parents would have supported such endeavors over more traditional paths to employment. Finally, to my wife, Casey, thanks for your love and support through the writing of an M.S. thesis and dissertation. Having you as my best friend through my graduate student career has made all the difference.
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Chapter I: General introduction

The four core chapters in my dissertation assess the fitness consequences of clutch size decisions and effects of mate change on the fitness of black brant (*Branta bernicla nigricans*; hereafter brant). Brant form perennial, socially monogamous pair bonds with partners remaining together and cooperating during winter, migration, and breeding (Bellrose 1980). Brant lay only one clutch of eggs (3-5) per breeding season and care for the brood of precocial young together. After fledging, brant juveniles migrate and cooperate with parents to acquire favorable foraging positions in wintering flocks (Poisbleau *et al.* 2006).

I address two core objectives in the current work. First, given that the distribution of brant clutches has a sharp right truncation with very few clutches consisting of more than five eggs (Chapter 2), I hypothesized that ultimate costs of reproduction may limit maximal clutch size in brant (Lack 1947). Secondly, I was interested in understanding if the long term pair bonds of brant were maintained due to fitness consequences of mate change and a lack of quality, unpaired individuals in the population (e.g., individuals having breeding experience) (Griffith *et al.* 2011). This second objective I address in Chapters 3–5. In these chapters the reader should note that I have chosen to combine divorces and widowing events into the same category (i.e., mate change) as has been done in investigations of barnacle geese (*Branta leucopsis*) (Forslund and Larsson 1991, Black 2001) and great tits (*Parus major*) (Culina *et al.* 2013). I did this because I was interested in the consequences of changing mates in general; not the consequences of
divorce versus widowing events. In these chapters I used longitudinal data on >6000 female and male brant spanning 25 years (1990–2014) including 748 females and 196 males who switched mates and bred with a new partner. It should also be noted that I have chosen to use females as the focal sex in chapters 2, 3, and 5. My reasoning for this was that females rarely disperse to other breeding colonies, which allows sampling of fitness components throughout their lives and larger sample sizes.

Brant are the smallest North American goose and breed from the mid-Russian Arctic, east to the mid-Canadian Arctic and south to the Yukon-Kuskokwim Delta (YKD) of Alaska, USA (Lewis et al. 2013). The population of brant I studied breeds at the Tutakoke River brant colony on the YKD, and winters as far south as estuaries on the coast of Bahia San Quentin, Baja California, Mexico. I have been fortunate to be able to continue the long-term work at TRC on brant that was begun in 1984 by my major advisor, Jim Sedinger, and his graduate students. Since 1986, >40,000 brant have been marked at this colony with uniquely identifiable, color tarsal bands. Each year, adults are monitored at nesting and captured during the brood rearing period with their goslings, many of whom are webtagged at the nest (Alliston 1975). Another outstanding part of this dataset is the long-term resighting efforts that have been conducted since 1989 during spring migration at the Strait of Georgia, British Columbia, Canada and on the wintering grounds at Bahia San Quentin, Baja California, Mexico resulting in >125,000 live resights of brant during the non-breeding season. Dr. Sean Boyd (Science and Technology branch, Environment Canada) has managed the British Columbia dataset and David Ward (U. S. Geological Survey, Alaska Science Center) the Mexico resight data.
They have both graciously shared these rich datasets with me and will be co-authors on the publications that emerge from two of chapters included in this dissertation. By combining the TRC dataset, live sights during the non-breeding season, and recoveries of brant by hunters I was able to estimate true survival (i.e., not biased by permanent emigration) which is impossible to do in many studies of wild, migratory animals (Kendall et al. 2013). Much of the following work draws heavily on modern capture-mark-recapture (CMR) methods to obtain unbiased estimates of the demographic parameters of interest (e.g., true survival, breeding probability, and prefledging survival).

The chapters of this dissertation have been prepared in accordance with the journals for which they are intended. Chapters 2 and 4 are intended for submission to the *Journal of Animal Ecology*. Chapter 3 is prepared for submission to *Behavioral Ecology* and Chapter 5 will be submitted to the *Auk*. Because some chapters are prepared for North American journals and others British journals the reader will notice variations in terms including: brant and band (North American usage) versus brent and ring (British) depending upon the intended journal.

In my second chapter I used manipulations of clutch and brood sizes, performed from 2008-2012, to test for effects of incubation and brood rearing effort on residual reproductive value of brant. Specifically, I used the Barker robust design capture-recapture model (Kendall et al. 2013) in Program Mark (White & Burnham 1999) to estimate true survival and breeding probability of female brant as a function of the number of eggs incubated or goslings in her brood. My prediction was that female brant
forced to care for clutches or broods larger than the maximal number of eggs laid by brant (five) would have reduced future breeding probability or survival.

In my third and fourth chapters, I investigated whether mate change influences fitness components of brant. In chapter three I hypothesized that mate change would reduce the number of goslings fledged by females who have switched mates in the current year. Further, if there are reproductive costs of mate change, I wanted to understand if they were caused by a lack of familiarity between pair members (Black 2001; Sanchez-Macouzet, Rodriguez & Drummond 2014) or whether such costs were due to breeding with an inexperienced male (Naves, Cam & Monnat 2007). Thus, I predicted that if mate familiarity was the primary determinant of reproductive success, newly formed pairs would always fledge fewer goslings than familiar pairs. Alternatively, if male breeding experience was that primary determinant of reproductive consequences in females who changed mates; I expected that females who bred for the first time with an experienced male would be as successful as females breeding with a familiar mate, while those breeding with an inexperienced male would fledge fewer goslings. I tested for costs of mate change with respect to relative initiation date, clutch size, initial brood size using a Generalized Linear Mixed Models. I tested for mate change costs in prefledging survival using a Cormack-Jolly-Seber CMR analysis on individually webtagged goslings (Alliston 1975) in program MARK (White & Burnham 1999).

In chapter four I was interested in the long-term benefits of, and rates of mate retention, by brant. While many researchers have investigated the reproductive
consequences of mate change in birds, I know of only one study that attempted to estimate the long-term consequences of breeding with a new mate (Culina et al. 2013). My objectives in chapter 4 were to first determine if changing mates affected true survival, future breeding probability, or breeding fidelity to TRC (females who are alive, but not breeding at TRC are in a permanent non-breeding state). I used the Barker robust design CMR framework in Program Mark to achieve this goal (White & Burnham 1999; Kendall et al. 2013). Second, I was interested in estimating mate fidelity between familiar partners and those breeding together for the first time. For this objective I used the Multi-state robust design in program MARK.

In chapter 5, my first objective was to estimate the proportion of female brant that pair with an inexperienced breeder after changing mates. Females breeding with inexperienced males have reduced reproductive success (Chapter 3) so if the proportion of females apparently forced to repair with inexperienced males is high; most females will have a short-term disincentive to change mates. Further, I wanted to investigate patterns of assortative mating in brant as I expected that both sexes may benefit from and thus attempt to breed with larger, older, and more experienced partners. Finally, I was interested in understanding if mate fidelity in brant was influenced by dissimilarities in breeding experience between partners, reproductive success of individual pairs, or overall productively of TRC (apparent nest success and gosling growth rates) using a multi-state robust design CMR framework.
References


Chapter II: Reproductive effort affects residual reproductive value in a long-lived nidifugous bird

Alan G. Leach*a,b, James S. Sedinger a, Thomas V. Riecke a,b, Amanda W. Van Dellen a,b, David H. Ward c, and W. Sean Boyd d

a Department of Natural Resources and Environmental Science, University of Nevada-Reno, 1664 N. Virginia St., Reno, NV 89557 USA

b Program in Ecology, Evolution, and Conservation Biology, University of Nevada-Reno, 1664 N. Virginia St., Reno, NV 89557 USA

c U. S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA

d Science and Technology Branch, Pacific Wildlife Research Centre, Environment Canada, RR1 – 5421 Robertson Rd., Delta, British Columbia V4K 3N2, Canada

* Corresponding author: aleach@cabnr.unr.edu

RH: Residual reproductive value of brent geese
Summary

1. Estimation of trade-offs between current reproduction and future survival and breeding probability of long-lived vertebrates is essential to understanding optimal reproductive investment.

2. To our knowledge no study has combined experimental manipulation of reproductive effort with robust capture-mark-recapture techniques to estimate trade-offs between current reproduction and residual reproductive value (including future breeding probability) in an avian species with precocial young.

3. We used a seven year mark-recapture dataset that included five years of clutch and brood size manipulations to estimate long-term consequences of reproductive decisions in black brent geese (Branta bernicla nigricans). We hypothesized that the sharp truncation of the distribution of brent clutches at greater than five eggs is, at least partially, a result of long-term fitness consequences for females laying larger clutches.

4. We found that future breeding probability was maximized (0.82 ± 0.10 (± 95% confidence interval) for females tending broods of four goslings (i.e., the most commonly laid clutch sizes contain 4–5 eggs) and lower for females tending smaller (e.g., two goslings) (0.65 ± 0.15) or larger broods (e.g., six goslings) (0.70 ± 0.21). Additionally, survival of brent females tended to decline as the number of goslings reared increased (β = -0.52 ± 0.55).
5. Our results suggest that long-term demographic consequences for adult female
brent affect the fitness value of different clutch sizes and, therefore, the
optimal allocation of nutrients to the current reproductive bout. Our study
modifies, rather than replaces, earlier work on proximate regulation of clutch
size in precocial species. Nutrient limitation may play a role in regulating the
size of smaller clutches as originally proposed by Lack (1967).

**Key-words:** Barker robust design, brood size, costs of reproduction, Lack’s clutch,
Life-history, optimal clutch size, trade-offs

**Introduction**

Understanding how trade-offs between life-history traits shape the evolution of optimal
reproductive effort (i.e., that which maximizes fitness) has long been a goal of
evolutionary biologists (Lack 1947; Williams 1966; Stearns 1992). David Lack (1947)
suggested that optimal clutch size in species with altricial young was determined by the
ability of parents to provision and ultimately fledge the maximal number of young (i.e.,
“Lack’s clutch”). The ideas underlying “Lack’s clutch” have now been applied across a
broad range of species including mammals, reptiles, and insects (Godfray, Partridge &
Harvey 1991; Hardy, Griffiths & Godfray 1992; Aubret et al. 2003; Koivula et al. 2003;
Hamel et al. 2010). Experimental testing of the Lack clutch has revealed that birds often
produce clutches that are smaller than the maximal number of offspring they can fledge
(Dijkstra et al. 1990; Stearns 1992; Vanderwerf 1992; Monaghan & Nager 1997),
suggesting that the Lack clutch is modified by trade-offs between current reproduction and residual reproductive value (RRV) of adults (Williams 1966; Vanderwerf 1992; Monaghan & Nager 1997). Reductions in RRV can result from either reduced survival or decreased future fecundity (Stearns 1992).

Detecting negative covariation among life-history traits is often difficult. For example, heterogeneity in individual quality often results in high quality individuals both investing more in current reproduction and surviving at greater rates than low quality individuals (van Noordwijk & de Jong 1986; Yoccoz et al. 2002; Sedinger et al. 2008; Hamel et al. 2009). An additional problem for detecting trade-offs is that avian reproductive bouts can be separated into four discrete phases: the decision to breed, egg production, incubation, and rearing offspring to independence. Studies of life-history optimization may fail to detect trade-offs with RRV, if focusing on only one of these periods (Monaghan & Nager 1997; Visser & Lessells 2001). Thus, to observe trade-offs in the presence of heterogeneity in individual quality investigators must (1) experimentally manipulate effort in as many breeding phases as possible (Mappes, Koskela & Ylonen 1995; Monaghan & Nager 1997; Visser & Lessells 2001); and (2) assess impacts of reproductive investment on survival and each of the four phases of reproduction during the current and subsequent breeding seasons.

Lack of the general availability of appropriate capture-mark-recapture (CMR) approaches has meant that many early studies attempted to estimate adult survival using methods such as return rates (Boulinier et al. 1997; Townsend & Anderson 2007), that are known to be biased (Lebreton et al. 1992). The potential for there to be fitness consequences of not being encountered at a study area depend on whether the return rate
is affected by changes to a component of fitness (e.g., survival) or detection probability (Boulinier et al. 1997). For example, if manipulation of reproductive effort causes individuals to subsequently nest in areas of a breeding colony less accessible to researchers (e.g., the periphery) the reduced return rate of such individuals would be influenced by detection probability, with potentially no effect on fitness. Robust CMR approaches also allow estimation of an important, but often overlooked component of fecundity, which is the frequency with which an individual decides to breed (Kendall, Nichols & Hines 1997; Sedinger et al. 2008; Souchay, Gauthier & Pradel 2014).

Separately estimating survival and breeding probability is essential to understanding trade-offs between allocation to current and RRV for long-lived species because fitness is more sensitive to survival and may be preserved to the detriment of breeding (Stearns 1992; Saether & Bakke 2000; Hamel et al. 2010; Rotella et al. 2012).

Most studies of optimal clutch size in birds have focused on species with altricial young, primarily based on the belief, dating to Lack (1967), that altricial young require greater parental investment than precocial young (Safriel 1975; Lessells 1986). Species with precocial young have received less attention, although a few studies have assessed optimal clutch size (Safriel 1975; Rohwer 1985; Lessells 1986; Rockwell, Findlay & Cooke 1987; Lepage, Gauthier & Desrochers 1998; Loonen et al. 1999). Though ultimate regulatory mechanisms have been proposed (e.g., egg viability, incubation capacity, and costs of brood-rearing) (Arnold, Rohwer & Armstrong 1987; Schindler & Lamprecht 1987; Sandercock 1997), the general consensus, has been that clutch size in precocial species is proximally regulated by female nutritional status. Though more recently, hypotheses have been refined to state that individuals simultaneously optimize
the timing of nest initiation with clutch size (Drent & Daan 1980). Generally, findings are consistent with the notion that capital breeders (e.g., arctic nesting geese) simultaneously optimize both the timing and size of their clutches, contingent on their nutritional states during winter and spring (Prop & de vries 1993; Bety, Gauthier & Giroux 2003). Proximal nutrient limitation of clutch size has been most readily accepted in arctic nesting geese, though because they are capital breeders, hypotheses have been refined to focus on nutrients stored prior to breeding (Ryder 1970; Ankney & Macinnes 1978). However, as Arnold and Rohwer (1991) pointed out, the apparent plausibility of the nutrient limitation hypothesis has often led to its acceptance without widespread tests of alternative or additional mechanisms of clutch size regulation.

Further, observations of clutch size distributions, egg replacement, and variation in pre- and post-laying nutritional states appear to be inconsistent with nutrient reserves completely regulating clutch size in precocial species. Such observations include clutch removal experiments that reveal an astounding ability of precocial birds to replace eggs without reductions in clutch size or egg volume (Arnold & Rohwer 1991; Yogev, Ar & YomTov 1996). Other anomalies include populations where individuals laying the smallest clutches have lower post-laying nutrient reserves than individuals laying the largest clutches (Arnold & Rohwer 1991) and large among-individual variation in post-laying nutrient reserves (Eichholz & Sedinger 1999). If pre-laying nutrient reserves solely regulate clutch size in precocial species we might expect that the distribution of clutches would closely resemble the distribution of nutrient reserves among individuals before egg laying and that all individuals would have similar post-laying nutrient reserves (Arnold & Rohwer 1991). Finally, the relatively abrupt upper limit to clutch size
distributions in numerous species, including black bren con geese (*Branta bernicla nigricans*, hereafter brent, Fig. 2-1a) suggests selection against individuals producing clutches larger than the observed maximum because such clutches reduce fitness through either fewer recruited young or reduced RRV.

We used five years of experimental manipulations of clutch and brood sizes of brent combined with CMR methods to assess the effects of current reproduction on RRV of mature female brent. We hypothesized that brent would experience reduced RRV when incubating clutches or rearing broods with offspring in excess of the largest clutches typically laid by brent (five eggs). Specifically, we predicted that trade-offs between current reproduction and future breeding probability act as an important selective force shaping maximal clutch size in this long-lived, migratory species with precocial young.

**Materials and methods**

**STUDY AREAS AND SPECIES**

Brent breed in coastal habitats from the Yukon-Kuskokwim Delta (YKD), Alaska, west to the mid-Russian Arctic and east to the mid-Canadian Arctic (Lewis *et al.* 2013). Brent are gregarious throughout the annual cycle, wintering in, and migrating through, coastal lagoons from the Alaska Peninsula, USA to Baja California, Mexico where they forage mainly on *Zostera marina* (Sedinger *et al.* 1993). Brent form long-term, year-round, socially monogamous pair-bonds and family groups remain together through the offspring’s first winter (Bellrose 1980). Brent are capital breeders using stored reserves for ~22% of the nutrients in the average clutch (Ankney 1984). Brent females are determinate layers, typically laying clutches of 3–5 eggs with a sharp truncation of larger
clutches (Fig. 2-1a), and assume all incubation duties during the 24 day incubation period (Lindberg & Sedinger 1997; Eichholz & Sedinger 1998). Within 24–48 hours of the first hatching activity brent goslings disperse with parents to terrestrial brood rearing areas where they forage mostly on *Carex subspathacea* (Flint, Sedinger & Pollock 1995; Sedinger, Eichholz & Flint 1995). Brood rearing responsibilities of female brent include brooding goslings during inclement weather, providing vigilance against predators, and taking aggressive actions towards intruding conspecifics (Sedinger, Eichholz & Flint 1995).

We conducted the nesting portion of our study at the Tutakoke River brent colony (hereafter TRC; 61°15′N, 165°37′W), Alaska, USA from 2008–2014. Though the current numbers of breeding brent at TRC are only half those during the 1990s, the number of brent nests remained relatively stable during our study (Wilson 2014). Winter resighting efforts occurred at Bahia San Quintin, Baja California, Mexico during three winters 2010-2013. Resighting efforts during spring migration occurred in the Strait of Georgia, British Columbia, Canada from 2009-2014.

MARKING AND REENCOUNTER

Since July 1986 we have marked adult (2+ years old), immature (1 year old), and gosling brent at ringing drives during adult remigial molt (Sedinger *et al.* 2008). Individuals were marked with USGS metal tarsus rings and 2.5 cm tall plastic coloured tarsus rings engraved with a unique alphanumeric code. We determined sex with a cloacal examination (Owen 1980). Approximately, 40% of the breeding females at TRC were colour ringed and uniquely identifiable during our study. As soon as egg laying began (May 10th - May 28th) we used 20–60X spotting scopes to read colour rings of female
brent after flushing them from their nests (Sedinger et al. 2008). During the adult wing moult in late-July we conducted ringing drives on seven brood rearing areas at TRC, recording recaptures of breeding females (i.e., those with brood patches) (Sedinger et al. 2008; Nicolai et al. 2014). During winter and spring migration we used Questar 35–150X telescopes (Questar, New Hope, Pennsylvania, USA) to read colour rings of brent at gritting bars as water level dropped following high tide (Ward et al. 2004). We obtained ring recovery information of brent harvested from autumn 2008-spring 2014 from the Bird Banding Laboratory in Patuxent, Maryland, USA (U.S. Geological Survey). All handling of animals was approved by Institutional Animal Care and Use committees at the University of Alaska Fairbanks and the University of Nevada Reno (most recent protocol number 00056).

MANIPULATION OF REPRODUCTIVE EFFORT

Our objectives for manipulating reproductive effort were three-fold. First, we created clutches and broods that exceeded the maximal clutch typically laid by brent geese (i.e., five eggs). We reasoned that the only way to test if incubation and/or brood rearing costs shaped maximal clutch size was to induce brent to care for clutches and broods larger than the maximal clutch size. Secondly, we wanted to decouple individual quality (e.g., laid clutch size) from incubated clutch and reared brood size (see introduction for reasoning). Lastly, we manipulated clutch and brood sizes of females in the same breeding season to reduce correlation between incubated clutch and brood size, thus allowing for independent estimation of the potential long-term effects of each breeding phase.
As soon as nesting began we intensively searched the nesting colony daily to determine nest initiation dates and clutches sizes (CS) of nests attended by ringed female brent. We only calculated initiation dates for nests found with one or two eggs and little or no down (i.e., found during egg laying). We considered nests found with one egg to have been initiated on the day of discovery while nests found with two eggs were initiated the day prior. Once a clutch was complete (i.e., no new eggs for 48 hours) it was eligible for experimental manipulation. We only moved eggs between clutches having the same number of eggs and initiation date to maintain hatching synchrony (Nicolai, Sedinger & Wege 2004). All clutch manipulations were done within ~72 hours of clutch completion. Eggs were carried in insulated bags between nests that were typically < 75 meters apart. Thus, eggs were out of a nest less than five minutes. Nests were subsequently checked 2-3 times during incubation to record any predation of eggs. Since our goals were to create a range of manipulated clutch and brood sizes, including those larger than naturally occur, not all females were subjected to equal numbers of eggs and goslings added or subtracted. We subtracted any eggs predated during incubation from the final manipulated clutch size (MCS) value used in our analysis.

We monitored nests of marked females daily during hatch. At hatch we moved pipped eggs, wet goslings (i.e., hatched within the last 1-2 hours), or dry goslings between nests at the same stage of hatching. After the brood had left the nest we visited all nests again to record dead goslings or unhatched eggs and subtracted them from the final brood size to calculate the number of goslings leaving the nest (GLN).
STATISTICAL ANALYSES

Our study included seven primary occasions (i.e., breeding seasons) each having two secondary occasions during which we assumed the population was closed to immigration and emigration: (1) nesting, and (2) ringing during the adult wing moult. We used the Barker robust design in program MARK implemented via RMark (Laake 2013) to estimate effects of current reproduction on true survival and the probability of temporary emigration (i.e., skipped breeding) from TRC (Kendall et al. 2013). The Barker robust design analyzes patterns of individual encounters across secondary occasions to separately estimate the probability of detecting an individual at least once during a primary occasion, conditioned on its presence, from the probability that an individual was present (synonymous with breeding in our study). Further, this mark-recapture framework combined live reencounter information of individuals at TRC and during the non-breeding season (winter and spring migration) with dead recoveries to (1) improve precision in estimates of true survival and temporary emigration, and (2) reduce terminal bias in true survival estimates (Kendall et al. 2013; Penaloza, Kendall & Langtimm 2014). We assessed the effects of violation of the closure assumption between secondary occasions elsewhere (Sedinger, Lindberg & Chelgren 2001) and found minimal (< 2%) bias in estimates of breeding probability associated with up to 20% emigration between secondary occasions.

In our study, the Barker robust design allowed modeling of 10 parameters: true survival ($S$), probability an individual that died between $t$ and $t+1$ was found dead and reported ($r$), probability of resighting during the non-breeding season conditioned on being alive ($R$), probability that an individual was observed alive before it died during a
non-breeding season \((R')\), probability an individual was present and available for encounter at TRC given availability the year before \((A^-)\), probability an individual was present and available for encounter at TRC given absence the year before \((A')\), probability an individual did not permanently emigrate from TRC after time \(t\) \((F)\), probability an individual was initially encountered at TRC during nesting conditioned on being available during that breeding season \((p_{nesting})\), probability an individual was initially encountered at TRC during ringing conditioned on being available during that breeding season \((p_{ringing})\), and the probability that an individual encountered at nesting was recaptured at ringing \((c)\). Because we restricted all encounters at TRC to breeding female, temporary emigration from TRC was equivalent to skipping breeding (Sedinger et al. 2008).

We constructed most individual encounter histories starting with the first breeding encounter after initial ringing (Sedinger et al. 2008). However, a subset of females receiving clutch and/or brood manipulations were caught and ringed on their hatching date \((n = 103)\). Because these females could positively bias estimates of true detection we did not allow them to contribute to estimates of \(p_{nesting}\) and \(p_{ringing}\) in their ringing year. We separated females into two groups: (1) those experiencing a reproductive manipulation by investigators (i.e., manipulated group), and (2) those not experiencing a reproductive manipulation during the course of the study (i.e., nonmanipulated group). If a female experienced a reproductive manipulation in any breeding season during the study she was placed in the manipulated group for the entire study. Our objective for including nonmanipulated females was to improve precision in \(r, R, p_{nesting}, p_{ringing}\), and \(c\). Finally, we limited our analysis to females detected during nesting at least once during
our study. Our reasoning for this was that the probability a female was detected at nesting was greater than during ringing drives (Sedinger, Lindberg & Chelgren 2001) and we did not want to include females potentially nesting outside the colony and therefore only available for encounter at ringing.

For brent in the manipulated group we only modeled effects of CS, MCS, and GLN for the year following manipulation, thereby, avoiding a mixture of natural and manipulated reproductive effects for these females. We considered CS of each female to be a proxy for individual quality in year \( t \) (Yoccoz et al. 2002; Hanssen et al. 2003). The covariate MCS was used to test for relationships between incubated clutch size in year \( t \), survival to \( t+1 \), and breeding probability \( (A^-) \) in \( t+1 \). The covariate GLN was used to test for relationships between brood-rearing effort in year \( t \), survival to \( t+1 \), and breeding probability \( (A^-) \) in \( t+1 \). We only modeled the effects of CS, MCS, and GLN for females successfully leaving the nest with a brood in year \( t \) (i.e., GLN > 0). Our reasoning for this was that our objective in this paper was to understand the fitness consequences of incremental changes in the costs of incubation and brood rearing and their implications for the evolution of maximal clutch size, not the costs of successful vs. failed breeding.

Based on earlier work with this population which indicated that survival and breeding probability varied with age we created a time varying age covariate to control for variation in true survival and breeding probability with age (Sedinger, Lindberg & Chelgren 2001; Sedinger et al. 2008). All females were assigned a continuous time-varying age covariate (AGE; range = 2–26). Approximately, 30–35% of females breeding at TRC are of known age (i.e., banded as a gosling or one year-old); females
ringed as adults were assumed to be 2 years old when first captured. All covariates were
z-standardized to mean = 0 and SD = 1 within groups.

We corrected for overdispersion caused through extra binomial variation by
adjusting $\hat{c} = 1.11$ (Sedinger et al. 2007; Nicolai et al. 2014), because there is not a
customized goodness-of-fit procedure for the Barker robust design (Kendall et al. 2013).
This adjustment resulted in model selection being more conservative regarding inclusion
of variables and increased the variance of parameter estimates to account for any lack of
independence among individuals. We set $F$ to 1.0 to reflect the fact that once female
brent begin nesting at TRC they are faithful to the site for future breeding attempts
(Lindberg et al. 1998; Sedinger et al. 2008). We set $R' = 0.0$ as was done in a previous
analyses of data from this population (Nicolai et al. 2014). We only modeled effects of
were used for their reencounter information only to reduce sampling correlation between
temporary emigration and survival at the end of our time series (Penaloza, Kendall &
Langtimm 2014).

We reasoned that previous manipulations of reproduction would not affect
detection probability of an individual breeding at TRC in year $t$. We hypothesized that a
behavioural response to previous reproductive effort could be manifested in two ways:
(1) females would nest in other areas of the colony in subsequent year(s) (Lindberg &
Sedinger 1997), or (2) females might be less attentive to the nest when approached by
investigators, both of which could affect $p_{nesting}$. However, given the large geographic
area at which the ringing drives were conducted (Nicolai & Sedinger 2012) neither of
these nesting behaviours would preclude a female from being captured during brood rearing in year $t$.

Our first model selection step was to find the optimal base model for all parameters. We did this by first finding the best group (manipulated versus nonmanipulated) and temporal structure for $R$, $r$, $p_{nesting}$, $p_{ringing}$, and $c$. We then found the group, temporal, and AGE structure for $S$, $A''$, and $A'$ that minimized the QAICc score. Next we used the best performing model from step one to test hypotheses using CS, MCS, and GLN. We included two-way interactions between CS and MCS, CS and GLN, and MCS and GLN. We also tested models having quadratic effects of MCS and GLN. We used $\Delta$QAICc and 95% confidence intervals on parameter estimates to draw inferences about the relative support for each model and parameter. Models within 2 QAICc units of the best model were considered competitive (Burnham and Anderson 2002).

**Results**

We encountered 1906 breeding female brent during the course of our study. Of these females we manipulated the clutch and/or brood size of 386 female brent (72 in more than 1 year) from 2008–2012. From 2008–2012, we experimentally manipulated 297 clutches (Fig. 2-1b) and 253 broods (Fig. 2-2b). Across all years we directly manipulated the clutch size and brood size of 76 reproductive attempts in the same year. We documented 92 cases where we manipulated only the clutch size, but unhatched eggs or dead goslings resulted in a smaller GLN than MCS. We manipulated only the final brood size for 177 breeding attempts. The range of manipulated clutch sizes we created was larger than those generally laid by brent and the distribution was more uniform with six
eggs being the most common MCS (Fig. 2-1b). Overall, MCS and GLN were moderately correlated \( (r = 0.59, P < 0.001) \). However, for females that incubated manipulated clutches larger than 5 eggs there was no correlation between MCS and GLN \( (r = 0.09, P = 0.36) \). Our manipulations resulted in CS being only weakly correlated with MCS \( (r = 0.29, P < 0.001) \) and GLN \( (r = 0.24, P < 0.001) \).

Our base model included an effect of group and AGE on \( S \), an intercept only structure on \( r \), annual variation in \( R \), a Markovian structure for temporary emigration with annual variation in \( A'' \), and an intercept only structure for \( A' \), detection probabilities that varied with group, year, and secondary occasion, and \( c \) that varied with year. The Markovian structure for temporary emigration meant that breeding in year \( t \) influenced the probability of breeding in year \( t+1 \). Our best supported model included an additive group, AGE, and GLN structure on \( S \), and a year and quadratic GLN effect on \( A'' \). This model was clearly supported over our base model \( (\Delta QAIC_c = 17.3; \text{Table 2-1}) \). We had nine competitive models from our candidate set (Table 2-1). Of these two included an MCS effect, four a linear effect of GLN, three a quadratic effect of GLN, and one a CS effect on \( S \). While four competitive models included CS, none included MCS, and all included a quadratic effect of GLN on \( A'' \). The most supported model not including a quadratic effect of GLN on \( A'' \) had a \( \Delta QAIC_c = 6.2 \) (Table 2-1).

We report parameter estimates (± 95% CIs) from the best supported model. Survival declined with age for all females \( (\beta = -0.43 \pm 0.11) \). For females in the manipulated group survival declined linearly with brood size \( (\beta = -0.52 \pm 0.55; \text{Fig. 2-3}) \). The linear and quadratic effects of GLN on \( A'' \) were \( 0.43 \pm 0.37 \) and \( -0.57 \pm 0.27 \), respectively. As a result, future breeding probability increased for females attending
brood sizes from 1 to 4 and then declined (Fig. 2-4). The best supported models including an effect of MCS ($\beta = 0.32 \pm 0.79$) on $S$ ($\Delta\text{QAICc} = 1.4$; Table 2-1) and CS ($\beta = 0.32 \pm 0.40$) on $S$ ($\Delta\text{QAICc} = 1.1$; Table 2-1), indicated the 95% CIs for these parameter estimates strongly overlapped zero. The best supported model including an effect of CS on $A''$ ($\Delta\text{QAICc} = 0.5$; Table 2-1) indicated the 95% CIs for the parameter estimate also strongly overlapped zero ($\beta = 0.22 \pm 0.34$).

The probability of dead brent being found and reported was constant across groups and years (0.08 ± 0.02). Resighting probability during the non-breeding season varied from < 0.01 in 2009-2010 to 0.12 (± 0.02) in 2012-2013. The probability of breeding in $t + 1$ for females that did not breed in $t$ ($A'$) was constant across years (0.20 ± 0.08). For females in the manipulated group $p_{\text{nesting}}$ ranged from 0.58 (± 0.06) in 2010 to 0.96 (± 0.04) in 2008, while $p_{\text{ringing}}$ ranged from 0.12 (± 0.03) in 2010 to 0.68 (± 0.22) in 2008. Recapture rates for individuals encountered at nesting ($c$) varied from 0.12 (± 0.03) in 2013 to 0.27 (± 0.03) in 2012.

**Discussion**

Our study is one of very few to combine CMR methods with manipulation of effort in multiple breeding phases to estimate trade-offs between current reproduction, true survival and breeding probability in a long-lived vertebrate. As predicted we found a trade-off between current reproduction and future breeding probability in brent geese, however, the relationship was not linear. The positive relationship between brood size and future breeding probability for females tending broods of up to four goslings is consistent with the widespread observation that social status in winter improves with family size in geese (Raveling 1970; Gregoire & Ankney 1990), including brent
(Poisbleau et al. 2006; Poisbleau, Guillon & Fritz 2010). We hypothesize that our imposition of smaller broods on some individuals, increased the probability of complete brood failure post-hatch (Rockwell, Findlay & Cooke 1987), which lowered their social status and ability to store nutrients during winter and spring (Black et al. 1992). Reduced acquisition and storage of nutrients, in turn, negatively influenced breeding probability (Lamprecht 1986; Black & Owen 1989; Poisbleau et al. 2006). This mechanism could also explain the lack of a strong clutch size effect on future demographic rates in our study, despite our prediction that clutch size correlated positively with individual quality (Yoccoz et al. 2002; Hanssen et al. 2003). While clutch size is a response to individual quality at time \( t \) (Hanssen et al. 2003), our results indicate a carryover effect of reproductive success on individual quality in brent the next year (Poisbleau, Guillon & Fritz 2010). Thus, an individual’s future quality is related to not only relatively fixed attributes (e.g., body size), but also, at least partially, to a positive feedback acting through the effect of successful reproduction on winter social status and future breeding (Lamprecht 1986; Black & Owen 1989; Poisbleau, Guillon & Fritz 2010; Sedinger et al. 2011).

We explain the reduction in breeding probability by females tending broods larger than 4–5 goslings as follows. At hatch female brent are in the poorest body condition of the year and begin to replenish nutrient reserves during brood-rearing (Ankney 1984). During brood-rearing, vigilance and aggression by parents increases with brood size in geese, while foraging efficiency declines (Schindler & Lamprecht 1987; Sedinger & Raveling 1990; Williams, Loonen & Cooke 1994). As a result, initiation of moult is delayed (Williams, Loonen & Cooke 1994) and body mass reduced for adults tending
larger broods (Lessells 1986). Thus, we hypothesize a negative relationship between brood size and post-hatch nutritional state which is, at least partially, responsible for the reduction in future breeding probability exhibited by females tending the largest broods.

We found some evidence for a negative relationship between brood size and survival; however, there was less support for this effect relative to that for breeding probability, because the brood size effect on survival was not included in all competitive models and its 95% CIs overlapped zero. Regardless, our results suggest the possibility that adult survival declined, but breeding probability improved as brood size increased up to four goslings suggesting a trade-off between survival and breeding probability as brood size increased. As a result individuals tending fewer goslings than the most common brood size survived at greater rates, but had a lower probability of future breeding. The precise mechanism underlying declining survival with increasing brood size, however, remains unknown.

It is unclear why we failed to find support for an effect of incubated clutch size on residual reproductive value in adult female brent. Our results, however, are consistent with a study of female common eiders (Somateria mollissima) that found that the fitness costs of increased incubation effort were not paid in terms of reduced return rate, but rather in decreased future clutch size (Hanssen et al. 2005). Further, our study does not rule out the possibility of within-year effects of clutch size on fitness, including egg hatchability (Rockwell, Findlay & Cooke 1987) and negative effects of delayed hatching of larger clutches (Eichholz & Sedinger 1998) on gosling growth rates (Cooch et al. 1991; Sedinger & Flint 1991). Thus, our current assessment of the fitness costs of producing and incubating different sized clutches is likely somewhat conservative.
To our knowledge our study is the first to demonstrate effects of incremental changes in brood size on future survival and breeding probability in a species with precocial young. It is unclear why we found long-term fitness effects while many studies report equivocal results (Santos & Nakagawa 2012). We attribute this discrepancy, at least partially, to our use of robust CMR approaches and the fact that our high detection rates of breeding females at TRC improved the power of our analyses. Additionally, given the small number of natural clutches larger than five laid by brent, we would have failed to find costs associated with rearing larger broods without manipulations and suspect observational studies of other nidifugous birds would face similar problems.

Our results suggest selection, through reduced survival and breeding probability, acts against females producing clutches larger than those commonly laid, in the case of brent, five eggs. We found that this selection pressure acts not through the number of eggs incubated, but through the number of goslings reared. Breeding probability seems to be maximized for females attending broods corresponding to the most common clutch sizes (4–5 goslings; Fig. 2-4). Our study does not address factors leading to clutches smaller than four eggs, although the superior breeding probability of females tending the most common brood sizes suggests a proximate nutrient limitation precluding some female brent from producing larger clutches (Lack 1967; Ryder 1970; Ankney & Macinnes 1978; Raveling 1979). Our results complement work we report elsewhere indicating that per capita prefledging survival is maximized for brent broods with 4-5 goslings. Before suggesting final conclusions concerning optimal clutch size in brent we need to integrate additional within- and among-year fitness consequences of clutch size decisions.
Acknowledgements

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Data accessibility

The mark-recapture input file (.txt file format) containing all the data used in this paper will be deposited in the Dryad Digital Repository before the final version of this manuscript is published.

References


Kendall, W.L., Barker, R.J., White, G.C., Lindberg, M.S., Langtimm, C.A. & Penaloza, C.L. (2013) Combining dead recovery, auxiliary observations and robust design...


Table 2-1. Final model selection results for Barker robust design mark-recapture models examining variation in true survival ($S$) and breeding probability in year $t+1$ ($A^+$) based upon reproductive effort in year $t$ for female brent breeding at the Tutakoke River brent colony, Alaska, USA from 2008–2014. QAICc, $\Delta$QAICc (difference in QAICc between best and the focal model adjusted for $\hat{c} = 1.11$), $k$ (number of estimated parameters in model $i$), $w_i$ (weight of evidence for model $i$ being the best model), and QDeviance for all candidate models are shown.

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\[ S(g + \text{AGE} + \text{CS} + \text{GLN}^2) \cdot A \sim (\text{yr} + \text{GLN}) \]
\[ S(g + \text{AGE} + \text{MCS}) \cdot A \sim (\text{yr} + \text{GLN}^2 + \text{MCS}^2) \]
\[ S(g + \text{AGE} + \text{GLN}) \cdot A \sim (\text{yr} + \text{GLN}) \]
\[ S(g + \text{AGE} + \text{MCS}^2) \cdot A \sim (\text{yr} + \text{CS} + \text{GLN}^2 + \text{MCS}) \]
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\[ S(g + \text{AGE} + \text{CS} + \text{MCS} + \text{CS}^2) \cdot A \sim (\text{yr} + \text{CS} + \text{GLN} + \text{MC}) \]
\[ S(g + \text{AGE} + \text{GLN} + \text{MCS}) \cdot A \sim (\text{yr} + \text{CS} + \text{GLN}) \]
\[ S(g + \text{AGE} + \text{CS} + \text{MCS} + \text{CS}^2) \cdot A \sim (\text{yr} + \text{CS} + \text{GLN}^2 + \text{MCS}) \]
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\[ S(g + \text{AGE} + \text{GLN} + \text{MCS}) \cdot A \sim (\text{yr} + \text{CS} + \text{GLN}) \]

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S(g + \text{AGE} + \text{GLN}) & A \sim (\text{yr} + \text{CS} + \text{GLN}) & 37 & 15035.9 & 7.5 & 0.00 & 14961.30 \\
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\]
| S(g+AGE+GLN^2) A’(yr+MCS) | 36 | 15042.3 | 13.9 | 0.00 | 14969.73 |
| S(g+AGE+CS+GLN^2) A’(yr+CS+MCS) | 38 | 15042.5 | 14.1 | 0.00 | 14965.87 |
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| S(g+AGE) A’(yr+CS+MCS^2) | 36 | 15043.3 | 14.9 | 0.00 | 14970.74 |
| S(g+AGE+GLN^2+MCS^2) A’(yr+CS+MCS^2) | 40 | 15043.4 | 15.1 | 0.00 | 14962.75 |
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| S(g+AGE+GLN) A’(yr+MCS^2) | 36 | 15043.6 | 15.3 | 0.00 | 14971.07 |
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| S(g+AGE) A’(yr+MCS^2) | 35 | 15044.2 | 15.9 | 0.00 | 14973.72 |
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| S(g+AGE+GLN^2+MCS^2) A’(yr+MCS^2) | 39 | 15044.5 | 16.2 | 0.00 | 14968.65 |
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| S(g+AGE) A’(yr+CS+GLN+CS*GLN) | 36 | 15048.4 | 20.1 | 0.00 | 14975.85 |
probability an individual was initially encountered at TRC during nesting condition on being alive (R) was allowed to vary across years, probability that an individual was observed alive before it died during a non-breeding season conditioned on being alive (R') was fixed at 0, probability an individual was present and available for encounter at TRC given absence the year before (A') was constant across groups and years, probability an individual did not permanently emigrate from TRC after time t (F) was fixed at 1.0, probability an individual was initially encountered at TRC during nesting condition on other parameters:

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Notes: Only structures for true survival (S) and breeding probability in year t+1 (A") are shown. All models considered had the following structure on other parameters:
being available during that breeding season \( (p_{nesting}) \) was allowed to vary by group and year, probability an individual was initially encountered at TRC during ringing conditioned on being available during that breeding season \( (p_{ringing}) \) was allowed to vary by group and year, and the probability that an individual encountered at nesting was recaptured at ringing \( (c) \) was allowed to vary by year. Groups \( (g) \) were manipulated (female brent receiving a clutch and/or brood manipulation during the study) and nonmanipulated brent. The covariate CS was the number of eggs laid by a female brent in year \( i \). The covariate MCS was the final number of eggs a female brent incubated after manipulation and minus any predated eggs. The covariate GLN was the number of goslings a female brent left the nest with after investigator manipulation.
Figure 2-1. Proportion of clutches sizes (a) laid by brent in the manipulated group and (b) created by investigators through manipulations at the Tutakoke River brent colony, Alaska, USA in 2008–2012.
Figure 2-2. Frequency distributions of the number of goslings leaving the nest (GLN) of (a) nonmanipulated brent and (b) manipulated brent at the Tutakoke River brent colony, Alaska, USA in 2008–2012.
Figure 2-3. Probability (as well as its 95% confidence band) that female brent tending manipulated brood sizes (GLN) of 1-7 survived the following year at the Tutakoke River brent colony, Alaska, USA.
Figure 2-4. Probability (as well as its 95% confidence band) that female brent tending manipulated brood sizes (GLN) of 1-7 bred the following year at the Tutakoke River brent colony, Alaska, USA.
Chapter III: Mate breeding experience, not pair familiarity improves reproductive performance in a long-lived bird

Alan G. Leach* a, b and James S. Sedinger a

a Department of Natural Resources and Environmental Science, University of Nevada-Reno, 1664 N. Virginia St., Reno, NV 89557 USA

b Program in Ecology, Evolution, and Conservation Biology, University of Nevada-Reno, 1664 N. Virginia St., Reno, NV 89557 USA

* Corresponding author: aleach@cabnr.unr.edu

RH: Reproductive costs of mate change in brant

Key words: prefledging survival, precocial young, mating systems, mate change, long-term pair bonds.
Abstract

Factors contributing to fitness costs of mate change in species that exhibit bi-parental brood care are debated among ecologists. We tested whether mate familiarity or prior breeding experience of the new mate was the most important determinate of reproductive success of black brant geese (*Branta bernicla nigricans*). We considered the potential effects of mate change on a number of reproductive traits including relative nesting date, clutch size, brood size at hatch, and prefledging survival of offspring. We modeled potential variation in relative nest initiation dates, clutch size, and initial brood size using generalized linear mixed models in Program R. We estimated prefledging survival of offspring using Cormack-Jolly-Seber models in Program MARK using reencounters of uniquely webtagged goslings. We found that mate change had a minimal effect on relative nest initiation date and clutch size, and no effect on initial brood size in brant. However, females that changed mates and bred with an inexperienced male had goslings with 35% lower prefledging survival rates ($\phi = 0.19 \pm 0.04$ [95% CI]) than those breeding with a familiar, experienced male ($\phi = 0.30 \pm 0.04$). In contrast, females that changed mates and bred with an experienced male actually had goslings with higher prefledging survival rates ($\phi = 0.46 \pm 0.10$) than those breeding with a familiar mate. Our findings support the hypothesis that mate change in brant can result in reduced reproductive success if females pair with an inexperienced breeder.
Introduction

Social monogamy is the dominant avian mating strategy, with 90% of bird species exhibiting this form of mating behavior (Lack 1968; Emlen & Oring 1977). The benefit of monogamy during the breeding season in birds, in comparison to other taxa (e.g., mammals), is thought to result from improved breeding success through shared incubation and/or bi-parental care of offspring (Lack 1968; Emlen & Oring 1977; Schneider & Lamprecht 1990). Within-season improvements in reproductive success, however, do not seem to explain retention of a social mate across multiple breeding seasons, a behavior which is exhibited by many long-lived birds (Sanchez-Macouzet, Rodriguez & Drummond 2014). One explanation for why some individuals remain paired to the same mate is that mate retention may improve or maintain reproductive success across years (Coulson 1966).

Perennial social monogamy could improve reproductive success through at least two non-mutually exclusive mechanisms. First, if the availability of high quality, potential replacement mates (e.g., experienced) is low individuals may benefit from mate retention rather than risking pairing with a low quality mate (Forslund & Larsson 1991; Dhondt & Adriaensen 1994; Griffith, Pryke & Buttemer 2011). Second, if reproductive success increases with pair bond duration, through for example, improved coordination among pair members (e.g., in raising offspring) mate retention may be favored (Black 2001; van de Pol et al. 2006; Sanchez-Macouzet, Rodriguez & Drummond 2014).

Despite the interest of biologists in species with perennial social monogamy, relatively few studies have investigated the implications of mate change for annual reproductive success in long-lived birds with precocial young (Cooke, Bousfield &
Sadura 1981; Forslund & Larsson 1991). The few studies attempting to assess the consequences of mate change or mate loss for reproductive performance in wild populations of precocial birds have produced equivocal results (Cooke, Bousfield & Sadura 1981; Martin et al. 1985; Forslund & Larsson 1991; LeSchack, Afton & Alisauskas 1998). One reason for the paucity of studies estimating multiple aspects of reproductive performance in relation to mate change in birds with precocial young is that key components of fitness may be difficult to measure. For example, it may be difficult to separate dispersal of young from mortality prior to fledging (Lebreton et al. 1992).

Thus, a key component of fitness, prefledging survival, is difficult to estimate in species with precocial young, in contrast to species with altricial young which can simply be counted in the nest before fledging (Flint, Sedinger & Pollock 1995).

Other factors also make quantification of costs of mate change challenging. First, before concluding that there are costs of mate change, investigators must ensure that poor reproductive performance after a mate change is not the result of inexperienced or otherwise less successful individuals being more likely to change mates (Cooke, Bousfield & Sadura 1981; Sanchez-Macouzet, Rodriguez & Drummond 2014). This necessitates long-term studies that build longitudinal histories of uniquely identifiable individuals, but such studies are difficult to maintain (Clutton-Brock & Sheldon 2010). After controlling for the inherent reproductive performance of the focal individual, investigators can then attempt to determine if the cost of mate change is caused by acquisition of an inexperienced or otherwise lower quality mate (Forslund & Larsson 1991; Naves, Cam & Monnat 2007), or lack of familiarity between mates (Black 2001; Sanchez-Macouzet, Rodriguez & Drummond 2014). Many studies have focused on the
effects of female attributes (e.g., experience or age) on reproductive success, but fewer studies have considered if attributes of the social partner also directly influence fitness (Coulson 1966; Auld, Perrins & Charmantier 2013). If a partner’s attributes, such as previous breeding experience, influence fitness of the focal individual, retaining such a mate across breeding seasons will be beneficial if such partners are in short supply, as in many socially monogamous taxa (Griffith, Pryke & Buttemer 2011). An issue plaguing studies of pair bond duration and reproductive success is the positive covariation that arises between mate familiarity and the breeding experience of each member of the pair (Black 2001; Naves, Cam & Monnat 2007; Sanchez-Macouzet, Rodriguez & Drummond 2014). Therefore, investigators should take advantage of mate changes that allow for a natural disassociation of partner age, breeding experience, and pair bond duration (Sanchez-Macouzet, Rodriguez & Drummond 2014).

We investigated the costs of mate change in black brant geese (*Branta bernicla nigricans*; hereafter brant) using 25 years of data collected from 1990–2014 at the Tutakoke River brant colony, (hereafter TRC; 61°15′ N, 165°37′ W), Yukon-Kuskokwim Delta (YKD), Alaska, USA. Brant are socially, but not completely genetically monogamous with 5–6% of offspring resulting from extra-pair paternity (Lemons et al. 2015). Brant pairs, as in most species of geese, remain in close contact throughout the annual cycle until death or divorce (Black 2001). Generally, in geese, it is thought that male assistance during breeding is most beneficial during nest initiation and brood rearing, because males defend resources that may increase reproductive success (LeSchack, Afton & Alisauskas 1998). In contrast, females can successfully incubate
and hatch a clutch in the absence of a mate, albeit with increased alertness and conspecific harassment (Martin et al. 1985; LeSchack, Afton & Alisauskas 1998).

Divorce occurs in geese (i.e., breakage of the pair bond while both mates remain alive), but generally fewer than 5% of pairs ultimately divorce in most species (Owen, Black & Liber 1988; Ens, Choudhury & Black 1996). However, when considering both divorce and widowing events simultaneously 12% of female brant change mates annually (Chapter 4). Because the average life span for brant is 7–8 years, approximately 50% of female brant will breed with more than one mate during their lifetime (Chapter 4). Thus, mate change is a common occurrence in female brant with potentially important fitness consequences. The TRC is one of 4 major brant colonies on the YKD and, at the beginning of our study, ~20% of the brant population bred at TRC (Sedinger et al. 1993). Brant exhibit sex-specific natal philopatry with breeding females having greater fidelity (0.86) than males (0.20) (Lindberg et al. 1998; Sedinger et al. 2008). Given this sex specific philopatry, the fact that TRC represents a relatively small proportion of the total breeding population, and that pairs are formed during winter (Bellrose 1980), many females changing mates formed pair bonds with males that had not bred previously at TRC (Chapter 5).

Our objectives were to: (1) determine if mate change affects reproductive success, including: clutch size, relative nest initiation date, initial brood size and prefledging survival of goslings, and (2) understand whether male breeding experience or familiarity of partners influences the effects of mate change. If mate familiarity affects reproductive success we predicted that females undergoing a mate change would fledge fewer goslings than those retaining their mate regardless of the breeding experience of their new partner.
Alternatively, if male experience determines the consequences of mate change, we predicted that females who changed to a new, but experienced mate would perform as well as females who were breeding with a familiar mate. Alternatively, females breeding with a new, but inexperienced male, however, would not fledge as many young.

**Materials and methods**

**STUDY SITE AND SPECIES**

Most brant breed in coastal habitats on the YKD, and the north slope of Alaska (Lewis *et al.* 2013). Females do not start breeding until 2 years of age with most recruiting by the age of 5 (Sedinger, Lindberg & Chelgren 2001). Brant females lay determinate clutches of predominantly 3–5 eggs (Eichholz & Sedinger 1998). Most brant nests are initiated within a 14 day period each year at TRC (Lindberg, Sedinger & Flint 1997). Soon after hatching (24–48 hours) brant family groups disperse to terrestrial brood rearing areas where goslings forage mostly on *Carex subspathacea* (Sedinger, Eichholz & Flint 1995). Females have sole responsibility for incubating clutches and brooding goslings (Martin *et al.* 1985; Sedinger & Raveling 1990). During the breeding season male brant aid in acquisition of a nesting location (LeSchack, Afton & Alisauskas 1998), partake in aggressive interactions with conspecific family groups to reduce harassment and improve rates of forage intake by goslings during brood-rearing, and aid in protection against predators of offspring (e.g., Glaucous gulls *Larus hyperboreous*) (Sedinger, Eichholz & Flint 1995).

We conducted the nesting portion of our study at the TRC from 1990–2014. During our study, breeding densities of brant at TRC increased from 1100 nests in 1986
to >5000 nests in the mid-1990s and then declined to < 2500 nests in 2014 (Sedinger et al. 1998; Wilson 2014).

FIELD METHODS

Each summer since July 1986 we have marked adult (2+ years old), immature (1 year old), and gosling brant with USGS metal tarsus rings and 2.5 cm tall plastic colored tarsus rings engraved with a unique alphanumeric code during mass ringing drives (~2000 individuals ringed annually) conducted during the adult remigial molt (Sedinger et al. 1997). We sexed brant using cloacal examination (Owen 1980). We conducted ringing drives ~30 days after hatch on seven brood rearing areas at TRC, recording rings of previously marked adults, and checking all individuals for the presence of a webtag (see below) regardless of whether or not they were ringed (Sedinger et al. 2008; Nicolai et al. 2014). During ringing drives breeding females were identified by the presence of a brood patch (Sedinger, Lindberg & Chelgren 2001; Sedinger et al. 2008). Though breeding males have no such identifying mark, we assumed all adult males caught at ringing had attempted to breed that year. We believe this assumption is justified for three reasons: (1) we targeted brood rearing flocks for capture, (2) most non-breeding brant molt at distant locations, and (3) < 2% of adult females caught lacked a brood patch (J. S. Sedinger, unpublished) indicating they had not nested in the current year. Due to the fact that one ringing drive (Punoarat, see below) requires traveling through the ocean by boat we only sampled this area opportunistically during years with favorable weather (Nicolai & Sedinger 2012). The proportion of breeding females and males at TRC that were color-ringed and uniquely identifiable during our study was approximately 50%. On average, we identified the mate of 86% of brant who bred each year.
In addition to our ringing at TRC, brant were periodically marked at other colonies on the YKD (Lindberg et al. 1998; Fondell et al. 2011), and breeding (Ward et al. 2004) and molting sites on the arctic coastal plain of Alaska (Bollinger & Derksen 1996) during the period of our study. These individuals provided a sample of male brant with known histories, not ringed at TRC, who paired with females breeding at TRC.

During egg-laying and incubation we used 20–60X spotting scopes to read color rings of nesting brant (Sedinger et al. 2008). We also recorded observations and mating status of color-marked adult brant tending goslings during brood-rearing from 3-7 meter towers and of non-breeding brant opportunistically at TRC (Sedinger, Lindberg & Chelgren 2001). The probability that a brant >3 years-old breeding at TRC was encountered at least once during nesting, brood-rearing, or ringing was >70% during our study (Sedinger, Lindberg & Chelgren 2001).

Each summer during egg laying and incubation we searched TRC for nests attended by ringed female brant to determine clutch size and initiation date. If nests were found during egg laying we back dated the initiation date assuming 1 egg was laid per day. For nests found during incubation, but with an observed hatch date, we back calculated the initiation date (in Julian days) assuming 26 days of incubation beginning on the second egg (Lindberg, Sedinger & Flint 1997). To standardize nest initiation dates across years we calculated a relative initiation date by subtracting the median initiation date for that year from that of a given nest (Schamber, Sedinger & Ward 2012). We monitored nests of marked females daily during hatch. We applied uniquely coded fish fingerling tags to goslings while still in the nest (Alliston 1975; Sedinger & Flint 1991). We captured and weighed a sample of breeding females at the nest on their hatching date.
(< 200 females annually); all females trapped on the nest were checked for webtags. We visited nests after the family group had left to record dead goslings, unhatched eggs and determine the number of goslings that left the nest (GLN).

We recorded pairs during three separate periods; at the nest, while rearing broods and opportunistic resights of individuals not associated with a nest or brood at TRC. We established mate changes in three ways. First, we concluded a female had changed mates in year \( t \) if she was breeding with a different ringed mate in year \( t-1 \) than in year \( t \). Secondly, if a female was previously observed with a color-ringed male, but observed with an unmarked mate in year \( t \). In this case we did not consider females observed with a mate having only a metal tarsus ring to have undergone a mate change, because a small percentage (0.2%) of brant lost their color rings annually (Sedinger et al. 1997). Lastly, if a female was previously observed with an unmarked mate and was seen in year \( t \) with a mate that was ringed previous to the last sighting with the unringed mate we assigned a mate change. Partially as a result of male dispersal after pair bond termination (Lindberg et al. 1998) we recorded ~75% fewer mate change events for males than females. Due to the small sample size of mate changes involving a focal male, we only investigated effects of mate change on female reproductive events in this paper.

To ensure that any effects on reproductive success of mate change were not due to breeding experience of the female, we removed first and second breeding attempts for each female from all analyses. This is consistent with observation that breeding success of female geese improves until the third attempt (Cooke, Bousfield & Sadura 1981; Sedinger et al. 1998).
CLUTCH SIZE, RELATIVE INITIATION DATE AND GOSLINGS LEAVING THE NEST

In separate analyses we constructed generalized linear mixed models with clutch size, relative initiation date, and GLN as response variables, using the lmer function of the lme4 package (Bates et al. 2014) in program R 3.1.2 (R core team 2014). To test for effects of male experience on reproductive success we created a categorical variable PAIRSTAT that included four categories: (1) FAITHFUL, females nesting with an experienced mate for at least the second time and who did not change mates during the rest of their lifetime, (2) PRE-SWITCH, females nesting with an experienced mate for at least the second time, but who switched to a new mate for a future breeding attempt, (3) SWITCH MALE EXP, females who had switched mates in year \( t \) and whose new mate was ringed and previously observed breeding at TRC at least twice, (4) SWITCH MALE NON-EXP, females who had switched mates in year \( t \) and whose new mate was either (1) ringed and previously observed breeding at TRC less than twice or (2) whose new mate was unringed. We acknowledge that unringed males had unknown histories, however, given the male dispersal among colonies and the high encounter rates of brant at TRC we reason that most unringed males mated to females who switched mates in year \( t \) had limited (i.e., < 2 previous breeding attempts) or no previous breeding experience at TRC. Further, given the high rates of pair fidelity and an operational sex ratio skewed towards females (Lemons et al. 2012), it is likely that many unringed males paired to females that had changed mates were young and/or previously unpaired (Forslund & Larsson 1991).

We included relative initiation date and female tarsus length in models examining variation in clutch size and GLN to control for the effects of timing of breeding and
female body size on number of eggs laid (Sedinger, Flint & Lindberg 1995; Schamber, Sedinger & Ward 2012). For our model considering variation in GLN we included clutch size as an explanatory variable. For each component of fitness we built one model and assessed the effect of PAIRSTAT by examining effect sizes and 95% CIs on regression parameters. If 95% CIs overlapped zero we concluded no effect of a regression parameter. We z-standardized the covariate for female tarsus (mean = 0, SD = 1) and assigned missing observations a covariate value of 0. We used female ID as a random effect to account for multiple observations of individual females (Schamber, Sedinger & Ward 2012).

PREFLEDGING SURVIVAL

We estimated prefledging survival using the live recaptures (CJS) model in program MARK implemented via the program R (R core team 2014) package RMark (Laake 2013). To create capture histories of webtagged goslings we organized webtag encounters into 3 occasions: (1) initial release at nest, (2) direct recaptures at ringing during hatching year, and (3) all subsequent recaptures of webtagged individuals (Nicolai & Sedinger 2012). We only included goslings that had mothers captured as adults in a brood rearing area we sample at ringing. Because female brant are largely faithful to brood rearing areas (Lindberg & Sedinger 1998), this restriction reduced the probability that failure to capture webtagged goslings resulted from their mothers using brood rearing areas we did not sample. Our approach depended on the assumption that probability of capture was independent of the experience of the male mate, which we believe was reasonable because of the high fidelity of females to brood rearing areas. We allowed for full time variation in apparent survival and recaptures rates between these three occasions
in all candidate models. As a result, we could estimate apparent survival and recapture rates of webtagged goslings during their hatching year, but survival following fledging and capture probability in the third occasion were not estimable (Nicolai & Sedinger 2012). We did not consider models with annual time varying covariate effects, because our goal was to estimate the average effect of PAIRSTAT across years. Finally, we created a binomial variable BRA that indicated whether goslings were attended by a female that reared her broods in a regularly sampled brood-rearing area (BRA = 0) or at the Punorat brood rearing area (BRA = 1). This variable was included in all models to explain variation in recapture rates. We only included goslings released from 1990–2010 in our analysis to allow at least 4 years of live recaptures after the release of each cohort.

To account for a potential lack of independence in survival among brood mates we adjusted $\hat{c} = 1.20$, this overdispersion value was calculated from an analysis of the entire dataset (Nicolai & Sedinger 2012). This adjustment resulted in model selection being more conservative regarding inclusion of variables and increased the variance of parameter estimates to account for any lack of independence among brood mates. We considered models having the effect of PAIRSTAT (modeled as separate groups) on apparent gosling survival and recapture rates.

We used Akaike model weights and 95% confidence intervals on parameter estimates to make inferences about the relative support for each variable in the model. For all analyses we report parameter estimates from the best performing model ± 95% confidence intervals.
Results

CLUTCH SIZE, RELATIVE INITIATION DATE AND GOSLINGS LEAVING THE NEST

We recorded clutch size and initiation dates for 2406 brant nests, of these we determined the GLN for 1637 nests. Of nests for which we determined clutch size and initiation dates 1484, 444, 51, and 427 were attended by mothers in the FAITHFUL, PRE-SWITCH, SWITCH MALE EXP, and SWITCH MALE NON-EXP categories, respectively. Of nests for which we determined GLN 1010, 310, 44, and 273 were attended by mothers in the FAITHFUL, PRE-SWITCH, SWITCH MALE EXP, and SWITCH MALE NON-EXP categories, respectively. The average clutch size for FAITHFUL mothers was 4.22 (± 0.05; Fig. 3-1). Females who had switched to an inexperienced mate initiated their nests 0.48 (± 0.26) (Fig. 3-2) days later and incubated clutches that were 0.17 (± 0.10) eggs smaller (Fig. 3-1) than FAITHFUL females. Females in the PRE-SWITCH category had similar relative initiation dates (β = -0.06 ± 0.29) (Fig. 3-2) and laid clutches of similar size (4.23 ± 0.09) (Fig. 3-1) to females in the FAITHFUL category. Though estimates of initiation date (β = -0.32 ± 0.63) and clutch size (4.21 ± 0.25) for females in the SWITCH MALE EXP category indicated these metrics were similar to females in the FAITHFUL category, the 95% CIs for these estimates was relatively large compared to other categories (Fig. 3-1 & Fig. 3-2). Despite smaller clutches of females in the SWITCH MALE NON-EXP group GLN estimates for all groups varied less than 0.17 goslings and all 95% CIs broadly overlapped indicating no substantial variation in initial brood size among groups (Fig. 3-3).
PREFLEDGING SURVIVAL

We released 6671 webtagged goslings from 1990–2010. We subsequently recaptured 1131 goslings during their initial hatching year and 157 webtagged individuals as one-year olds or adults at TRC. Of the goslings we released 3813, 1843, 130, and 736 were attended by mothers in the FAITHFUL, PRE-SWITCH, SWITCH MALE EXP, and SWITCH MALE NON-EXP categories, respectively. The majority of goslings we released (5612; 84.2%) had mothers that used a brood rearing area we regularly sampled.

For models investigating the effect of mate change on prefledging survival our most parsimonious model included an effect of PAIRSTAT on apparent gosling survival and an effect of mother’s brood rearing area on recapture rates (Table 3-1). Our most parsimonious model was well supported in relation to the next best model (ΔQAICc = 5.14; wi = 0.07) which included the effect of PAIRSTAT on both apparent survival and recapture rates (Table 3-1). The best supported model was also clearly supported over the null model which only included the effects of time (i.e., sampling occasion: (1) hatching year or (2) encountered as an adult) on apparent survival and recapture rates, and BRA on recapture rates (ΔQAICc = 30.70; wi = 0.00; Table 3-1). Parameter estimates from the best supported model indicated that goslings attended by females in the FAITHFUL (ϕ = 0.30 ± 0.04) and PRE-SWITCH (ϕ = 0.32 ± 0.04) categories had similar prefledging survival (Fig. 3-4). Goslings attended by females in the SWITCH MALE EXP (ϕ = 0.46 ± 0.10), however, had greater prefledging survival than those in the SWITCH MALE NON-EXP (ϕ = 0.19 ± 0.04) category (Fig. 3-4). As predicted, we recaptured goslings reared by mothers using regularly sampled brood-rearing areas at greater rates (p = 0.66 ± 0.07) than those using the Punoarat area (p = 0.19 ± 0.07).
Discussion

We found strong evidence that mate change reduced the reproductive success of female brant. However, this cost was only incurred by females remating with males that had little or no breeding experience (i.e., < 2 previous breeding attempts) at the colony we studied. Further, we found that females that switched to a new, but experienced male had similar (or better in the case of prefledging survival) reproductive performance to females that bred with an experienced, familiar mate. This was despite the fact that females breeding with a mate that would remain paired with (FAITHFUL) and females who would breed with another mate in the future (PRE-SWITCH) were, on average, nesting with their mate for the 3.72 (SD = 1.99) and 3.61 attempts (SD = 1.70), respectively. These results do not support the hypothesis that reproductive success is greater for pairs who are familiar with each other in brant. Rather, the benefit of mate fidelity, at least in terms of within-year reproductive success, is largely the result of retaining an experienced partner. Females breeding with an inexperienced male can expect to fledge 1/3 fewer goslings.

We are confident that our finding that females who switch to an inexperienced mate suffer reduced reproductive success is a cost of mate change and not an artifact of female experience or quality for two reasons. First, we removed all breeding attempts by inexperienced females (< 2 previous nesting attempts) from our analyses. Second, because of our long-term longitudinal dataset, we were able to estimate reproductive success of the same females before and after they changed mates. We found that before females switched mates they performed similarly to females that did not change mates
(i.e., the FAITHFUL group) in all reproductive metrics (Figs. 3-1–3-4). This result indicates that the reduction in reproductive success for some females after mate change was not due to the inherently low quality of these females, but rather a true cost of mate change.

We hypothesize two non-mutually exclusive mechanisms to explain the effects of male experience on clutch size and relative initiation date. First, the reduction in clutch size could result from females paired to an inexperienced mate experiencing reduced rates of nutrient storage prior to egg laying and therefore investing less in breeding (Ankney & Macinnes 1978; Drent & Daan 1980). Alternatively, inexperienced males may be less attentive during laying (Cooke, Bousfield & Sadura 1981) and as a result their nests may be more likely to be expropriated by another pair after laying 1-2 eggs. Thus, we were more likely to find these females incubating their smaller continuation clutches. This mechanism would also explain the delay in initiation date as we would have found continuation nests 1-2 days after females had actually laid their first egg. Regardless, females of all pair status categories left the nest with a similar number of goslings indicating that mate change had a negligible effect on pre-hatch offspring production. These results are in agreement with other studies that found minimal reduction in clutch size and slight delay in clutch initiation in female geese following mate change (Cooke, Bousfield & Sadura 1981; Macinnes & Dunn 1988; Forslund & Larsson 1991). Our results combined with results from other studies suggest that clutch size and nest initiation date is determined primarily by attributes of the female.

The two other studies that investigated the effect of mate change on prefledging survival in precocial species had equivocal results; no effect was detected in lesser snow
geese (*Chen caerulescens*) (Cooke, Bousfield & Sadura 1981), while a reduction in prefledging survival followed mate change in barnacle geese (*Branta leucopsis*) (Forsslund & Larsson 1991). We hypothesize that the discrepancy between Cooke et al. (1981) and our study and Forsslund and Larsson (1991) is partially methodological. Cooke et al. (1981) indicated that their inability to document a reduction in prefledging survival may have resulted from a small sample size. Additionally, Forsslund and Larsson (1991) found that females who switched to relatively older males (i.e., more experienced) had greater reproductive success than those remated with younger males. We hypothesize that the reduced survival of brant goslings attended by an inexperienced male is related to reduced male attentiveness, lesser aggression towards conspecifics, and reduced vigilance for predators of goslings.

In conclusion, our results suggest that reproductive success in brant is influenced by parental experience rather than familiarity between members of the pair. Our results are in agreement with studies of kittiwakes, *Rissa tridactyla* (Naves, Cam & Monnat 2007) and at least one sub-population of barnacle geese (Forsslund & Larsson 1991). Alternatively, studies on the blue-footed booby, *Sula nebouxii* (Sanchez-Macouzet, Rodriguez & Drummond 2014) and oystercatchers (*Haematopus ostralegus*) found a positive relationship between pair duration and annual reproductive success while controlling for parental experience and age. Black (2001) found a positive association between pair bond duration and lifetime reproductive success in barnacle geese, but did not directly assess annual reproductive performance of pairs. We believe that more long-term studies of the benefits of mate retention for annual reproductive success are
necessary before a full understanding of the mechanisms favoring mate retention across a broad spectrum of taxa is possible.

**Funding**

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**References**


Table 3-1. Performance of Cormack-Jolly-Seber models investigating prefledging survival of webtagged goslings hatched at the Tutakoke River brent colony, 1990–2010.

Mother’s pair status (PAIRSTAT) is as follows: 1) Faithful, females breeding with a familiar mate who will not change mates in the future, 2) Pre-switch, females breeding with a familiar mate in year $i$ who will change mates in the future, 3) Switch, male exp; females breeding with an unfamiliar mate that has bred at least twice at TRC, 4) Switch, male non-exp; females breeding with an unfamiliar mate that is either ringed and bred less than twice at TRC or who is unmarked and assumed to have little to no experience at TRC. The variable BRA indicates whether goslings were attended by a female that rears her broods in regularly sample brood-rearing areas or at the Punorat brood-rearing area.

<table>
<thead>
<tr>
<th>Model structure</th>
<th>k</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>QDeviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phi(occ+PAIRSTAT)p(occ+BRA)</td>
<td>8</td>
<td>0.00</td>
<td>0.88</td>
<td>5889.59</td>
</tr>
<tr>
<td>Phi(occ+PAIRSTAT)p(occ+PAIRSTAT+BRA)</td>
<td>11</td>
<td>5.14</td>
<td>0.07</td>
<td>5888.71</td>
</tr>
<tr>
<td>Phi(occ)p(occ+PAIRSTAT+BRA)</td>
<td>8</td>
<td>5.53</td>
<td>0.06</td>
<td>5895.12</td>
</tr>
<tr>
<td>Phi(occ)p(occ+BRA)</td>
<td>5</td>
<td>30.70</td>
<td>0.00</td>
<td>5926.30</td>
</tr>
</tbody>
</table>
Figure 3-1. Predicted clutch sizes (± 95 CIs) laid by female brant as a function of pair status at the Tutakoke River brent colony (TRC), 1990–2014. Female’s pair status is described as follows: (1) faithful, females breeding with a familiar mate and who will not change mates in the future; 2) pre-switch, females breeding with a familiar mate in year i but who will change mates in the future; 3) switch, male exp, females who are breeding with an unfamiliar mate that has bred at least twice at TRC; 4) switch, male non-exp, females who are breeding with an unfamiliar mate that is either ringed and bred less than twice at TRC or who is unmarked and assumed to have little to no experience at TRC. Number of clutches is indicated below each error bar.
Figure 3-2. Predicted relative initiation date (± 95 CIs) of nests by female brant as a function of pair status at the Tutakoke River brent colony (TRC), 1990–2014. Female’s pair status is described as follows: (1) faithful, females breeding with a familiar mate and who will not change mates in the future; 2) pre-switch, females breeding with a familiar mate in year $i$ but who will change mates in the future; 3) switch, male exp, females who are breeding with an unfamiliar mate that has bred at least twice at TRC; 4) switch, male non-exp, females who are breeding with an unfamiliar mate that is either ringed and bred less than twice at TRC or who is unmarked and assumed to have little to no experience at TRC. Number of clutches for which initiation date was determined is indicated below each error bar.
Figure 3-3. Predicted number of goslings leaving the nest (± 95 CIs) as a function of female pair status at the Tutakoke River brent colony (TRC), 1990–2014. Female’s pair status is described as follows: (1) faithful, females breeding with a familiar mate and who will not change mates in the future; 2) pre-switch, females breeding with a familiar mate in year $i$ but who will change mates in the future; 3) switch, male exp, females who are breeding with an unfamiliar mate that has bred at least twice at TRC; 4) switch, male non-exp, females who are breeding with an unfamiliar mate that is either ringed and bred less than twice at TRC or who is unmarked and assumed to have little to no experience at TRC. Number of clutches for which the number of goslings leaving the nest was determined is indicated below each error bar.
Figure 3-4. Prefledging survival estimates (± 95 CIs) from webtagged goslings as a function of mother’s pair status at the Tutakoke River brent colony (TRC), 1990–2010. Female’s pair status is described as follows: 1) faithful, females breeding with a familiar mate and who will not change mates in the future; 2) pre-switch, females breeding with a familiar mate in year $i$ but who will change mates in the future; 3) switch, male exp, females who are breeding with an unfamiliar mate that has bred at least twice at TRC; 4) switch, male non-exp, females who are breeding with an unfamiliar mate that is either ringed and bred less than twice at TRC or who is unmarked and assumed to have little to no experience at TRC. Number of webtagged goslings is below each error bar.
Chapter IV: Long-term fitness benefits of mate fidelity in brent geese

Alan G. Leach*a,b, James S. Sedinger a, Thomas V. Riecke a,b, David H. Ward c, and W. Sean Boyd d

a Department of Natural Resources and Environmental Science, University of Nevada-Reno, 1664 N. Virginia St., Reno, NV 89557 USA

b Program in Ecology, Evolution, and Conservation Biology, University of Nevada-Reno, 1664 N. Virginia St., Reno, NV 89557 USA

c U. S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA

d Science and Technology Branch, Pacific Wildlife Research Centre, Environment Canada, RR1 – 5421 Robertson Rd., Delta, British Columbia V4K 3N2, Canada

* Corresponding author: aleach@cabnr.unr.edu

RH: Demographic benefits of mate retention in brent geese
Introduction

Social monogamy is the ubiquitous mating strategy in avian species with >90% of birds exhibiting social monogamy during the breeding season (Lack 1968; Emlen & Oring 1977). Within-season breeding cooperation and monogamy is thought to have evolved in most birds because the necessity of bi-parental brood care results in an inability of males to effectively care for the offspring of more than one female per season (Emlen & Oring 1977). However, the reason that individuals of some species form long-term, socially monogamous pair-bonds, with the pair remaining in close contact throughout the year, is less clear. There are several hypotheses regarding the advantages of mate retention, such as, the mate “familiarity” effect which states that pairs remaining together improve their fitness, because of a “fine-tuning” of efforts (Black 2001; Sanchez-Macouzet, Rodriguez & Drummond 2014). Further, individuals may remain faithful to the current mate if few unpaired, high quality, replacement mates are available (Dhondt & Adriaensen 1994; Ens, Choudhury & Black 1996). Alternatively, for species in which the pair remains in close proximity and coordinates efforts throughout the annual cycle, such as in Arctic nesting geese, individuals remaining with the same mate throughout the non-breeding season may maintain a higher social status than those who change mates during winter (Black 2001).

While many studies have assessed the effects of mate change on within-season reproductive success in birds; the long-term demographic benefits of mate fidelity remain largely unexplored. We know of only two investigations of the long-term benefits of mate fidelity; one study investigated effects of mate death (due to human harvest) prior to the breeding season on true survival and breeding probability of black brent geese.
(Branta bernicla nigricans; hereafter brent) (Nicolai et al. 2012) and the other explored apparent survival and recapture rates of great tits (Parus major) who were breeding with a new partner after mate change (Culina et al. 2013). However, the inferences of Culina et al. (2013) concerning the demographic benefits of mate retention were limited, because of their inability to differentiate mortality from permanent emigration. Additionally, although rates of mate fidelity in wild bird populations are of substantial interest, few studies, have estimated mate fidelity using robust capture-mark-recapture (CMR) analyses which account for processes that can bias parameter estimates of interest, such as detection and permanent emigration (Lebreton et al. 1992; Boulinier et al. 1997; Culina et al. 2013). To date, we know of only one study (Culina et al. 2013) that attempted to estimate mate fidelity using CMR techniques. This paucity of information regarding the rates of mate fidelity and long-term effects of mate change represents an important limitation to our understanding of the evolution of mating systems and the benefits of long-term pair-bonds.

Explanations for the lack of studies estimating mate fidelity and its demographic consequences are likely three fold. First, estimating survival and breeding probability requires long-term data on a large sample of uniquely marked individuals with high reencounter rates (Sedinger, Lindberg & Chelgren 2001). Second, most studies are unable to independently estimate true survival and permanent emigration, because individual reencounter data from the entire range of the focal species are unavailable (Culina et al. 2013; Kendall et al. 2013). Third, most studies are unable to separately estimate detection of an individual from its probability of absence from the breeding area (i.e., skipped breeding) (Kendall, Nichols & Hines 1997; Sedinger et al. 2008). This
results in most investigators ignoring or being unable to estimate an important component of fitness, which is the decision to breed (Kendall, Nichols & Hines 1997; Sedinger, Lindberg & Chelgren 2001; Souchay, Gauthier & Pradel 2014).

We use 25 years of mark-recapture data collected on brent at the Tutakoke River brent colony (hereafter TRC), Yukon-Kuskokwim Delta, Alaska, USA, to assess the demographic consequences of mate change. Specifically, we estimated the costs of mate change to true survival (i.e., unbiased by permanent emigration), future breeding probability, and fidelity to the breeding site (i.e., TRC). Our interest in breeding site fidelity (i.e., 1 – permanent emigration) stems from the fact that female brent (and possibly most males also) who permanently emigrate from their breeding colony are unlikely to breed elsewhere and thus enter a permanent non-breeding state (Sedinger et al. 2008).

The current work builds on a previous investigation of the effect of mate loss (due to human harvest) prior to the breeding season on rates of survival and breeding in brent (Nicolai et al. 2012). However, we predicted that even after successfully breeding with a new partner, brent may still suffer long-term fitness consequences of mate change. We expected that costs of mate change would be paid in terms of reduced future breeding probability and not survival, because fitness in long lived species, such as brent, is most sensitive to survival and thus typically preserved (Stearns 1992; Saether & Bakke 2000).

**Materials and methods**

**STUDY AREAS AND SPECIES**

We used live resights and recaptures of breeding brent at TRC from 1990–2014 in the current study. We collected live resight data on brent during winter at up to 3 lagoons
along the western coast of Baja California, Mexico (Sedinger et al. 2011) and during spring migration in the Strait of Georgia, British Columbia, Canada. During our period of study the number of brent breeding at TRC ranged from 2000–8000 pairs (Wilson 2014). Coastal habitats from the Central Russian arctic, east to the Yukon-Kuskokwim Delta (YKD), the north slope of Alaska, and the mid-Canadian Arctic serve as breeding areas for brent (Lewis et al. 2013). Brent winter in, and migrate through, coastal estuaries from the Alaska Peninsula, USA to Baja California and mainland, Mexico. Brent do not begin breeding until at least two years of age (Sedinger, Lindberg & Chelgren 2001). Brent exhibit a perennial socially monogamous mating strategy, with partners working together throughout the annual cycle to acquire nutrients needed for survival and breeding and cooperate in rearing young (Bellrose 1980). Additionally, when breeding is successful, brent offspring cooperate with parents in wintering flocks in order to maximize the families’ social status and forage intake (Poisbleau et al. 2006). Though socially monogamous, adults participate in extra-pair copulations (EPC), as a result, 8% of eggs at TRC result from EPCs (Lemons et al. 2015).

MARKING AND REENCOUNTERT

We have marked adult (2+ years old), immature (1 year old), and gosling brent in ringing drives during the adult remigial moult at TRC since July 1986 (Sedinger et al. 2008). We captured individuals in mass drives (up to 2000 individuals per year) and marked them with U.S. Geological Survey metal rings and coloured tarsus rings (2.5 cm tall) engraved with a unique alphanumeric code. We determined the sex of each individual using cloacal examination (Owen 1980). To date, we have ringed >40,000 brent at TRC (J. S. Sedinger, unpublished data). During ringing we were able to determine if a female brent
had bred in the current year by the presence of a brood patch (Sedinger et al. 2008). Male brent have no such identifying plumage to indicate breeding, regardless we assumed all adult males captured in a ringing drive had attempted to breed that year. Our reasoning for this assumption was that (1) most non-breeding brent moulted in distant locations (Bollinger & Derksen 1996), and (2) < 2% of adult females captured lacked brood patches (A. G. Leach, unpublished data) indicating few nonbreeders were present in our ringing drives. Approximately, 50% of the breeding brent at TRC were colour ringed and uniquely identifiable during our study. During winter and spring migration we used Questar 35–150X telescopes (Questar, New Hope, Pennsylvania, USA) to read colour rings of brent that were acquiring grit at sand bars after the water level dropped following high tide (Ward et al. 2004). We obtained ring recovery information of brent harvested from autumn 1990-spring 2014 from the Bird Banding Laboratory (U.S. Geological Survey). We received approval of all handling and marking of animals by Institutional Animal Care and Use committees at the University of Alaska Fairbanks and the University of Nevada Reno (most recent protocol number 00056).

Each summer during egg laying at TRC we systematically searched 48 50 m plots every four days and used 20–60X spotting scopes to read colour rings of nesting brent (Sedinger et al. 2008). Additionally, we searched the remainder of the colony, outside our random plots, for nests attended by at least one marked brent. Our nest searching efforts resulted in 500–1000 nests with at least one ringed parent being monitored annually, with the rings of parents typically being read at least twice. During the post-hatching period we recorded observations and mating status of colour marked adult brent tending goslings from 3–7 meter towers (Sedinger, Lindberg & Chelgren 2001). We also
opportunistically read the rings of brent at TRC that were not associated with a nest or brood during a particular observation; these individuals were non-breeding, had not yet initiated nesting, or were failed breeders. These opportunistic observations were not used to construct capture histories (see below), but allowed more opportunity to identify an individual’s mate in year $t$.

We established mate changes using three scenarios. First, if an individual was observed with a different ringed mate in time $t$ than previously. Second, we assigned a mate change if an individual was previously with a marked mate, but observed with an unmarked mate in year $t$. In this case we did not record a mate change if the mate only had a metal tarsal ring in year $t$, because a small percentage (0.2%) of brent lose their colour rings annually (Sedinger et al. 1997). Finally, if an individual was previously observed with an unmarked mate, but observed in year $t$ with a mate that was ringed before the last sighting with the unringed mate we assigned a mate change. On average, we identified the mate of 86% of adult brent detected breeding at TRC annually.

**Statistical analyses**

**ESTIMATING MATE FIDELITY**

We estimated mate fidelity using the Huggins closed capture multi-strata robust design module (MSRD) (Kendall & Nichols 2002) in program MARK (White & Burnham 1999). We built all models using the program R (R core team 2014) package RMark (Laake 2013). We estimated transitions among four strata based on mating status for our analysis: (1) faithful, brent that were breeding with the same ringed mate for at least the second time, (2) individuals who were breeding with a new mate in year $t$ who was previously ringed, (3) individuals who were breeding with a new mate in year $t$ who was
unringed, and (4) individuals that had a ringed mate in year $t$, but it was uncertain how many times the pair had bred together previously. The fourth strata allowed individuals who had switched to an unringed mate the opportunity to eventually transition back to the faithful state after we ringed the new mate.

We only assigned a mating state to individuals who were breeding at TRC in year $t$ (i.e., seen at a nest and/or caught in a ringing drive) and who had been observed breeding on at least two previous seasons at TRC making them at least five years old. By censoring reencounters of individuals breeding for the first or second time we aimed to reduce any effects of inexperienced focal individuals in our dataset as they could be more likely to change mates (Culina et al. 2013). We assigned individuals to the faithful state in year $t$, if the focal individual bred and the mate’s identity was not determined, but the individual was observed with the same ringed mate before and after year $t$. Otherwise we had to identify both the focal individual and its mate in year $t$, to assign a state. Individuals not observed breeding were assigned a “0” in their capture history for both secondary occasions during that breeding season. If an individual was seen breeding, but was inexperienced or the mate status was not determined we assigned a “.” to the capture history for both secondary occasions in year $t$.

We constructed a candidate set of models that allowed for variation among sexes and strata in apparent survival and transition probabilities. We also considered models that allowed for variation in detection among years, secondary occasions, and intercept-only structures for apparent survival and transition probabilities. Models were evaluated using AICc model weights, and assessment of 95% confidence intervals for parameter estimates (Burnham and Anderson 2002). We did not test for, or adjust, our parameter
estimates for overdispersion, because we know of no standard method for assessing
overdispersion in MSRD models. However, estimates of $\hat{c}$ are generally < 1.2 in other
analyses of this dataset (Sedinger et al. 2007), and given the small set of non-nested
models we tested overdispersion likely resulted in little bias in precision of estimates
(Sedinger et al. 2011).

DEMOGRAPHIC COSTS OF MATE CHANGE
To estimate the long-term demographic costs of mate change we used the Barker robust
design (BRD) (Kendall et al. 2013) module in program MARK. We constructed all
models using the program R (R core team 2014) package RMark (Laake 2013). While
the MSRD produces estimates of apparent survival of individuals in each stratum we
chose to estimate demographic parameters with the BRD for several reasons. First, we
were interested in estimating the effects of mate change on three demographic parameters
(1) true survival (i.e., unconfounded by permanent emigration), (2) breeding probability,
and (3) breeding fidelity to TRC. The only demographic parameter estimated in our
MSRD models was apparent survival, which is confounded with permanent emigration.
Secondly, we were interested in estimating breeding probability; while the MSRD can be
used to estimate this parameter it necessitates at least two states (1) observed breeding in
year $t$ and (2) not observed breeding in year $t$. Because we were estimating state
transitions between mate fidelity and mate change (see below) adding breeding states to
our analysis would have added substantial complexity to our transition probabilities and
model convergence would have been unlikely.

Our analysis spanned 25 breeding seasons, each having two secondary occasions
(nesting and ringing during the adult wing moult) between which we assumed the
population was closed to immigration and emigration. We used the Barker robust design in program MARK implemented via RMark (Laake 2013) to build models and estimate demographic parameters to assess costs of mate change. The BRD combines closed (within a breeding season) and open (between breeding seasons) periods to estimate a number of demographic (e.g., survival) and nuisance (detection) parameters (Kendall et al. 2013).

We modeled the following parameters using the BRD: true survival ($S$), reporting rate ($r$), probability of resighting during the non-breeding season ($R$), probability that an individual was observed alive, but later died during a non-breeding season ($R'$), probability an individual was available for encounter at TRC given availability in year $t-1$ ($A''$), probability an individual was available for encounter at TRC given absence in year $t-1$ ($A'$), probability an individual did not permanently emigrate from TRC after time $t$ ($F$), probability that an individual who was breeding at TRC, was initially encountered at TRC during nesting ($p_{nesting}$), probability that an individual who was breeding at TRC, was initially encountered at TRC during ringing ($p_{ringing}$), and the probability of being recaptured at ringing given encounter at nesting ($c$). We restricted all encounters at TRC to breeding brent, thus, temporary emigration was equivalent to skipping breeding (Sedinger et al. 2008).

For all analyses we constructed capture histories using information collected from breeding seasons 1990–2014. We did not begin capture histories at initial ringing, but rather at first breeding reencounter at TRC. We separated brent into groups by sex. We limited our analysis to individuals detected during nesting at least once during our study. Our reasoning for this was that the probability a breeding brent was detected at nesting
was greater than during ringing drives and we did not want to include brent potentially nesting outside the colony and therefore only available for reencounter at ringing (Sedinger, Lindberg & Chelgren 2001).

We created a time varying age covariate to control for age-specific variation in demographic rates (Sedinger, Lindberg & Chelgren 2001; Sedinger et al. 2008). All individuals were assigned a continuous time-varying age covariate (AGE; range = 2–26). Brent ringed as adults were assumed to be 2 years old when first captured (Sedinger, Lindberg & Chelgren 2001). We z-standardized the individual age covariate (mean = 0 and SD = 1) within groups (White & Burnham 1999). To test the hypothesis that mate change affects demographic rates of brent, we created the time-varying covariate MCH. For the variable MCH we assigned a value of “1” if an individual was breeding for the first time with a new mate in year \( t \), a value of “-1” if an individual was breeding with a familiar mate (i.e., at least one previous breeding attempt together) and a “0” otherwise.

We accounted for any lack of independence between individuals by adjusting \( \hat{c} = 1.11 \) (Sedinger et al. 2007; Nicolai et al. 2014), because there is not a procedure for assessing overdispersion in the Barker robust design (Kendall et al. 2013). We set \( R' = 0.0 \) as was done in a previous analysis of data from this population (Nicolai et al. 2014). We only modeled covariate effects after the 1990–2010 breeding seasons. However, we included reencounter information from 2011–2014 to reduce sampling correlation between temporary emigration, permanent emigration, and true survival at the end of our time series (Penaloza, Kendall & Langtimm 2014). To ensure that any demographic costs of mate change were not the result of inclusion of inexperienced breeders we did not model mate change effects until the focal individual had bred at TRC at least twice
previously. This is consistent with earlier work in this population reporting that breeding probability in Brent increases until age five (Sedinger, Lindberg & Chelgren 2001). All Brent that were involved in reproductive manipulations performed at TRC were removed from the current analysis (Leach unpublished manuscript).

We approached model selection as a two-step process. Our first model selection step was to find the best performing base model for all parameters. We did this by first finding the best group and temporal structure for \( p_{nesting} \), \( p_{ringing} \), and \( c \), then \( r \), \( R \), and finally \( S \), \( A'' \), \( A' \), and \( F \). Next we considered linear and quadratic effects of AGE on \( S \), \( A'' \), \( A' \), and \( F \). For the second step of the model selection process we used the best performing model (i.e., lowest QAICc score) from step one to test hypotheses about costs of mate change. We tested hypotheses by building models which containing the effect of MCH on true survival (\( S \)), breeding probability (\( A'' \)), and breeding fidelity (\( F \)) to TRC. In a separate modeling exercise we constructed models testing the hypothesis that individuals who remated with an experienced partner would suffer lower costs of mate change than those breeding with a new, but inexperienced partner. After finding the best base model we performed separate analyses for females and males. We used \( \Delta \text{QAICc} \) scores, model weights, and 95% confidence intervals on parameter estimates to draw inferences about the relative support for each model and parameter (Burnham & Anderson 2002). We report all parameter estimates ± 95% confidence intervals and considered a parameter to be unsupported if the CIs overlapped 0.
Results

RATES OF MATE FIDELITY

This analysis included 1429 females and 956 males who had bred with a ringed mate in at least one year at TRC. Models including effects of an interaction between sex and stratum on survival failed to converge and were removed from consideration. The best performing model included additive effects of sex and stratum on apparent survival, an interaction between sex and all transition probabilities, and effects of year and secondary occasion on probability of detection at TRC. This was the only model receiving support ($w_i = 1.0$; Table 4-1). Models without state specific transition probabilities were clearly not supported (All $\Delta$AICc > 4040) (Table 4-1). Models without stratum (All $\Delta$AICc > 94) and sex (All $\Delta$AICc > 57) effects on apparent survival were also not supported (Table 4-1). Parameter estimates from the best performing model indicated that rates of mate retention in year $t+1$ for brent breeding with a familiar mate in year $t$ was $0.881 \pm 0.017$ for females and $0.952 \pm 0.013$ for males. However, for individuals who had switched mates in year $t$ the probability of mate fidelity was reduced to $0.277 \pm 0.163$ for females and $0.343 \pm 0.246$ for males (Fig. 4-1).

DEMOGRAPHIC COSTS OF MATE CHANGE

This analysis included 3021 and 3039 mature female and male brent, respectively. From 1990–2010, we documented 748 and 196 first breeding attempts after mate change for female and male brent, respectively. All parameter estimates provided hereafter are from the best performing model with error represented by 95% CIs adjusted for $c = 1.11$.

The best performing base model included effects of sex and AGE on true survival, and annual variation in $r$ and $R$. As is typical in this population we found a strong
Markovian structure for breeding probability (Sedinger et al. 2008); brent who were absent from TRC in year $t-1$ bred at lower rates than those present in year $t-1$. Given presence at TRC in year $t-1$ breeding probability in year $t$ ($A$) was influenced by sex (Table 4-2), with males on average being less likely to breed in $t+1$ ($\beta = -0.42 \pm 0.23$) than females. Given absence from TRC (i.e., skipped breeding) in year $t-1$ the only variable that influenced breeding probability in year $t$ ($A'$) was sex, with males on average being less likely to breed in $t+1$ ($\beta = -0.57 \pm 0.50$) than females after skipping breeding in year $t$. Adult breeding fidelity to TRC was influenced by sex and the interaction between sex and AGE. The probability a breeding brent was detected at TRC varied among years and secondary occasions. The probability a breeding brent was recaptured at ringing given detection at nesting varied only by year.

Survival declined for females ($\beta = -0.53 \pm 0.06$) and males ($\beta = -0.31 \pm 0.08$) with AGE. Males had, on average, age specific survival rates ($\bar{x} = 0.863 \pm 0.012$) that were $\sim 2\%$ lower than those of mature females ($\bar{x} = 0.886 \pm 0.004$). Males who skipped a breeding attempt had lower probability of breeding in $t+1$ ($0.17 \pm 0.07$) than females ($0.31 \pm 0.07$). Breeding fidelity to TRC also declined for females ($\beta = -0.76 \pm 0.36$) and males ($\beta = -0.38 \pm 0.22$) with AGE. As has been previously reported in brent (Lindberg et al. 1998; Sedinger et al. 2008) we found that mature females, on average, had higher breeding site fidelity ($F$) to TRC ($0.985 \pm 0.004$) than males ($0.932 \pm 0.027$). The probability a brent that died and was reported varied from ($0.047 \pm 0.028$) in the winter of 2000-2001 to ($0.211 \pm 0.077$) in the winter of 2012-2013. The probability of a brent being detected alive during the non-breeding season varied from ($0.009 \pm 0.006$) in the winter of 2009-2010 to ($0.339 \pm 0.028$) in the winter of 1992-1993.
For models considering the effect of mate change on female demographic rates
the best model included the effect of mate change on survival and breeding probability
(Table 4-2). This model was a clear improvement over the base model (ΔAICc = 50.47;
Table 4-2). The best model examining the effect of mate change on male demographic
rates included the effect of MCH on survival, breeding probability, and breeding fidelity
to TRC (Table 4-3). Again this model was a clear improvement over the base model
(ΔAICc = 75.57; Table 4-3). Parameter estimates from the best models indicated that
survival was reduced for females (β = -0.24 ± 0.12) and males (β = -0.35 ± 0.19) who
were breeding with a new mate in year $t$ (Fig. 4-2). Likewise, the probability of breeding
in $t+1$ was reduced for females (β = -0.89 ± 0.33) and males (β = -2.07 ± 0.60) who were
breeding with a new mate in year $t$ (Fig. 4-3). Breeding fidelity to TRC tended to be
greater for males who returned to TRC and bred again with a new partner (β = 0.68 ±
0.71).

Discussion

To our knowledge we provide the first evidence of the long-term benefits of breeding
with a familiar mate for a long-lived bird. Culina et al. (2013) made strides in
understanding long-term benefits of mate fidelity in great tits, but they could not separate
survival from permanent emigration nor estimate breeding probability. We hypothesize
that reduced survival and breeding probability of individuals in newly formed pairs is, at
least partially, explained by the low fidelity of members of these pairs to each other.
Brent, as in most geese, have a strong social hierarchy in their wintering flocks, with
family groups dominating pairs of adults without offspring and pairs dominating
singletonst (Black & Owen 1989; Gregoire & Ankney 1990; Poisbleau et al. 2006;
Poisbleau, Guillon & Fritz 2010). This social hierarchy is positively related to forage acquisition during winter (Black et al. 1992; Stahl et al. 2001) and future breeding probability (Sedinger et al. 2011). Thus, the low mate fidelity among partners in newly formed pairs likely leads to a reduction of winter social status after pair bond breakage, and as a consequence reduced survival and breeding probability associated with finding a new mate (Black 2001; Stahl et al. 2001; Nicolai et al. 2012). We are unsure why males are less likely than females to breed at TRC in year \( t+1 \), after breeding with an unfamiliar mate in year \( t \), but this discrepancy in breeding probability could also be directly related to the reduced fidelity of newly formed pairs. Perhaps males are unable to find a new mate or pair with a female who breeds at another colony for their next breeding attempt(s).

However, we cannot be sure that lower mate fidelity is only reason for mate change costs; perhaps a finely-tuned repertoire between mates which helps to maximize nutrient gain and reduce conflict with conspecifics during the non-breeding season is disrupted after mate change (Black, Prop & Larsson 2007; Culina et al. 2013). However, this explanation seems unlikely, because Leach (Chapter 3) found that new pairs composed of experienced partners fledged more goslings than familiar pairs indicating that mate familiarity apparently is not necessary to successfully raise a brood. We suspect that to fully understand mechanistic links between mate fidelity and demography researchers will need to study social rank and behaviour of brent with known mating histories throughout the annual cycle, possibly by incorporating experimental mate removals.
We are confident that the costs of mate change we report are not confounded with individual quality for three reasons. First, Nicolai et al. (2012) demonstrated that female brent suffered lower survival (but not breeding probability) after human harvest of their mate. In light of these results the authors reasoned that only high quality females are able to survive to remate and breed again; these individuals were the basis of our current analysis. Second, we only modeled costs of mate change for experienced breeders who have higher inherent demographic rates (e.g., breeding probability) compared to younger birds (Sedinger, Lindberg & Chelgren 2001). We acknowledge there is still heterogeneity in breeding probability among brent 5 years and older (Sedinger et al. 2008), however, since we limited the current analysis to individuals breeding for at least the third time we likely eliminated many brent that breed only sporadically. Finally, in the current analysis, the average age of a female that had changed mates was 9.41 years \((SD = 3.90)\) as such we expect that phenotypic mortality selection had, by this point, reduced the number of low quality individuals in each birth cohort (Curio 1983; Cam et al. 2002). Despite the relatively advanced average age of remated females this was unlikely to have biased our results, because (1) the average age of females breeding with a familiar mate was similar 8.32 \((SD = 3.52)\) and (2) we modeled age related variation in survival.

The rates of mate change for females breeding with a familiar mate (~12% annually) would result in a female who began breeding at the age of two and lived to 8 years of age (average lifespan of brent = 7.3 years) having almost a 53% chance of switching mates. Additionally, we suspect we underestimated the number of pair-bond terminations, because we only included individuals who returned to TRC and bred with a new mate following mate change. It is likely that many widows and divorcees died
before acquiring a new mate and breeding again at TRC (Nicolai et al. 2012). Given that the oldest brent observed during the study was at least 26 years old; we hypothesize that for most individuals to achieve maximal longevity (and perhaps lifetime fitness) they need to efficiently acquire a new partner following mate death or divorce. Further, to maintain successful breeding, the replacement mate must be an experienced (i.e., ≥ 2 previous breeding attempts) TRC breeder (Chapter 3). We suspect that because of the constrained mate choice options in monogamous populations (Griffith, Pryke & Buttemer 2011) such as brent, many individuals are precluded from achieving their maximum lifetime fitness, because of their inability to replace mates.

While as many as 90% of partnerships between familiar mates end due to death (A. G. Leach, unpublished data), the low rates of mate retention for females breeding with an unfamiliar mate (28%) suggests that a large proportion of these partnerships end in divorce, because rates of widowing cannot explain such high rates of mate change. We hypothesize that reduced mate fidelity in newly formed pairs could result from discrepancies in experience between pair members resulting in reduced reproductive success and a resulting incentive to change mates.

We found that males breeding at TRC have ~2% lower survival rates than females. This would seem to partially explain why males tend to have greater rates of mate fidelity as they are less likely to be widowed. Our variation is sex-specific survival rates is in contrast to another recent survival rate analysis on YKD brent (Sedinger et al. 2007). We suspect that the discrepancy in our estimates with Sedinger et al. (2007) results from differences in methodology: whereas Sedinger et al. (2007) used ring-recovery only models (Brownie et al. 1985) we used a joint live encounter-dead recovery
approach (Kendall et al. 2013). As a result of the low recovery rates of ringed brent (< 2% annually) the power of ring-recovery only models is reduced for this dataset (Sedinger & Nicolai 2011), when compared to the large numbers of live breeding and non-breeding reencounters we were able to incorporate to improve precision (Barker 1997; Kendall et al. 2013). Sedinger et al. (2007) were thus less likely to be able to detect a relatively small difference (i.e., 2%) in survival between the sexes. With this discrepancy in survival, pairs formed when both partners were 2 years old would have 41% of males versus 48% of female members alive by age 8. We suspect that male survival is reduced because they participate in more aggressive interactions with conspecifics (Sedinger, Eichholz & Flint 1995) and potential offspring predators than females, which could result in increased mortality rates.

The reduced survival rates of males may also have indirect fitness consequences to females beyond those they widow. Lower survival of adult males further skews the sex ratio in brent, which begins in early life from reduced survival of male relative to female goslings (Lemons et al. 2012). Lemons et al. (2012) hypothesized that the excess numbers of females during early adulthood resulted in ~13% of female goslings permanently emigrating from TRC (Sedinger et al. 2008), because they are unable to acquire a mate and breed. We further suspect that this continued reduction of the proportion of males in the population precludes some females from replacing their mates following termination of their partnerships. Additionally, many females who are able to replace a mate likely have to settle for young, inexperienced males to the detriment of reproductive success (Chapter 5).
In conclusion, we provide evidence for the first time in a long-lived bird that individuals breeding with a familiar mate have higher survival and breeding propensity than individuals breeding with a new mate. We did not expect that mate familiarity would affect survival in this species, because as in other long-lived species, fitness is most sensitive to survival and typically preserved to the detriment of reproduction (Stearns 1992; Saether & Bakke 2000). We think that the reduction of true survival and breeding probability we found for brent of both sexes who are breeding with a new mate represents a large disincentive to changing mates.

Our findings in the current paper and those of Nicolai et al. (2012) demonstrate that though researchers typically focus on how mate fidelity affects reproductive success, they should also consider the effects of mate change to survival and breeding probability when trying to understand the evolution of mating systems (Culina et al. 2013). We believe that the social benefits of being paired during the winter have, at least partially, shaped the evolution of the perennial socially monogamous mating system of brent. As such, mate retention is favored to not only improve reproductive success, but also to continuously have a partner during the non-breeding season who helps to acquire nutrients essential to survival and breeding (Black, Prop & Larsson 2007). We also suspect that brent benefit from mating with partners that are not only good parents, but have superior longevity, thereby reducing the frequency of mate change. While the current findings shed light on the relative rates of mate fidelity and its long-term benefits in brent it does not address causes of mate change. We investigate factors that affect rates of mate retention in brent elsewhere (Chapter 5).
Acknowledgements

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Data Accessibility

The mark-recapture input file (.txt file format) containing all the data used in this paper will be deposited in the Dryad Digital Repository before the final version of this manuscript is published.
References


*Biometrics, 53,* 666-677.


Table 4-1. Performance of multi-state robust design mark-recapture models investigating mate retention of experienced (breeding for at least the third time) brent at the Tutakoke River brent colony, 1990–2014. We included four strata in our analysis: (1) faithful (F), females that were paired with the same banded mate for at least two consecutive years, (2) females who had a new mate in year $t$ who was previously banded (C), (3) individuals that had a new mate in year $t$ who was not banded (U), and (4) individuals that had a banded mate in year $t$, but whose familiarity with we were uncertain (M).

<table>
<thead>
<tr>
<th>Model structure</th>
<th>$k$</th>
<th>$\Delta$AICc</th>
<th>$w_j$</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
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<td>$S(\text{sex+stratum})Psi(\text{stratum<em>tostratum</em>sex})$</td>
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<td>0.00</td>
<td>1.00</td>
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<td>$S(\text{stratum})Psi(\text{stratum*tostratum})$</td>
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<td>$S(\text{sex})Psi(\text{stratum*tostratum})$</td>
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<td>4195.77</td>
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<td>40481.39</td>
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Table 4-2. Models examining effects of mate change (MCH) on survival ($S$), breeding probability ($a''$), and breeding fidelity ($F$) to the Tutakoke River brent colony, for mature female brent from 1990–2010.

<table>
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<th>$w_i$</th>
<th>QDeviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S(sex<em>age+MCH)a''(sex+MCH)F(sex</em>age)$</td>
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<tr>
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</tr>
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<td>$S(sex<em>age)a''(sex)F(sex</em>age+MCH)$</td>
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<td>32.79</td>
<td>0.00</td>
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</tr>
<tr>
<td>$S(sex<em>age)a''(sex)F(sex</em>age)$</td>
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<td>50.47</td>
<td>0.00</td>
<td>106691.5</td>
</tr>
</tbody>
</table>

*Notes:* Only structures for true survival ($S$), breeding probability in year $t+1$ ($a''$), and breeding site fidelity ($F$) are shown. All models considered had the same structure on all other parameters.
Table 4-3. Models examining effects of mate change (MCH) on survival (S), breeding probability (a''), and breeding fidelity (F) to the Tutakoke River brent colony, for mature male brent from 1990–2010.

<table>
<thead>
<tr>
<th>Model structure</th>
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<th>wi</th>
<th>QDeviance</th>
</tr>
</thead>
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<tr>
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</tr>
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<td>S(sex<em>age)a''(sex+MCH)F(sex</em>age)</td>
<td>112</td>
<td>8.45</td>
<td>0.01</td>
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<tr>
<td>S(sex<em>age)a''(sex+MCH)F(sex</em>age+MCH)</td>
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<td>113</td>
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<td>111</td>
<td>75.57</td>
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<td>106691.47</td>
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**Notes:** Only structures for true survival (S), breeding probability in year \( t+1 \) (a''), and breeding site fidelity (F) are shown. All models considered had the same structure on all other parameters.
Figure 4-1. Probability (± 95% CI) that brent breeding with a familiar mate (at least one previous breeding attempt together) versus those breeding with a new mate retain that mate into the next breeding season at the Tutakoke River brent colony, Yukon-Kuskokwim Delta, Alaska, USA from 1990–2014. Estimates are from the best performing Huggins closed capture multi-strata robust design capture-recapture model.
Figure 4-2. Probability (± 95% CI) of surviving to year \( t+1 \) for brent breeding with a familiar mate (at least one previous breeding attempt together) versus those breeding with a new mate in year \( t \) at the Tutakoke River brent colony, Yukon-Kuskokwim Delta, Alaska, USA from 1990–2010. Estimates are from the best performing Barker robust design capture-recapture model.
Figure 4-3. Probability (± 95% CI) of attempting to breed in year $t+1$ for brent breeding with a familiar mate (at least one previous breeding attempt together) versus those breeding with a new mate in year $t$ at the Tutakoke River brent colony, Yukon-Kuskokwim Delta, Alaska, USA from 1990–2010. Estimates are from the best performing Barker robust design capture-recapture model.
Chapter V: Patterns of assortative mating and mate retention in black brant

Alan G. Leach*\textsuperscript{a, b} and James S. Sedinger\textsuperscript{a}

\textsuperscript{a} Department of Natural Resources and Environmental Science, University of Nevada-Reno, 1664 N. Virginia St., Reno, NV 89557 USA

\textsuperscript{b} Program in Ecology, Evolution, and Conservation Biology, University of Nevada-Reno, 1664 N. Virginia St., Reno, NV 89557 USA

* Corresponding author: aleach@cabnr.unr.edu

RH: Patterns of mating in brant geese
Introduction

Mate retention between breeding seasons can affect not only individual fitness but potentially population dynamics by determining the number of reproducing pairs and their productivity (Culina et al. 2013). One mechanism by which mate change can affect fitness is if the focal individual is forced to breed with an inexperienced mate, such as in kittiwakes, *Rissa tridactyla* (Naves, Cam & Monnat 2007). Similarly, prefledging survival of black brant goslings (*Branta bernicla nigricans*; hereafter brant) was reduced by 35% if the mother was partnered to a male that was an inexperienced breeder (i.e., < 2 previous breeding attempts) (Chapter 3). Additionally, female brant who are breeding with a new partner have low rates of mate retention (28%) compared to females breeding with a familiar mate (88%), which potentially contributes to the reductions in future survival and breeding probability of brant who change mates (Chapter 4). Leach (Chapter 4) hypothesized that low rates of mate retention by newly formed pairs may be the result of most females being forced to repair with inexperienced males, resulting in these females changing mates again in an attempt to repair with an experienced male.

We suspected that most females who lost a mate through death or divorce would have to settle for an inexperienced replacement mate for several reasons. First, annual divorce rates in geese tend to be low (i.e., generally <10%) resulting in most pair bonds ending from death of a partner (Black, Choudhury & Owen 1996). Second, Leach (Chapter 4) found that male brant have survival rates that are ~2% less than females resulting in fewer males being widowed than females, this disparity in mortality likely further skews the sex ratio towards females, a trend that begins in the prefledging stage of their life cycle (Lemons et al. 2012). Finally, while adult female brant have breeding site
fidelities near 1.0 (Sedinger et al. 2008) adult males are less likely to continue breeding at a colony (~0.94) (Lindberg et al. 1998). Lindberg et al. (1998) hypothesized that this sex-specific variation in philopatry resulted from males that repair with females from other breeding colonies after loss of their mates or dissolution of the pair-bond through divorce. Thus, because many males that are experienced breeders remain paired until their death, there is likely an excess of unpaired experienced females compared to similarly aged males, and because some experienced males who are widowed or divorced repair with a female from another colony, we expected that most unpaired male brant would be inexperienced.

Despite the potential lack of available experienced males in the population, we still expected that there may be weak positive assortative mating by age and breeding experience in brant as individuals of both sexes may try to repair with an experienced breeder to avoid costs of mate change (Lamprecht 1986; Forslund & Larsson 1991). Further, adults may mate assortatively by body size if there are direct fitness benefits of having a large mate (e.g., improved reproductive success) as has been demonstrated in barnacle geese (Branta leucopsis) (Choudhury, Black & Owen 1996) or indirect benefits to offspring (i.e., heritability of advantageous traits) (Jiang, Bolnick & Kirkpatrick 2013). Body size in female brant is positively related to fitness through increased fecundity, because larger females can store greater amounts of nutrients to invest in clutches (Ankney & Macinnes 1978; Sedinger, Flint & Lindberg 1995). Adult male geese of large body size may achieve a greater dominance ranking through improved likelihood of success during conspecific contests, which benefits female nutrient acquisition during winter and thus future reproductive success (Poisbleau, Guillon & Fritz 2010).
Additionally, if body size in brant is heritable, which is common in many animals (Mousseau & Roff 1987), including geese (Larsson & Forslund 1992), pairs consisting of large partners may be more likely to produce large goslings which have fitness advantages over smaller conspecifics (Sedinger, Flint & Lindberg 1995; Sedinger, Herzog & Ward 2004; Sedinger & Chelgren 2007). Thus, we hypothesized that brant of both sexes could benefit from acquiring a structurally large mate and therefore would pair in a positive assortative fashion by body size.

Mate retention in many birds species is positively related to successful reproduction (Dhondt & Adriaensen 1994; Dubois & Cezilly 2002). Brant colonies on the Yukon-Kuskokwim Delta (YKD), Alaska, experience substantial annual variation in reproductive success, due largely to periodic nesting failures resulting from egg predation by arctic foxes (Vulpes lagopus) (Sedinger et al. 2015). After a breeding failure, brant migrate to distant locations to molt. This has the effect of reducing future forage availability for goslings on sedge (Carex subspathacea) grazing lawns, because these sedges require continuous grazing to maintain the nutritious growth form that will support gosling growth (Person et al. 2003). As a result of arctic fox predation, declining gosling growth rates, and lower first year survival, recruitment of goslings at the Tutakoke River brant colony (TRC), YKD, has declined substantially since 2000 (Sedinger et al. 2015). Thus, we hypothesized that rates of mate retention by brant may be affected by not only the individual reproductive success of the pair, but the productivity of their breeding colony, because males have the ability to repair and breed at other potentially more productive colonies.
We used 25 years of data collected on uniquely marked brant at the Tutakoke River brant colony, \((61^\circ15\,N, 165^\circ37\,W)\), YKD, Alaska, USA, in the current study. Our first objective was to test for factors that influenced mate retention, including previous breeding experience of partners, annual nest success, and growth rates of goslings. We expected that female brant who acquired inexperienced mates would be more likely to change mates again. Further, we predicted that rates of mate retention in brant would be positively related to annual nest success and gosling growth rates. We also expected positive assortative mating by age, breeding experience and body size in brant, because of potential advantages to each sex of having a more experienced, larger partner. Finally, we were interested in understanding how long it took brant pairs to achieve maximal rates of mate retention after mate change.

**Methods**

**STUDY AREA AND SPECIES**

The TRC is located on the Bering sea coast in southwestern Alaska with most brant nesting within 1 km of the coast in sedge meadows and islands with sedge cover on tidal mud flats (Lindberg, Sedinger & Flint 1997). During our study the number of brant nests at TRC has declined from 7400 to 2400 nests since 2000 (Wilson 2014). Female brant only lay one clutch per breeding attempt; clutches typically contain of 4-5 eggs (Flint & Sedinger 1992), and females assume all incubation duties (Eichholz & Sedinger 1999). Arctic-nesting geese, including brant, form long-term, socially monogamous pair-bonds with partners remaining in close proximity during the entire year (Bellrose 1980). Males exhibit aggressive behavior toward conspecifics, thereby, reducing disturbance during foraging for females during the non-breeding season (Black & Owen 1989), aiding in
nest site acquisition (LeSchack, Afton & Alisauskas 1998), and defense of the family
group from intruding conspecifics during the brood rearing period (Sedinger, Eichholz &

MARKING AND REENCOUNT

Since 1986 we have captured brant in mass drives (up to 2000 individuals) during adult
remigial molt and individually marked them with U.S. Geological Survey metal bands
and colored tarsus bands (2.5 cm tall) engraved with a unique alphanumeric code
(Sedinger et al. 1997). At banding we were able to age brant as (1) young of the year, (2)
immature (1 year old) and (3) adult (2+ years old) by inspecting plumage characteristics
(Sedinger et al. 2008). We used cloacal examination to determine the sex of all
individuals (Owen 1980). We recorded recaptures of all previously marked brant.

Further, we weighed (± 10 g) recaptured adult brant and measured (± 0.01 mm) their
culmen and tarsus (Sedinger, Flint & Lindberg 1995). If an adult was measured in more
than one year we averaged measurements of their culmen and tarsus lengths. We did not
average adult mass measurements because mass could vary among years. During
banding drives we identified females who had nested in the current year through the
presence of a brood patch (Sedinger et al. 2008). We assumed all adult males captured
during brood rearing had attempted to breed even though males do not have brood
patches. Our reasoning for this assumption was that (1) most non-breeding brant molted
at distant locations, such as the north slope of Alaska (Bollinger & Derksen 1996), and
(2) < 2% of adult females captured lacked brood patches (A. G. Leach, unpublished data),
indicating that all adults we captured in banding drives had likely bred that year. We
considered all brant that had bred less than twice prior to the current year to be
inexperienced breeders, because in geese reproductive success increases until the third breeding attempt (Cooke, Bousfield & Sadura 1981; Sedinger, Lindberg & Chelgren 2001).

Periodically, during our study period, brant were captured and banded at other breeding colonies (Lindberg et al. 1998; Ward et al. 2004; Fondell et al. 2011) and molting sites on the arctic coastal plain of Alaska (Bollinger & Derksen 1996). Brant marked away from TRC provided us with a sample of birds with known histories potentially available to pair with females breeding at TRC. All handling and marking of animals at TRC was approved by Institutional Animal Care and Use committees at the University of Alaska Fairbanks and the University of Nevada Reno (most recent protocol number 00056).

During nest initiation we searched 48 randomly placed plots (50 meter radius) and documented all new brant nests at four day intervals once ~10% of nests had been initiated. Outside these plots we searched the entirety of TRC for nests attended by at least one marked brant. We confirmed the identity of parents at most nests on at least one additional visit. During the study we monitored 500–1000 brant nests annually. Nests were visited at least once during incubation and then daily at hatch to determine fates. We determined that a nest was successful if at least one gosling left the nest with parents. We estimated apparent nest success by dividing the number of successful plot nests by the total found on plots each year (Sedinger et al. 2006).

During the brood-rearing period we recorded observations and mating status of adult brant tending goslings from 3–7 meter towers (Sedinger, Lindberg & Chelgren 2001). Finally, we identified brant that were not associated with a nest or brood during a
particular observation; these individuals were non-breeding, had not yet initiated nesting, or were failed breeders. If an adult was seen at a nest, with a brood, or caught in a brood rearing drive we considered it to have bred in that year. Additionally, if the focal individual was not detected, but its mate was seen breeding we assumed the focal individual also bred.

We established mate changes using three scenarios. First, if an individual was observed with a banded mate in year $t$ that was different from a banded individual it was observed with previously. Second, if an individual was previously with a banded mate, but observed with an unmarked mate in year $t$ we determined a mate change had occurred. In this case we did not record a mate change if the mate had a USGS metal tarsal band in year $t$, because a small number (0.2%) of brant lose their color markers annually (Sedinger et al. 1997). Finally, if an individual was previously observed with an unmarked mate, but seen in year $t$ with a banded mate that was marked before the last sighting with the unbanded mate we assigned a mate change. To avoid potential pseudoreplication we only used females as the focal pair member in all analyses.

Statistical analyses

PATTERNS OF ASSORTATIVE MATING BY SIZE, BREEDING EXPERIENCE, AND AGE

For assessment of assortative mating by body size we included all brant known to have bred at TRC with a marked mate. We used intra-pair correlations of tarsus and culmen length to test for assortative mating by body size. We do not believe that brant assort directly by these specific structural measurements, rather these metrics are proxies for overall body size, an attribute by which they may select mates (Ankney 1977). For our
assessment of relationships of body mass of partners we only used cases where both members of the pair were measured during the same brood rearing period (i.e., year). If partners were weighed together in more than one year we randomly selected one set of masses for analysis.

For our investigation of correlation between age and breeding experience of partners we only used cases where a female had switched mates in the given year and the new mate was previously marked. The use of previously marked males allowed us to have a record of the previous breeding history of each individual in the pair prior to its establishment. We only compared the age and previous number of breeding attempts at TRC of each individual during their first nesting attempt together. We estimated correlations between morphological characteristics, age, and breeding experience between partners using Pearson’s product-moment correlation with the function cor.test in the stats package of program R 3.1.2 (R core team 2014).

FACTORS AFFECTING MATE FIDELITY
To assess factors affecting mate fidelity we used the Huggins closed capture multi-strata robust design module (MSRD) (Kendall & Nichols 2002) in program MARK (White & Burnham 1999). We used the program R (R core team 2014) package RMark (Laake 2013) to build and rank models. We included four strata in our analysis: (1) faithful (F), females that were paired with the same banded mate for at least two consecutive years, (2) females who had a new mate in year $t$ that was previously banded (C), (3) individuals that had a new mate in year $t$ that was not banded (U), and (4) individuals that had a banded mate in year $t$, but it was unclear if they had bred with their partner previously (M). The fourth strata allowed individuals who had switched to an unbanded mate the
opportunity to eventually transition back to the faithful state after we banded the new mate. We acknowledge that our approach combines mate changes due to both mortality and divorce. We chose to organize the analysis in this way because male dispersal precluded us from assigning divorce in many cases due to low detection of males not breeding at TRC. Thus, we were interested in factors affecting mate retention in general, because of the negative effects of mate change on individual fitness and colony productivity (Chapters 3 & 4).

We only assigned a stratum to females who bred at TRC in year $t$ (i.e., seen at a nest and/or caught in a banding drive) and were experienced breeders (i.e., at least two previous breeding attempts). If a female’s mate was not observed in year $t$, but she was observed with the same banded mate before and after year $t$ we assumed she was with the same mate in year $t$. Females we did not observe breeding in year $t$ were assigned a zero value in their capture history during that breeding season. If an individual was observed breeding, but its mate was not identified we assigned a “.” to the capture history for both secondary occasions in year $t$. By building capture histories with a “.”, we were able to censor individuals during years when they bred, but their mating status was unknown. This censoring precluded individuals from influencing transition probabilities in the given year, while allowing them to remain in the analysis. However, because we determined the mating status of 86% of brant breeding at TRC annually these censoring events were relatively infrequent.

We created the covariate HATCH which was assigned a value of “1” for successful nesting attempts (i.e., at least one gosling left the nest), “-1” for failed attempts and “0” if success or failure was undetermined. To assess the general productivity of
TRC in a given year we created two covariates (1) NEST SUCCESS and (2) MEAN GOS MASS. NEST SUCCESS was the apparent nest success on the colony each year. The covariate GOS MASS was the average mass of goslings in a given year. To assess the effects of mate familiarity on mate retention we created the variable BOND, which was the number of years a pair remained mated (new pairs were assigned a value of “0”). Finally, we created the variable MATE EXP, females breeding with a male that was apparently nesting for the first or second time were assigned a value of “-1”, if a female’s mate was breeding for third or greater attempt we assigned a value of “1”, otherwise a value of “0” was assigned. We only assessed the effects of BOND and MATE EXP for females that had switched to a marked mate. Our reasoning for this was twofold; we could only accurately assess (1) the duration of the pair-bond and (2) the previous experience of the mate when the new mate was already marked. In all models, we limited covariate effects to transitions of remaining faithful to the same mate or from breeding with a new marked mate to transitioning to being faithful to that mate. We z-standardized all continuous covariates (White & Burnham 1999).

Based on an earlier analysis (Chapter 4) we built a null model that allowed for variation in apparent survival by stratum, all possible transition probabilities, full annual variation in detection probabilities, variation in detection between secondary occasions, and full annual variation in recapture rates (c). We fixed transition probabilities from stratum F to M, C to M, U to F, M to U, and M to M to zero because these transitions are biologically impossible. We also built models that allowed for full time variation and a time trend on transition rates. We used the models with time variation to provide a comparison to our covariate models. Also, parameter estimates from models allowing for
time variation provided an opportunity to assess the hypothesis that rates of pair fidelity may be declining at TRC which could be exacerbating the decline in productivity the colony has experienced since 2000 (Sedinger et al. 2015). We assessed support for models by assessing ΔAIC values, model weights, and 95% confidence intervals for parameter estimates (Burnham & Anderson 2002). We did not adjust our parameter estimates for overdispersion because we know of no standard method for assessing overdispersion in MSRD models. However, estimates of $\hat{c}$ have generally been small (i.e., < 1.2) in other analyses of this dataset (Sedinger et al. 2007), and given the small set of non-nested models we considered, overdispersion likely resulted in little bias in precision of parameter estimates (Sedinger et al. 2011).

**Results**

**PATTERNS OF ASSORTATIVE MATING**

We observed 273 cases where experienced female brant switched mates and the new mate was previously marked. In these cases the age of the pair members was more strongly correlated ($r = 0.26, P < 0.001$; Fig. 5-1) than their previous number of breeding attempts at TRC ($r = 0.16, P = 0.007$; Fig. 5-2). As expected, of the cases when females switched to a previously marked mate 64% of the males had previously bred at TRC one or fewer times. We measured the culmen and tarsus of each partner in 1295 pairs. We weighed each partner in the same breeding season in 663 cases. We found weak, but statistically significant positive correlations between tarsus ($r = 0.07, P = 0.012$; Fig. 5-3) and culmen ($r = 0.07, P = 0.016$; Fig. 5-4) lengths of partners. However, body mass during brood-rearing was more strongly correlated among pair members than structural measurements ($r = 0.28, P < 0.001$; Fig. 5-5).
FACTORS AFFECTING MATE RETENTION

Our analysis included the breeding histories of 1890 experienced female brant. We recorded 325 failed and 1375 successful breeding attempts by females breeding with a familiar mate in year \( t \). We recorded 23 failed and 76 successful breeding attempts by females breeding with a new mate in year \( t \). For females that repaired with a banded male, we documented 190 cases where experienced females switched mates and the replacement male was an inexperienced TRC breeder and 109 instances in which the new mate was experienced. Apparent nest success ranged from 16–88% \((\bar{x} = 70\%)\) across years. The average mass of goslings at 30 days of age ranged from 501–881 grams \((\bar{x} = 649\text{ grams})\) across years.

The best supported model attempting to explain variation in mate retention included a time trend \((w_i = 0.98; \text{Table 5-1})\). Parameter estimates from the time trend model indicated that mate retention has declined for females breeding with both familiar \((\beta = -0.028 \pm 0.014; \text{Fig. 5-6})\) and unfamiliar mates \((\beta = -0.06 \pm 0.06)\) over the course of the study. The next best supported model \((w_i = 0.02; \text{Table 5-1})\) included the effect of male breeding experience on rates of mate retention in newly formed pairs. Contrary to a priori predictions, females breeding with a new, but experienced male had lower rates of mate retention \((\beta = -0.47 \pm 0.40)\) than those repairing with an inexperienced male. The model assessing whether mate retention continued to increase after a pair had been mated for one year did not improve fit substantially over the null model \((\Delta \text{AIC} = 0.10)\). Correspondingly, the 95% CIs for the parameter estimate of BOND strongly overlapped zero \((\beta = -0.07 \pm 0.44)\), further indicating a lack of support for the hypothesis that rates of mate retention improve with the duration of the pair bond. Although models with
average gosling mass and nest success improved model fit slightly over the null model (ΔAICs < 2; Table 5-1), 95% CIs on these parameter estimates substantially overlapped zero. These results did not support our a priori prediction that annual colony productivity would be positively related to mate retention. Parameter estimates from the null model indicated that females who bred with a familiar mate in year \( t \) had a 0.017 (± 0.006) probability of switching to a new, but previously marked male in year \( t+1 \) and a 0.087 (± 0.010) probability of switching to a new, but unbanded partner. Thus, the majority of female brant who switched mates (80%) repaired with an unmarked male.

**Discussion**

We found that the great majority of females (~80%) who changed mates remated with an unbanded partner. Because of our high encounter and marking rates of brant breeding at TRC (Sedinger, Lindberg & Chelgren 2001), the majority of these unmarked males likely had little or no previous breeding experience at TRC. Further, of females that switched mates and repaired with a previously marked male the majority (64%) of these males had bred at most one time at TRC. When combined, these results suggest that as many as 90% of female brant that switch mates repair with a male that is an inexperienced TRC breeder.

However, we did detect weak assortative mating by age and breeding experience, at least among female brant that repaired with a marked male (Figs. 5-1 & 5-2). However, brant seem to assort less strongly by age than barnacle geese where 42% of individuals acquire a new mate that is the same age (Black & Owen 1995). In contrast we found that partners in only 17% of newly formed pairs were the same age. Additionally, in 64% of rematings the female was older than the male versus 19% of
cases where the male was older. In 80% of cases the female had more nesting experience at TRC than her replacement mate. We acknowledge that because many of the males in our analysis were not hatched at TRC and were first banded as adults we may have been more likely to underestimate their ages than those of females. However, this potential methodological bias would not seem to apply to breeding experience, which was also only weakly correlated between partners, because the rates of detection among 4+ year old brant breeding at TRC are similar among the sexes (Sedinger, Lindberg & Chelgren 2001). Another explanation for the relatively weak within-pair correlation of age and breeding experience is the fact that males breeding at TRC have lower survival rates than females (Chapter 4). As such, the sex ratio among older brant is likely increasingly skewed towards females resulting in many older, experienced females likely being forced to mate with younger, inexperienced males. However, by using previously marked males we likely positively biased the correlation between at least, breeding experience of partners, because a large proportion of females that change mates acquire an unbanded male who is unlikely to have had any prior breeding experience at TRC.

Similar to studies of barnacle geese (Forslund & Larsson 1991; Black, Prop & Larsson 2007) we found no evidence that reproductive performance of the individual pair; nor, productivity of the colony in general was related to mate retention. The lack of an effect of reproductive performance on mate retention in brant is in contrast to many other species of birds (Dubois & Cezilly 2002). We are unsure why this is the case, but it could be related to the fact that most nesting failures in brant are the result of arctic fox predation or flooding during high tide events (Sedinger et al. 2015). Brant pairs do not have the ability to prevent either of these causes of nest failure. Thus, at least from the
female perspective it is unlikely she would have fared better with a different mate in the face of fox predation and therefore it would not be advantageous to switch mates after cases of nesting failure due to fox predation. However, we did find that rates of mate retention at TRC have declined during our study by as much as 7%, though our results do not shed light on the causation of this decline. Regardless, the reduced rates of mate retention by brant are likely further reducing recruitment at TRC, because most females suffer from reduced reproductive success, survival, and breeding probability after mate change (Chapters 3 & 4).

Similar to great tits (*Parus major*) (Culina et al. 2013) female brant have much lower rates of mate retention after the initial nesting attempt with the unfamiliar partner (Chapter 4). Here we found that females reached peak rates of mate retention (88%) after breeding with a male for the second time. However, our results did not clarify why newly formed pairs have such relatively low rates of fidelity. Contrary to a priori predictions we found that females who repair with an experienced male tend to have lower rates of mate fidelity. Perhaps this result suggests that because experienced replacement males are in short supply these males are more selective of their mates and more likely to divorce females after the first breeding attempt (Edward & Chapman 2011). We can think of no mechanism, based upon the current data from this population, which would not favor females retaining experienced males as mates.

Our finding of weak correlations between the structural metrics of brant partners is similar to the findings of studies of barnacle geese (*Branta leucopsis*) (Choudhury, Black & Owen 1992) and lesser snow geese (*Chen caerulescens caerulescens*) (Ankney 1977; Davies, Rockwell & Cooke 1988). However, Atlantic brant (*Branta bernicla*
have been shown to mate assortatively based on the thickness and ornateness of their necklaces (Abraham, Ankney & Boyd 1983), indicating that brant apparently can use phenotypic cues for mate selection or recognition, but typically do not do so in the case of body size. Weak assortative mating by structural size could result from several causes. These may include: inconsequential fitness benefits of having a large mate, high search costs because few large individuals are unpaired (Parker 1983), or factors such as age, breeding experience, and personality being more important for reproductive success (Black, Prop & Larsson 2007; Chapter 3). More work will need to be done on heritability of body size and selection on focal individual and mate body size throughout the life cycle of brant before we can determine the potential benefits of having a large mate. We suspect that the stronger correlation of mass between partners resulted from a shared environment effect where partners forage under the same conditions and raise the same number of goslings, as has been found in barnacle geese (Choudhury, Black & Owen 1992). Unfortunately, we did not have a sufficient sample of masses of partners before they mated to directly test this hypothesis.

In conclusion, we demonstrate that as many as 90% of female brant that change mates have to repair with an apparently inexperienced TRC breeder. Elsewhere, we found that female brant that breed with an inexperienced male fledge 35% goslings (Chapter 3). Thus, the vast majority of females changing mates likely suffer reduced reproductive output for at least the first breeding attempt with these new, inexperienced mates (Chapter 3). Therefore, we believe that the perennial mating system of brant is favored, at least partially, because experienced replacement mates are generally lacking and as a result, most females suffer reproductive costs of mate change.


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Anchorage, AK, USA.
Table 5.1. Performance of multi-strata robust design mark-recapture models investigating mate retention of experienced (breeding for at least the third time) at the Tutakoke River brant colony, 1990–2014. We included four strata in our analysis: (1) faithful (F), females that were paired with the same banded mate for at least two consecutive years, (2) females who had a new mate in year $t$ who was previously banded (C), (3) individuals that had a new mate in year $t$ who was not banded (U), and (4) individuals that had a banded mate in year $t$, but whose familiarity with we were uncertain (M). Effects of covariates were restricted to females transitioning from “F” in year $t$ to “F” year $t+1$ or females transitioning from having switched to a new previously banded male (C) year $t$ to “F” year $t+1$. The variable BOND indicates the duration (in years) of a pair’s association together. The variable NS is the apparent nest success at TRC in a given year. The variable GOS_MASS is the average mass (30 days) of goslings at TRC in year $t$. MATE_EXP indicates whether a females mate is an experienced TRC breeder (i.e., $\geq 2$ previous breeding attempts) or not. The covariate HATCH indicates whether or not a pair left the nest with at least 1 gosling or not.

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Figure 5-1. Scatterplot of male and female age within brant pairs (n = 273) at the Tutakoke River brant colony, (61°15’N, 165°37’W), Yukon-Kuskokwim Delta, Alaska, USA from 1990–2014. We only included pairs in which the female was breeding with a new mate in year t and the male was previously banded. The diameter of each symbol is proportional to the number of pairs (minimum = 1; maximum = 12). Dashed gray line represents a 1:1 relationship between male and female traits.
Figure 5-2. Scatterplot of male and female breeding experience within brant pairs ($n = 273$) at the Tutakoke River brant colony, (61°15′N, 165°37′W), Yukon-Kuskokwim Delta, Alaska, USA from 1990-2014. We only included pairs in which the female was breeding with a new mate in year $t$ and the male was previously banded. The diameter of each symbol is proportional to the number of pairs (minimum = 1; maximum = 30). Dashed gray line represents a 1:1 relationship between male and female traits.
Figure 5-3. Scatterplot of male and female tarsus (mm) within brant pairs ($n = 1295$) at the Tutakoke River brant colony, (61°15'N, 165°37'W), Yukon-Kuskokwim Delta, Alaska, USA from 1990–2014. The diameter of each symbol is proportional to the number of pairs (minimum = 1; maximum = 30). Red dashed line represents the best fit least squared regression between male and female tarsus.
Figure 5-4. Scatterplot of male and female culmen (mm) within brant pairs ($n = 1295$) at the Tutakoke River brant colony, (61°15′N, 165°37′W), Yukon-Kuskokwim Delta, Alaska, USA from 1990–2014. The diameter of each symbol is proportional to the number of pairs (minimum = 1; maximum = 80). Red dashed line represents the best fit least squared regression between male and female culmen.
Figure 5-5. Scatterplot of male and female body mass (g) during brood rearing within brant pairs weighed in the same breeding season ($n = 663$) at the Tutakoke River brant colony, (61°15′N, 165°37′W), Yukon-Kuskokwim Delta, Alaska, USA from 1990–2014. Red dashed line represents the best fit least squared regression between male and female body mass.
Figure 5-6. Rates of mate fidelity of breeding female brant from 1990–2014 at the Tutakoke River brant colony, (61°15’N, 165°37’W), Yukon-Kuskokwim Delta, Alaska, USA estimated from a Multi-state robust design mark-recapture model. Transition rates represent the probability that female brant that bred with a familiar mate in year $t$ remained with that mate in year $t+1$. Estimates are shown ± 95% confidence intervals.