RESEARCH ARTICLE

Fitness heterogeneity in adult Snow and Ross's geese: Survival is higher in females with brood patches

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ABSTRACT
Life-history theory broadly predicts a fitness tradeoff between costs of raising offspring and parental survival. Waterfowl with precocial young face particularly high costs of egg production, incubation, and brood-rearing, but not all evidence supports a corresponding decline in survival. We used multi-state mark–recapture–recovery models to estimate annual probabilities of survival, reported mortality, and transition between 2 states for female Ross's Geese (*Anser rossii*) and Lesser Snow Geese (*A. caerulescens caerulescens*) that attempted nesting near Karrak Lake, Nunavut, Canada. States were possession of a brood patch (high likelihood of successful nesting, "B") vs. no brood patch (attempted nesting but failed, "N"). Based on over 43,000 birds marked from 2000 to 2015, we found that females of each species with a brood patch had consistently higher probabilities of survival than those without, subsequent to capture in early August. Virtually all of the state differences in survival were due to nonhunting mortality. These patterns are consistent with the concept of variable individual quality impacting vital rates across multiple seasons. Higher survival of females with brood patches may be linked to greater breeding success but also to a hypothesized dominance advantage afforded to family groups of geese during winter. Moreover, although hunting pressure can play a key role in regulating Arctic goose populations, it does not appear to affect this relationship between inferred breeding state and survival. Instead, coincident with recent declines in harvest rate in these populations, higher individual quality of breeding females appears to outweigh the higher hunting vulnerability of presumed parents with young. The potential influence of social dominance in reducing natural winter mortality among families may thus contribute to the survival advantage seen in successful, relative to failed, breeders.

Keywords: Arctic, brood patch, cost of breeding, goose, heterogeneity, individual quality, survival

Hétérogénéité de la condition physique chez les adultes d'*Anser caerulescens caerulescens* et d'*A. rossii*: la survie est plus élevée chez les femelles ayant une plaque incubatrice

RÉSUMÉ
La théorie du cycle biologique prédit de manière générale un compromis sur la condition physique entre les coûts d'élevage des jeunes et la survie des parents. Les espèces de sauvagine ayant des jeunes nidifuges font face à des coûts particulièrement élevés de production des œufs, d'incubation et d'élevage des jeunes, mais les preuves n'appuient pas toutes un déclin de la survie correspondant. Nous avons utilisé des modèles multi-états de capture-marquage-recapture afin d'estimer les probabilités annuelles de survie, la mortalité rapportée et la transition entre deux états pour les femelles d'*Anser rossii* et d'*A. caerulescens caerulescens* qui ont fait une tentative de nidification près du lac Karrak, au Nunavut, Canada. Les états comprenaient la possession d'une plaque incubatrice (probabilité élevée de succès de nidification, "B") et l'absence de plaque incubatrice (tentative de nidification sans succès, "N"). En se basant sur plus de 43 000 oiseaux marqués entre 2000 et 2015, nous avons trouvé pour chaque espèce que les femelles ayant une plaque incubatrice avaient des probabilités de survie systématiquement plus élevées que celles sans plaque incubatrice, après leur capture au début d'août. Pratiquement toutes les différences de survie entre les états étaient causées par la mortalité non liée à la chasse. Ces tendances sont cohérentes avec le concept de l'impact d'une qualité individuelle variable sur les taux vitaux pendant plusieurs saisons. La survie plus élevée des femelles avec des plaques incubatrices peut être associée à un succès de reproduction plus élevé mais également à un avantage hypothétique de la dominance accordé aux groupes familiaux d'oies en hiver. De plus, bien que la pression de chasse puisse jouer un rôle clé dans la régulation des populations d'oies dans l'Arctique, elle ne semble pas affecter cette relation entre l'état reproducteur inféré et la survie. Au lieu de cela, coïncidant avec les baisses récentes du taux de récolte dans ces populations, la qualité individuelle plus élevée des femelles reproductrices semble compenser la plus grande vulnérabilité à la chasse des parents avec jeunes présumés. L'influence potentielle de la dominance sociale dans la réduction de la mortalité hivernale naturelle parmi les

famílles peut ainsi contribuer à l'avantage de survie observé chez les individus reproducteurs ayant connu du succès en comparaison de ceux ayant échoué la reproduction.

Mots-clés: Arctique, coût de la reproduction, hétérogénéité, oie, plaque incubatrice, qualité individuelle, survie

INTRODUCTION

A tradeoff between an organism's investment in reproduction and its survival is predicted by life-history theory (Roff 1992, Stearns 1992, McNamara and Houston 1996) operating through physiological mechanisms, such as changes in hormonal regulation, metabolism, and immune function (Harshman and Zera 2007). Reproductive costs may be reflected in either reduced survival probability or lowered future reproductive success (Williams 1966), and "optimal" clutch size in birds was historically believed to reflect this balance between maximizing current reproductive output and the long-term fitness costs of breeding to future survival and potential reproduction (Lack 1947, Monaghan and Nager 1997). Some experimental studies have indeed supported changes in parental survival with brood-size manipulation (e.g., Nur 1984, Dijkstra et al. 1990), but not all evidence supports this correlation (e.g., De Steven 1980, Williams et al. 1994). Using a theoretical model for long-lived birds, Erikstad et al. (1998) connected the reproduction/survival tradeoff to environmental variability, where conditions must exceed a (population-specific) threshold so that fitness benefits of breeding outweigh consequent survival cost.

Fitness costs in altricial species (i.e. those that are developmentally immature at hatching) include high energetic demands of chick provisioning (e.g., Saether et al. 1993, Golet et al. 2004). Yet future productivity or survival in precocial species—where young are more mature at hatching—may also be affected by investments in egg formation and subsequent chick-rearing (e.g., Seddon and Nudds 1992, Viallefont et al. 1995, Monaghan and Nager 1997). For waterfowl in particular, the energetic demands of egg production and incubation, and thus female body condition, can constrain reproductive output (e.g., Ankney and MacInnes 1978, Wiebe and Martin 2000, Bêty et al. 2003). Arctic-nesting geese use a combined capital–income reproductive investment strategy, whereby necessary egg-laying nutrients are accumulated both during spring migration and after arrival at the breeding grounds (Gauthier et al. 2003, Traylor 2010, Hobson et al. 2011). Nutrient acquisition and conditions encountered during spring migration are particularly important predictors of reproductive success for geese in northern breeding areas (Alisauskas 2002, Mainguy et al. 2002, Reed et al. 2004) and can carry over to affect fitness in subsequent seasons (Morrissette et al. 2010, Juillet et al. 2012, Sedinger and Alisauskas 2014).

Any survival costs of reproduction by Arctic-nesting geese could therefore be incurred during one or more

phases of the breeding season: pre-breeding resource acquisition, egg-laying, incubation, brood-rearing, or post-fledging accompaniment of young in their first year. Egg-laying and incubation entail high energy and time commitments (Monaghan and Nager 1997) and, in some waterfowl species, breeding females may face elevated risks of predation during these periods (Arnold et al. 2012, DuRant et al. 2013). Brood-rearing females may spend less time feeding and more time in vigilance when offspring are young (Seddon and Nudds 1992, Williams et al. 1994), and brood-rearing can affect body condition and mass-gain of females before molt and migration (Arnold and Howerter 2012, Fondell et al. 2013). Finally, the risk from harvest is the primary cause of adult mortality for some (Gauthier et al. 2001) but not all (Alisauskas et al. 2011, Calvert et al. 2017) goose populations, and hunting kill may be amplified for parents that accompany young (Giroux and Bédard 1986, Francis et al. 1992), although Arnold and Howerter (2012) also observed reduced survival in successfully breeding Mallards (*Anas platyrhynchos*), which do not accompany their offspring after fledging.

Yet not all recent evidence supports a long-term fitness cost to reproduction among Arctic geese (Williams et al. 1994, Gauthier et al. 2001). Indeed, other long-lived birds have shown a positive correlation between breeding and survival, likely linked to individual variation in quality and experience (Sanz-Aguilar et al. 2008, Robert et al. 2012, Kennamer et al. 2016). For geese in particular, in which young typically remain with their parents throughout their first year, greater dominance of family groups during winter may afford breeders a fitness advantage over nonbreeders (Black and Owen 1989a, Gregoire and Ankney 1990, Stahl et al. 2001, Jónsson and Afton 2008), and these effects may carry over into subsequent years (e.g., Black and Owen 1989b, Poisbleau et al. 2006). As a result, individuals may exhibit positively correlated reproductive success and survival because of variation in their quality, and not because of any causal link between these 2 demographic parameters (e.g., Sedinger and Alisauskas 2014, Kennamer et al. 2016). For the purposes of this study, we adopt the definition of "individual quality" of Wilson and Nussey (2010) as "the axis of phenotypic variation that best explains variance in individual fitness," although we acknowledge that we are not directly quantifying the links among genotype, environment, phenotype, and fitness (see Bergeron et al. 2011). In the absence of tradeoffs between survival and fecundity (e.g., in cases of important individual heterogeneity: Gimenez et al. 2018), we suggest that high-quality

individuals are those with positively correlated probabilities of surviving and breeding.

The rapid population growth of Arctic-nesting geese in recent decades has renewed interest in cross-seasonal demographic links and the management implications of interconnected vital rates (Morrissette et al. 2010, Alisauskas et al. 2011, Juillet et al. 2012, Sedinger and Alisauskas 2014). Despite their designation as "overabundant" and the implementation of special harvest measures (Batt 1997, CWS 2013), increases in abundance have continued among Lesser Snow Geese (*Anser caerulescens caerulescens*, hereafter LSGO) and especially among Ross's Geese (*A. rossii*, hereafter ROGO; Alisauskas et al. 2012b, CWS 2014). There is evidence of density-dependent limitation in productivity and site fidelity of both species (Slattery 2000, Traylor 2010, Alisauskas et al. 2011, Wilson et al. 2016, Ross et al. 2017), although the continued availability of intact breeding habitat outside the main colonies may be buffering some of this density-dependence (Traylor 2010, Alisauskas et al. 2011, Conkin and Alisauskas 2017). If there is a survival cost or benefit to raising young in these populations, then changes in productivity could carry over into a corresponding change in adult survival.

The Karrak Lake colony in the Queen Maud Gulf Migratory Bird Sanctuary, in Canada's central Arctic, is an important nesting area for both LSGO and ROGO (Kerbes et al. 2014), where the total abundance of breeders grew from about 400,000 in 1993 to >1,100,000 by 2010 (Alisauskas et al. 2012b), with especially high growth among ROGO. Whereas nonbreeding by adults results in earlier flightless molt in July (Jónsson et al. 2013) and permits earlier migration south, adult females banded in August remain flightless later and include both successful and failed (attempted) breeders, inferred respectively from the presence or absence of a brood patch. Contrasting the survival of these 2 groups of female geese therefore provides an opportunity to better understand the potential survival costs or benefits of incubating and successfully rearing young and accompanying them during migration (which would only apply to successful breeders), in isolation from any costs incurred during egg-production or laying (which all of these banded females would have experienced to some extent).

We evaluated the potential survival cost (or benefit) associated with possession of a brood patch in LSGO and ROGO from 2000 to 2015 at Karrak Lake using multi-state mark–recapture–recovery models combining databases of bandings, live recaptures, and dead recoveries. If brood-rearing and accompaniment of young during later stages of the breeding season entails a survival cost, females with a brood patch are predicted to show lower survival probability than those without. This effect might also vary between species (given that ROGO have been increasing more

rapidly than LSGO). We therefore modeled survival (1) differentially by breeding status (presence/absence of brood patch) and species, and (2) with both full time-variance and linear temporal trends. Given the importance of adult survival to population growth of these species (Rockwell et al. 1997, Alisauskas and Rockwell 2001, Alisauskas et al. 2011), additional insight about various drivers of survival, such as those related to breeding costs or benefits, will be relevant to decisions about ongoing attempts at population reduction (Leafloor et al. 2012).

METHODS

Banding, Recapture, and Recovery Data

As part of a long-term demographic study in the Queen Maud Gulf Migratory Bird Sanctuary, both LSGO and ROGO were captured and banded during late-summer molt in August. Birds caught at this time were those that attempted egg-laying or nesting, because non-nesters molt earlier in July and have regained flight by August (Jónsson et al. 2013, Wilson et al. 2016). At the time of capture, adult females were examined for the presence of an incubation patch, or brood patch, a defeathered ventral area associated with full brood patch development (Jónsson et al. 2006b). For the purposes of this paper, we refer to this defeathered ventral area as the "brood patch," although full brood patch development has been defined to also include epidermal thickening, temporarily increased vascularization of the epidermis, and thickening of connective tissue (Jones 1971). Brood patch presence was determined visually or tactilely during banding to ensure that its presence was detected even if sometimes covered by surrounding contour feathers. The defeathered brood patch in ducks and geese results from their plucking contour and down feathers during egg-laying and incubation and placing them in nests, acting as insulation in addition to that provided by vegetation incorporated into nests (McCracken et al. 1997, Jónsson et al. 2006a). Geese may continue to pluck ventral feathers during incubation to replenish those lost from nests, but this plucking stops if a nest is terminated before hatch (either through abandonment or predation), after which some refeathering occurs by failed nesters (Cooper 1978). Thus we used presence of a brood patch for geese captured July 30 to August 13 as a state indicator of successful incubation: females were inferred to have been relatively successful incubators and likely successful nesters (hereafter state B) or to have failed at nesting during egg-laying or early in incubation (state N) that year. We assumed that no nonbreeding geese were captured in these samples of flightless birds, as nonbreeders typically molt and regain flight earlier in the summer (Jónsson et al. 2013); thus we assumed that all birds captured (state N or B) had at least attempted to breed (see Methodological

Considerations section below for further details on this assumption). Females with a brood patch in August could thus represent either (1) failures in mid to late incubation, (2) those that lost their goslings before capture, or (3) those that had successfully reared goslings until capture. Because of the probability that not all females with brood patches had successfully produced young that survived into the subsequent winter to accompany their parents, we view this model-based hypothesis test to be conservative (i.e. any survival effects on birds with a brood patch are likely underestimated). Corroboration with independent nest success and age ratio data (below) supported the validity of our state categorization.

We used banding and recapture data for adult (after-hatch-year, AHY) females of both species from the large brood-rearing area north of Karrak Lake (between 99.5° and 101.5° latitude) from 2000 to 2015, as well as dead-recovery data (from all causes, although note that hunting comprised >97% of recoveries) reported to the Bird Banding Laboratory from July 2000 to February 2016. We defined each year as beginning at the time of banding (Jul–Aug) and ending the following June, before the next banding season; for instance, the year "2000" refers to the 12-mo period from July 1, 2000, to June 30, 2001. We used only data from birds marked with uniquely coded leg bands, as neck bands affect survival of Arctic-nesting geese (Alisauskas and Lindberg 2002, Alisauskas et al. 2006, Wilson et al. 2016).

Our dataset included a total of 45,020 banded female birds, 1,793 live recaptures, and 2,819 dead recoveries. By species, these included 29,748 banded ROGO and 15,272 banded LSGO, 1,106 live recaptures of ROGO and 687 live recaptures of LSGO, and recoveries of 1,676 ROGO and 1,143 LSGO. The total number of birds assigned to each breeding state (N vs. B) at the time of capture are shown (Figure 1).

Multi-state Live–Dead Encounter Models

We fit multi-state live–dead models (Barker et al. 2005) to our data, which allow live recaptures, state transitions, and dead recoveries to be combined in the same analysis. These models are defined by 4 key parameters that we estimated through Program MARK (White and Burnham 1999): survival (S, the probability that an individual alive in one year survives to the following year), recapture (p, the probability that an individual alive and present in the study area is captured), transition (ψ, the probabilities of transition between states [with brood patch, B, or without, N], conditional upon the individual being alive), and reported mortality (r, the probability that an individual that dies will be found and its band reported to the Bird Banding Laboratory); these were all estimated on an annual basis
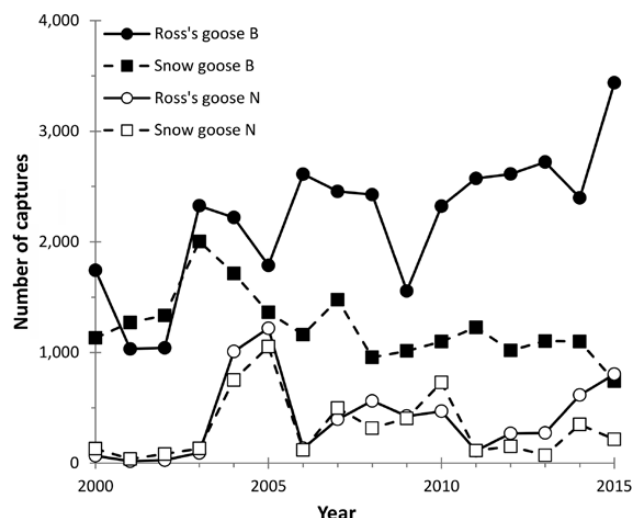
FIGURE 1. Annual capture totals for Ross's Geese and Lesser Snow Geese at Karrak Lake, Nunavut, from 2000 to 2015, by breeding state (successful breeding = B; failed breeding = N).

in our models. Note that because we used dead recoveries across the entire species range, our estimates of S can be considered representative of true survival, unbiased by permanent emigration (see Barker et al. 2005).

The most general model was $\{S(b*s*t)\ p(b*s*t)\ \psi_{B \to N}(s*t)\ \psi_{N \to B}(s*t)\ r(b*s*t)\}$, where all parameters vary across years (t), between species (s), and between brood and non-brood patch states (b). A goodness-of-fit test ("median ĉ," executed in Program MARK) on this model suggested no significant overdispersion of the data ($ĉ < 1$), so model selection was based on corrected AIC_c values (i.e. the Akaike Information Criterion adjusted for sample size but not for overdispersion; Akaike 1973, Burnham and Anderson 2002). Models were compared via difference in AIC_c values (ΔAIC_c, where the best-fit model is that with the smallest AIC_c value), as well as relative Akaike model weights (w_i), which sum to 1 and provide an index of support for each model relative to the total set of models (Burnham and Anderson 2002); cumulative weights for individual predictors were also explored as an alternative (see Methodological Considerations, below), as well as analysis of deviance for examining covariate effects. Note that because of the risk from lack of convergence of complex models, we fit each model to data several times using different initial parameter values to increase the probability that we arrived at the global (and not local) maximum of the likelihood. If deviance differed among these alternatives, we retained the model with the smallest deviance.

We built reduced models where we examined variation in each of the 4 key parameters, first allowing additive effects of species, state, and time, and subsequently testing

interactions between these factors. We determined the best structure of variation for one parameter at a time, and then combined the best-fit structures for each of these. Because our primary interest was in survival and transition probabilities, we first determined the best fit for r and p, and then retained those best-fit structures as we examined variation in S and ψ in more detail. Subsequently, we examined models where survival could vary linearly (*LinT*) across years (both additively and interactively by species and state) as linear changes in survival for these populations have been demonstrated in recent years (e.g., Alisauskas et al. 2011, Wilson et al. 2016). We also built some additional group-level covariate models as a preliminary analysis to explore influences of environmental/colony/physical conditions (where survival or transition probabilities could vary with mean local temperature, nest initiation date, abdominal fat, or colony abundance), but found no support for any of these on either S or ψ, nor any interaction with presence/absence of brood patch (i.e. all confidence intervals of effect size on the logit scale included 0), and therefore did not pursue these models further.

Interpretation of variation in r can be difficult because it is the quotient of 2 probabilities, $r = f/(1 - S)$ where f is known as the recovery probability, or the probability that the banded bird is shot, retrieved, and reported to the Bird Banding Laboratory (Brownie et al. 1985), so that f is expressed as a fraction of total mortality. Assuming that the probability of band reporting is equal between states of interest (and there is no a priori reason to assume such a difference), then recovery rate is a useful proxy of relative hunting pressure on each state. Thus, we estimate the derived parameter, $\hat{f}$, as

$$\hat{f} = \hat{r}(1 - \hat{S}) \text{ and}$$

$$\widehat{\text{var}}\left(\hat{f}\right) \approx \hat{r}^2 \cdot \widehat{\text{var}}\hat{S} - 2\left[\left(1 - \hat{S}\right)\hat{r}\right] \cdot \widehat{\text{cov}}(\hat{S}, \hat{r}) + \left(1 - \hat{S}\right)^2 \cdot \widehat{\text{var}}(\hat{r})$$

for each species and state of brood patch presence (Cooch and White 2019:B34).

Of the numerous candidate models that we considered, many were similarly ranked according to AIC$_c$ and relative AIC$_c$ weights. To deal with the inferential uncertainty arising from similar support for competing models, we used a model-averaging approach, as it is one that is often recommended for multi-model inference (e.g., Burnham and Anderson 2002, Burnham et al. 2011). Yet, some authors caution against drawing strong inference from very closely ranked models, especially if they differ by <2AIC and by only a single parameter (Arnold 2010), as is the case here for variation in reported mortality (r). As one alternative, the cumulative weight of evidence for a particular variable can be used to further inform its importance to variation in a given parameter (Burnham and Anderson 2002, Arnold 2010). For instance, although brood-patch variation in reported mortality was included in the top-ranked model (see Results below), the sum of AIC$_c$ weights for models including $r(b)$ {$\sum w$AIC$_c$ = 0.274} is lower than the sum of weights for models where reported mortality is invariant ($r.$) {$\sum w$AIC$_c$ = 0.548}. We therefore agree that conclusions should be drawn carefully, particularly regarding the effect of brood patch on reported mortality, yet maintain that the model-averaging approach taken here should sufficiently capture the important sources of variation in the parameters we estimated.

RESULTS

Several of our candidate models ranked very closely in AIC$_c$ values, and we therefore used model-averaged parameter estimates for inference (based on relative AIC$_c$ weights, w_i; Burnham and Anderson 2002; see Table 1). We used confidence intervals on effect sizes to infer the importance of each source of variation for each of the 4 key parameters, as well as the relative rankings of candidate models as supplemental information. A full table of all models considered is provided as supplementary information (Appendix Table 2).

Recapture probability p varied across years and also among groups, with higher p for females with brood patches than without, and higher p for LSGO than ROGO, but parallel temporal fluctuations between the 2 species (Figure 2A). Mean recapture estimates for birds with brood patches ranged 0–0.15 for ROGO and 0–0.27 for LSGO, but were very close to 0 throughout for females of either species without brood patches.

Transition probability ψ varied dramatically among years, covering the full range from 0 to 1. Estimates of ψ were parallel among species but with opposite species effects for the 2 directions: within a given year, transitions from successful- to failed-breeder status ($\psi_{B \to N}$) were higher for LSGO than ROGO, whereas transitions from failed- to successful-breeder status ($\psi_{N \to B}$) were higher for ROGO than LSGO (Figure 2B). An a posteriori comparison of $\psi_{N \to B}$ over the interval t to $t+1$ vs. an independent measure of mean annual apparent nest success in year $t+1$ (an index of group breeding success, measured as the proportion of detected nests that produce at least one gosling) supported our use of brood patch as a reasonable measure of relative success of incubating females (Figure 3A). Age ratios at the time of fledging (estimated from annual mass-capture of flightless geese between August 1 and 15, close to attainment of flight by both ages; Ross et al. 2017) were similarly correlated with $\psi_{N \to B}$, providing further support for our state categorization (Figure 3B).

TABLE 1. The top 10 models (general model in **bold**) describing multi-state live–dead encounters of female Ross's Geese and Lesser Snow Geese at Karrak Lake, Nunavut, from 2000 to 2015. Parameters estimated were annual probabilities of survival (S), recapture (p), transition between successful (B) and failed (N) breeding states ($\psi_{B\to N}$ and $\psi_{N\to B}$), and reported mortality (r). Subscripts indicate variation with breeding state (b), species (s), year (t), and additive (+) or interactive (*) combinations of these. For each model are shown the difference in sample size–corrected Akaike Information Criterion relative to the top model (ΔAIC_c), relative AIC_c weight (w_i), number of parameters (K), and deviance. A full table of model results is available in Appendix Table 2. The minimum AIC_c value (i.e. for the top model) was 52,103.22.

Model	ΔAIC_c	w_i	K	Deviance
S (b+s*t) p (b+s*t) $\psi_{B\to N}$ (s+t) $\psi_{N\to B}$ (s+t) r(b)	0.000	0.274	98	51,906.78
S (b+s*t) p (b+s*t) $\psi_{B\to N}$ (s+t) $\psi_{N\to B}$ (s+t) r(.)	0.359	0.229	97	51,909.15
S (t+b)*s) p (b+s*t) $\psi_{B\to N}$ (s+t) $\psi_{N\to B}$ (s+t) r(.)	0.817	0.182	98	51,907.60
S (b+s*t) p (b+s*t) $\psi_{B\to N}$ (s+t) $\psi_{N\to B}$ (t) r(.)	2.019	0.100	96	51,912.82
S (b+s*t) p (b+s*t) $\psi_{B\to N}$ (s+t) $\psi_{N\to B}$ (s+t) r(s)	2.123	0.095	98	51,908.91
S (b+s*t) p (b+s*t) $\psi_{B\to N}$ (s+t) $\psi_{N\to B}$ (s*t) r(.)	2.469	0.080	111	51,883.13
S (b+s*t) p (b+s*t) $\psi_{B\to N}$ (t) $\psi_{N\to B}$ (s+t) r(.)	4.995	0.023	96	51,915.80
S (b+s*t) p (s*t) $\psi_{B\to N}$ (s+t) $\psi_{N\to B}$ (s+t) r(.)	7.663	0.006	96	51,918.46
S (b+s+t) p (b+s*t) $\psi_{B\to N}$ (s+t) $\psi_{N\to B}$ (s+t) r(.)	7.895	0.005	82	51,946.81
S (b+s*t) p (b+s*t) $\psi_{B\to N}$ (s*t) $\psi_{N\to B}$ (s+t) r(.)	9.164	0.003	111	51,889.83
S (b*s*t) p (b*s*t) $\psi_{B\to N}$ (s*t) $\psi_{N\to B}$ (s*t) r(b*s*t)	156.844	0.000	248	51,761.30

Survival probability S varied across years and among groups (Table 1, Figure 2C), where the top models supported largely additive effects of brood patch for both species. Females with a brood patch had higher survival probabilities than those without a brood patch for both ROGO and LSGO, although there was some overlap of confidence intervals; effect size for brood patch presence in the best-fit model differed from zero (logit-link BetaS_b: mean = 0.517, 95% CI: 0.036–0.997). Survival varied across years independently for the 2 species, but with no clear directional tendency (Figure 2C). There was no support for models with a linear time-trend among years, regardless of brood patch or species (all confidence intervals for effect size on the logit scale included zero); ΔAIC_c was 295.27 for the best-fit model with linear time-trend {S ($b*s*LinT$) p ($b+s*t$) $\psi_{B\to N}$ ($s+t$) $\psi_{N\to B}$ ($s+t$) $r(.)$}.

There was little support for variation in reported mortality probability, r, across years or between species, but species-variance did appear among the top models (with marginal support for $r_{ROGO} > r_{LSGO}$). In contrast, an effect of brood patch presence (with higher reported mortality for those with, than without, a brood patch) was supported in the top-ranked model {$S(b+s*t)$ $p(b+s*t)$ $\psi_{B\to N}(s+t)$ $\psi_{N\to B}(s+t)$ $r(b)$}, where mean values were r_B = 0.167 (SE = 0.026) and r_N = 0.120 (SE = 0.011), although this effect was not strongly supported among most other top models; the logit-link effect size for breeding status effect on r in this top model was 0.385 (95% CI: −0.144 to 0.915). See the Methods (above) for a discussion of relative support for these effects. Recovery probability, f, was higher for females without a brood patch in the following hunting season than for those with a brood patch (Figure 2D). However, the mean difference in recovery rate for Ross's

and Snow geese was only 0.002 and 0.001, respectively, over the study, whereas the corresponding mean difference in survival between strata were 0.027 and 0.028. Thus, the difference in survival appeared to be due to nonhunting causes rather than to hunting.

DISCUSSION

We found that both Lesser Snow Goose and Ross's Goose females with brood patches had higher survival than females whose nesting presumably failed early in the season and so had stopped maintaining a brood patch. This pattern held across a 15-yr time span, despite some variation in mean survival over this period. Our findings therefore support the model of positive life-history correlations, which we suggest may be linked both to variations in individual "quality" (e.g., van Noordwijk and de Jong 1986, Blums et al. 2005) and to direct survival advantages gained by successfully breeding females.

Survival, Dominance, and Individual "Quality"
Traditional ecological theory predicts a negative relationship between current reproductive effort and future fitness, such that breeders are expected to suffer a survival cost relative to nonbreeders (Roff 1992, Stearns 1992, McNamara and Houston 1996). Yet alternative theories have instead supported positive correlations between life history traits, driven by variation in the "quality" of individual organisms (van Noordwijk and de Jong 1986, Blums et al. 2005, Arnold et al. 2012), as long as these traits are closely linked to fitness (Wilson and Nussey 2010). Both hypotheses support carryover effects across phases of the life cycle, resulting in strong links between seasonal vital rates (e.g., Marra et al. 1998, Sillett et al. 2000, Bearhop
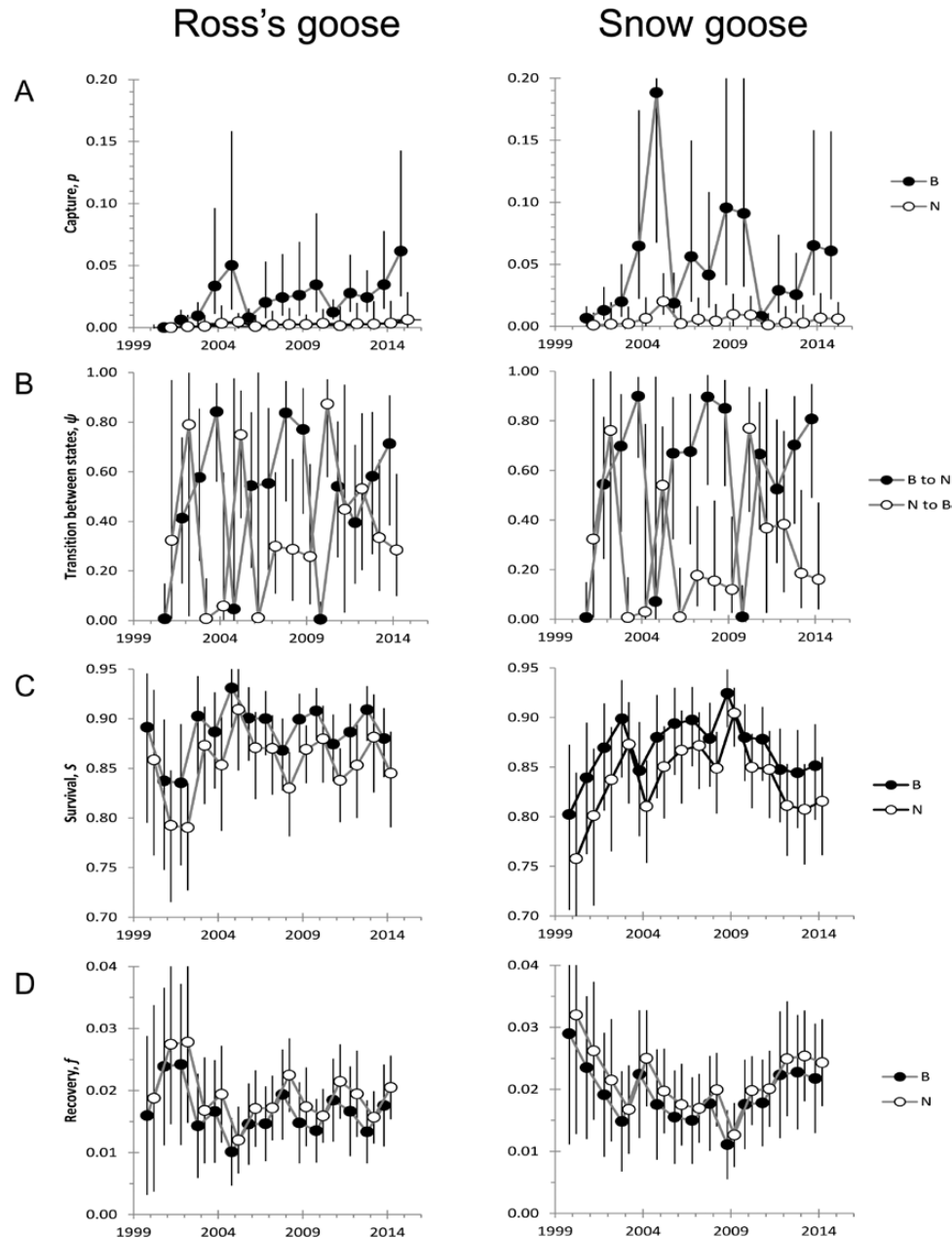
FIGURE 2. Annual estimates [mean (±SE)] of (**A**) recapture probability (*p*), (**B**) survival probability (*S*), (**C**) breeding-state transition probabilities (ψ) between failed and successful breeding states ($\psi_N \to_B$ and $\psi_B \to_N$), and (**D**) recovery probability (*f*), for Ross's Geese (ROGO, left column) and Lesser Snow Geese (LSGO, right column) breeding at Karrak Lake, Nunavut, from 2000 to 2015. Years indicated represent the 12-mo period from July to June, such that for example the estimate for 2000 covers the period from July 2000 through June 2001; estimates for the last year (2015–2016) were not estimable and are not shown. Estimates are derived from model-averaged values across multiple models, because of numerous closely ranked models.

et al. 2004, Juillet et al. 2012, Sedinger and Alisauskas 2014). Thus, despite long distances between seasonal habitats of many waterfowl populations, nutritional demands and environmental conditions in one season often entail important fitness consequences later in the life cycle (e.g., Drent et al. 2003, Morrissette et al. 2010, Juillet et al. 2012, Sedinger and Alisauskas 2014, Harms et al. 2015). For both

LSGO and ROGO at Karrak Lake, recent declines in body condition of breeding females have been linked to density-dependent regulation during spring migration (Traylor 2010), with negative consequences for recruitment (Ross et al. 2017, 2018).

Some recent experimental manipulations of nest success in long-lived birds have supported significantly
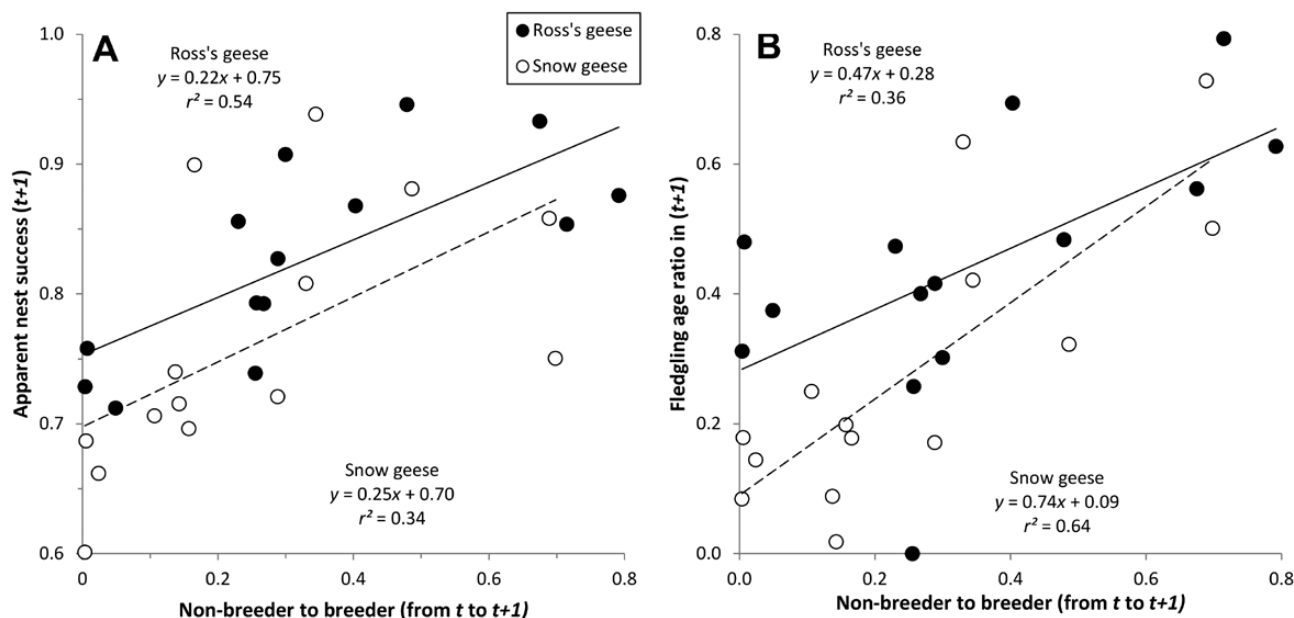
FIGURE 3. The relationship of model-averaged estimates of the probability of transition from failed to successful breeder states ($\psi_{N \to B}$) in from year t to year t+1 relative to (**A**) mean annual apparent nest success (an index of group breeding success, measured as the proportion of detected nests that produce at least one gosling) in year t+1, and (**B**) age ratios at fledging (ratio of fledglings:adults, estimated from annual mass-capture of flightless geese between August 1 and 15, close to attainment of flight by both ages), for Ross's Geese (ROGO) and Lesser Snow Geese (LSGO) nesting at Karrak Lake, Nunavut, from 2000 to 2015. Note that the 2 boundary estimates of $\psi = 1$ were from the first year of the study (2000).

negative associations between breeding success and survival. Through direct alteration of nest success of ROGO at Karrak Lake, Drake et al. (2018) showed that females with manipulated nest failures survived better than those with successful nests. This appears to contradict our findings, but the sample of birds drawn from the population in each study was quite different. For example, nests of female Ross's Geese studied by Drake et al. (2018) were manipulated during late incubation, and so did not include early nest failures. Consequently, both experimental and control birds were still nesting during late incubation and were likely of higher and less variable individual quality in that study than in this one. Geese in our study failed much earlier during nesting, and our failed-breeder class might also have included a small portion of nonbreeders (see Methodological Considerations below). Thus, we suggest that the paradox from opposite outcomes of the 2 studies is related to differences in the variance and degree of heterogeneity in female quality, and its consequences for successful nesting and subsequent survival probability. Another important difference is that Drake et al. studied neck-banded birds exclusively, which may have further reduced heterogeneity in the ability of nesting females not only to complete incubation but perhaps also in breeding. Neck bands approximately double mortality in both Ross's Geese (Alisauskas et al. 2006, 2012a; Caswell et al. 2012) and Snow Geese (Wilson et al. 2016) that nest near Karrak Lake. As well, breeding propensity by Greater Snow Geese

(*Anser caerulescens atlantica*) was 48% lower among neck-banded geese than it was for those without neck bands (Reed et al. 2005). Thus, Drake et al.'s (2018) experiment might have been focused on birds with a truncated distribution of individual fitness, if neck bands also reduced breeding propensity in Ross's Geese, while our results pertain to unmanipulated geese. Their experimental manipulation also found higher hunting recovery probabilities among failed nesters, which they interpreted as evidence for greater vulnerability of breeders to non-human causes (e.g., disease, predation) rather than to hunting mortality (Drake et al. 2018).

An experiment similar to that by Drake et al. (2018) on nest success in a long-lived seabird (Black-legged Kittiwake, *Rissa tridactyla*) also supported higher survival for manipulated failed breeders than for successful breeders or naturally failed breeders (Golet et al. 2004). Yet it should be noted that, in these studies, survival was measured from incubation onward, such that early-season mortality risks (e.g., time and energy costs of egg production and incubation; Monaghan and Nager 1997, Arnold et al. 2012) could be more important than when survival effects are thought to begin after incubation, as in our current study. Thus, experimental results may be contingent on the degree to which individual heterogeneity occurs in the sample of manipulated birds, such as heterogeneity in nest-success rates among the females that attempted breeding (B) in our study. We suggest that

such heterogeneity declines as the population of nesting birds is reduced through attrition as nest failures accumulate through incubation.

For geese, in which family groups normally remain together throughout the first year of gosling life, social dominance likely plays an important role in affording breeders an advantage that outweighs the potential costs of producing and raising young. Family groups are dominant over single birds or nonbreeders when competing for resources during nonbreeding seasons, through aggressive behaviors and greater access to preferred positions in feeding flocks (Black and Owen 1989a, Gregoire and Ankney 1990, Black et al. 1992). Social dominance of family groups over pairs or individuals has been confirmed for these 2 species in a study that revealed greater family cohesion, and thus greater dominance, among LSGO than ROGO during winter (Jónsson and Afton 2008). Our data supported similar advantages in both species for brood patch females over those without, likely because any family breakup in either species would occur well after the time of capture. Social status during winter also carries over to subsequent seasons' fitness, as dominant females or those with prolonged parental care are more likely to return to breed the following year (Black and Owen 1989b, Stahl et al. 2001), and body condition in one winter can influence dominance status in subsequent seasons (Poisbleau et al. 2006). This can result in positively correlated traits—and thus covariation in individual quality—across seasons (see also Sedinger and Alisauskas 2014, Kennamer et al. 2016). Although not all females with a brood patch would necessarily be accompanied by young through the winter (i.e. because of breeding failure before capture or juvenile mortality), this social dominance associated with family size in geese may further widen the gap in survival between successful vs. unsuccessful nesters. We are not aware of a direct test of the hypothesis that larger family size in geese confers survival advantages on the parents, although we predict that it does, by further increasing heterogeneity in individual quality and inclusive fitness. Nonetheless, we acknowledge that we cannot conclusively differentiate between intrinsic individual quality and the benefits of group living that are common to geese.

Mortality, Recapture, and Transition Probabilities

Successfully breeding adults might face additional survival costs if accompaniment by young exposes them to increased hunting risk, as has been suggested elsewhere (e.g., Giroux and Bédard 1986, Francis et al. 1992, Madsen 2010; although see Drake et al. 2018). However, differences between females with and without brood patches in recovery probability, f, were too small to account for the differences in overall survival. Although hunting mortality can be a major fraction of total mortality in Arctic-nesting geese (e.g., Rockwell et al. 1997, Gauthier et al. 2001; see also Juillet et al. 2012 for hunting effects on recruitment), this contrast implies that current harvest rate is too low to have any measurable survival consequence (see Alisauskas et al. 2011, Dufour et al. 2012, Calvert et al. 2017).

This apparent incongruity may also serve as further support for the importance of individual quality in driving relationships between reproduction and survival. In a previous study of LSGO vital rates, Francis et al. (1992) similarly found both higher survival and recovery rates of breeding relative to nonbreeding adults, which they linked to nonbreeding birds being in worse condition and therefore more susceptible to natural (i.e. nonhunting) causes of mortality. Thus, while hunting accounted for a greater fraction of total mortality for successful than failed breeders in our study, the concurrent higher total survival for successful breeders suggests both (1) that hunting mortality does not significantly influence survival probability (and/or there is a compensatory response to increased hunting mortality), and (2) that variations in individual experience and quality can drive such correlations between vital rates (e.g., Sedinger and Alisauskas 2014, Kennamer et al. 2016).

Capture probabilities were much lower for failed than successful breeders for both ROGO and LSGO, likely because some females with no brood patch may have failed early in incubation or even before capture and joined flightless flocks of nonbreeding geese (see Methodological Considerations below). Breeders failing early in incubation would likely regain flight earlier and remain less available for capture (Figure 2A) than more successful breeders with brood patches, many of whom would be accompanied by flightless young and thus much more prone to capture. While lower capture probability for females without brood patches might seem to be a problem, we suggest that exclusion of such birds that may have gained flight earlier than we were able to sample is an analytical benefit. Specifically, both groups of geese were flightless and so on the same molt schedule compared to females without brood patches that were not captured and probably joined the earlier-molting, nonbreeding groups of geese. In this way, a confounding effect of different molt schedules (and thus exposure to different weather or plant phenology) was avoided.

Estimated transition probabilities between successful- and failed-breeding states were highly variable and of low precision, as expected with such low capture probabilities. Transitions from failed- to successful-breeder states appeared to be generally higher among ROGO than LSGO, while successful-to-failed transition estimates were higher for LSGO than ROGO; this is consistent with evidence that ROGO experienced a more rapid increase (Leafloor et al. 2012, CWS 2014), greater nesting success (Ross et al. 2017), and greater nesting site fidelity (Wilson et al. 2016) than LSGO, all during a similar time period to our study.

Note, however, that the low precision of these estimates suggests cautious interpretation of these contrasts.

Methodological Considerations

Long-lived species such as geese are known to forego breeding in some years (Viallefont et al. 1995). As a result, some birds in our failed breeder (N) state could have joined an unobservable nonbreeding state (i.e. those that did not attempt to breed in a given year). The far lower capture probabilities for birds with no brood patch compared to those with a brood patch suggests that proportionally more females with no brood patch may have joined flocks composed of nonbreeding females. We attempted to address this problem by considering a third state to our models representing unobservable ($p = 0$) nonbreeders, thereby restricting our failed (N) state exclusively to birds that attempted to breed but were unsuccessful. However, because of the very low capture and recovery probabilities for all states, 3-state models never converged reliably. We therefore proceeded with the 2-state model outlined above, but caution that our results should be interpreted with this untested assumption in mind.

Because most geese in our study were marked as adults, we could not assess the importance of age or previous breeding experience to our evaluation of the survival costs or benefits of breeding in these populations. Reduced survival of first-time breeders, and thus presumably an elevated cost of reproducing among younger and inexperienced individuals, has previously been demonstrated for LSGO (Francis et al. 1992, Viallefont et al. 1995) as well as other long-lived birds (e.g., Cam and Monnat 2000, Barbraud and Weimerskirch 2005, Sanz-Aguilar et al. 2008). Although we did not have such data available here, more precise data on the age structure of marked geese could therefore help to isolate age effects from other sources of variation in survival. Information on breeding history could similarly corroborate (or contradict) the importance of individual quality and, if available, could be incorporated in a more complex multi-state model allowing for estimation of breeding propensity as well as success. Unfortunately, we could not address nonbreeding before capture, and non-captures during the study could have reflected either nonbreeding or breeding in a different location, preventing distinction of nonbreeding from breeding following dispersal.

Our preliminary covariate-model analyses provided no support for environmental or physical condition effects on survival or transition probabilities; there was far greater support for time variability in survival due to unmeasured variables than to the covariates considered from factors encountered during the breeding season. This is in line with the hypothesis that environmental covariates have minimal influence on adult survival in long-lived species (e.g.,

Morris and Doak 2004, Bjørkvoll et al. 2016). Instead of the group-level covariates that we applied broadly to entire species/state groups in the preliminary analyses (and for which we found little support), additional measures of individual variation could enhance future survival estimates, if individual quality is indeed an important predictor of the survival costs of reproduction. In fact, 2 recent studies of survival in breeding vs. nonbreeding seabirds (discussed above) emphasize the need to consider individual factors driving reproductive status, and not just the state itself (Golet et al. 2004, Robert et al. 2012). Collection of supplementary data on the quality (e.g., body condition) of each female at the time of marking would permit future analyses to incorporate these measures as individual covariates in models of survival and brood patch (e.g., White and Burnham 1999, Blums et al. 2005), and thus to clarify the possible mechanisms for links between these 2 parameters.

In ducks, numerous studies have supported reduced survival of breeders relative to nonbreeders, linked to such factors as the temporal and energetic costs of raising young and consequent increases in predation or migration mortality (e.g., Brasher et al. 2006, Arnold and Howerter 2012, Arnold et al. 2012, DuRant et al. 2013; although see Kennamer et al. 2016). But whereas young ducks remain with their parents only for several weeks (e.g., Afton and Paulus 1992), geese remain in family groups throughout their first year, and thus can benefit from dominance advantages afforded by family size. Given the apparent importance of social interactions to overwinter survival (Gregoire and Ankney 1990, Stahl et al. 2001, Jónsson and Afton 2008; above), this difference in family structure may largely account for the contrast between our findings and survival estimates for many ducks and other birds.

Conclusion

Rapid population growth of light geese and the corresponding alteration of Arctic and sub-Arctic nesting habitats resulted in their designation as "overabundant" and the implementation of additional harvest measures (Batt 1997, 1998; CWS 2013). Although there was an initial surge in hunting immediately after initiation of these special measures, relative harvest rate has not kept pace with increasing abundance (Alisauskas et al. 2012a, Johnson et al. 2012) and is particularly low for geese breeding in the Arctic (Alisauskas et al. 2011, Dufour et al. 2012). Alisauskas et al. (2012b) suggested that these populations are regulated by both survival at the metapopulation scale and local recruitment rates at the colony scale, supporting the importance of vital rate interactions across temporal and spatial scales.

Ross's Geese and Lesser Snow Geese nesting at Karrak Lake showed positively correlated breeding status (as indexed by brood patch presence) and survival, consistent with variations in individual quality that carry across

seasons (Van Noordwijk and De Jong 1986, Sedinger and Alisauskas 2014). Moreover, somewhat higher hunting-recovery probabilities of females with brood patches did not translate into any reduction in survival for either species. Links between inferred breeding status and survival thus appear to be more of a function of variation in individual quality than a direct cause and effect, and support other evidence that hunting mortality currently has a negligible effect on survival for both of these populations (e.g., Alisauskas et al. 2011), regardless of their breeding status.

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Appendix Table 2. Full list of models describing multi-state live–dead encounters of female Ross's Geese and Lesser Snow Geese at Karrak Lake, Nunavut, from 2000 to 2015. Parameters estimated were annual probabilities of survival (S), recapture (p), transition between successful (B) and failed (N) breeding states ($\Psi_{B \to N}$ and $\Psi_{N \to B}$), and reported mortality (r). Subscripts represent parameter variation with breeding state (b), species (s), year (t), linear time trend (*LinT*), and additive (+) or interactive (*) combinations of these. For each model are shown the difference in sample size–corrected Akaike Information Criterion (AIC$_c$) relative to the top model (ΔAIC$_c$), relative AIC$_c$ weight (w_i), number of parameters (K), and deviance.

Model	ΔAIC$_c$	w_i	K	Deviance
{S (b+s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(b)}	0	0.274	98	51,906.78
{S (b+s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	0.359	0.229	97	51,909.15
{S (s*t)(b*s) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	0.817	0.182	98	51,907.60
{S (b+s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(t) r(.)}	2.019	0.100	96	51,912.82
{S (b+s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(s)}	2.123	0.095	98	51,908.91
{S (b+s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s*t) r(.)}	2.469	0.080	111	51,883.13
{S (b+s*t) p (b+s*t) ΨBtoN(t) ΨNtoB(s+t) r(.)}	4.995	0.023	96	51,915.80
{S (b+s*t) p (s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	7.663	0.006	96	51,918.46
{S (b+s+t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	7.895	0.005	82	51,946.81
{S (b+s*t) p (b+s*t) ΨBtoN(s*t) ΨNtoB(s+t) r(.)}	9.164	0.003	111	51,889.83
{S (s*t)(b*s) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(b)}	10.648	0.001	99	51,915.42
{S (b+s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(t) r(b)}	11.326	0.001	97	51,920.12
{S (s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(b)}	11.618	0.001	97	51,920.41
{S (b+t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	13.154	0.000	81	51,954.07
{S (b+s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(t)}	14.328	0.000	112	51,892.98
{S (b+s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(s+t)}	18.741	0.000	113	51,895.38
{S (s+t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	21.103	0.000	81	51,962.02
{S (b+s*t) p (b+s*t) ΨBtoN(t) ΨNtoB(t) r(.)}	24.117	0	95	51,936.93
{S (s+b*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	25.321	0	97	51,934.11
{S ((b+s)*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	25.474	0	113	51,902.12
{S (b+s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(b+s+t)}	26.276	0	114	51,900.91
{S ((b*t)(b*s)) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	27.368	0	98	51,934.15
{S (b+s*t) p (b+s*t) ΨBtoN(t) ΨNtoB(s+t) r(b+s+t)}	27.568	0	113	51,904.21
{S ((b*t)) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	29.043	0	96	51,939.84
{S (s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	29.662	0	96	51,940.46
{S (b*s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	34.080	0	128	51,880.56
{S (b+s*t) p (b+s*t) ΨBtoN(s) ΨNtoB(s+t) r(.)}	36.996	0	83	51,973.90
{S (b+s*t) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(b+s*t)}	41.431	0	129	51,885.90
{S (b+s*t) p (b+t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	58.358	0	82	51,997.27
{S (b+s*t) p (b+s+t) ΨBtoN(s+t) ΨNtoB(s+t) r(b+s+t)}	58.963	0	100	51,961.73
{S (b+s*t) p (b+t) ΨBtoN(s+t) ΨNtoB(s+t) r(b)}	60.365	0	83	51,997.27
{S (b+s*t) p (b+s+t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	64.760	0	83	52,001.67
{S (b+s*t) p (b+s+t) ΨBtoN(s+t) ΨNtoB(s+t) r(b+s)}	65.460	0	85	51,998.35
{S (b+s*t) p (b+s+t) ΨBtoN(s+t) ΨNtoB(s+t) r(b+s*t)}	66.103	0	115	51,938.72
{S (b*s*t) p (b+s+t) ΨBtoN(s+t) ΨNtoB(s+t) r(b+s+t)}	81.385	0	115	51,954.01
{S (b+s+t) p (b+s+t) ΨBtoN(s+t) ΨNtoB(s+t) r(b+s+t) ALL ADDITIVE}	82.358	0	85	52,015.25
{S (b*t+s) p (b+s+t) ΨBtoN(s+t) ΨNtoB(s+t) r(b+s+t)}	93.653	0	100	51,996.42
{S (b+s*t) p (b+s) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	113.899	0	69	52,078.90

Appendix Table 2. *continued*

Model	ΔAIC_c	w_i	K	Deviance
{S B:B(g*t) S N:N(g*t) p B:B(g*t) p N:N(g*t) ΨBtoN(g*t) Ψ NtoB(g*t) r B:B(g*t) r N:N(g*t) -GENERAL}	156.844	0	248	51,761.30
{S (b*s*LinT) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	295.269	0	72	52,254.25
{S ((b+s)*LinT) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	306.535	0	70	52,269.53
{S (b+s*LinT) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	319.177	0	69	52,284.18
{S (b+s+LinT) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	327.876	0	68	52,294.88
{S (b*s) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	355.336	0	68	52,322.34
{S (b+s) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(b)}	355.743	0	68	52,322.75
{S (b+s) p (b+s*t) ΨBtoN(s+t) ΨNtoB(s+t) r(.)}	356.5800	0	67	52,325.59