



and Raveling 1981; Martin et al. 1985; Owen et al. 1988; LeSchack et al. 1998. Future costs to a female of incubating a clutch or rearing a brood alone has yet to be assessed, however. Divorce rates in geese are low (0.05; Ens et al. 1998), suggesting that costs, including reduced survival, of finding new mates are substantial in relation to potential lifetime reproduction (Choudhury 1995; McNamara and Forslund 1996).

No study has yet examined survival costs of mate loss in long-lived monogamous birds. Absence of such studies results in part from the difficulty of distinguishing between mortality and dispersal away from a breeding area. Burnham (1993) and Barker (1997) capture-mark-recapture (CMR) models use encounters at the local scale (e.g., breeding location) and at the global scale (e.g., ring recoveries) to separate permanent emigration from mortality, thereby allowing estimation of true survival and fidelity to a breeding area. We used human harvest of brant during a long-term study of uniquely marked individuals to estimate the effects of mate loss on reproductive success, fidelity to the breeding area, and true survival of adult female brant. Adult female brant do not disperse from their breeding colony once they have nested there (Sedinger et al. 2008), so emigration was synonymous with nonbreeding. Because of the importance of mates for access to resources, we predicted that mate loss would affect both survival and reproductive success in brant.

## MATERIALS AND METHODS

### Field methods

Brant are long-distance migrants that breed in high latitude ( $\approx 60^\circ$  N) coastal habitats from the mid-Canadian arctic, west to Russia, and south to the Yukon-Kuskokwim Delta, Alaska (Reed et al. 1998). Brant winter in coastal lagoons from the Alaska peninsula in the north, to mainland Mexico in the south (Reed et al. 1998; Ward et al. 2004). We conducted the nesting

estimate both true annual survival and fidelity to TRC (Burnham 1993; Barker 1997; White and Burnham 1999). Because adult females are nearly completely faithful to TRC (fidelity = 1.0; Sedinger et al. 2009), dispersal after mate loss was almost certainly associated with nonbreeding by females that lost their mates. The Barker model, thus allowed us to distinguish between survival and breeding costs of mate loss. We conditioned the initial release into the study on the first time females were seen nesting and their marked mate was identified. We used subsequent encounters on breeding areas (nesting and/or brood rearing), reports of harvested birds from USGS-Bird Band Laboratory, and resightings from wintering areas to construct encounter histories. We excluded pairs where both individuals were shot in the same day to eliminate confounding between a shared mortality risk and fitness costs to females of losing their mates. We report the following parameters from the Barker analysis:  $S$  (true annual survival),  $p$  (encounter probability at the TRC),  $r$  (reporting rate, the probability that an individual died [including being shot] during the nonbreeding season and the ring was reported),  $R$  (probability an individual alive during the breeding season was observed during the preceding nonbreeding period),  $F$  (fidelity of individuals to the TRC). All individuals that were "reported" in this study were shot by hunters; thus, differences in reporting rates reflected differences in the underlying mortality process, combined with differences in harvest rates. Ring recovery rates (as distinguished from reporting rates) represent the probability that an individual was shot by a hunter, and the ring was reported to the U.S. Geological Survey Bird Banding Laboratory (Brownie et al. 1985). Recovery rates, thus represent a direct index of harvest rate, which can be transformed to an estimate of harvest rate if ring reporting rates (as a component of recovery rates) are known (Nichols et al. 1995). The terminology here can be confusing. Reporting rates that are components of ring recovery rates are different parameters from the reporting rates we estimated in our analyses. Ring recovery rates can be approximated from estimates of Barker reporting rates ( $r$ ) using the formula  $f = r / (1 - S)$  (Barker 1997; White and Burnham 1999; Nicolai et al. 2005).

We used 2 separate sets of year-specific individual covariates in which individuals were assigned 0 for no mate loss and 1 for mate loss. For the first covariate (cov1), females received a 1 in the year their mate was shot and a 0 in all other years. This covariate allowed us to assess the impact of mate loss on survival and fidelity of females to TRC only in the year after mate loss. In the second covariate (covF), we assigned females a 1 in the year of mate loss and in all subsequent years. This second covariate allowed us to examine lifetime effects of mate loss. We only considered models that allowed encounter probability ( $p$ ) at TRC and resighting probability ( $R$ ) in winter to vary by year. We constrained parameters in the Barker model so our estimates of fidelity to TRC were derived only from effects of permanent emigration (Barker 1997; Nicolai 2010).

Our modeling approach had 3 steps. First, we considered all possible models that allowed survival ( $S$ ), reporting rate ( $r$ ), and fidelity ( $F$ ) to TRC to vary by year ( $t$ ), or we constrained parameters to be constant across years. Second, we used the best supported model in the first stage and considered models in which cov1 was used to explain variation in survival and reporting rate, and covF was used to explain variation in fidelity to TRC. These models allowed us to examine whether loss of a mate influenced either survival or fidelity to TRC. We only allowed covF rather than cov1 to explain variation in fidelity to TRC because for females that were alive but never returned, we could not determine when permanent emigration actually occurred. Last, in the best supported model from level 2, we tested models where we replaced cov1 with covF

for explaining survival and reporting rate to examine the hypothesis that loss of a mate had lifetime consequences for survival. At this stage, we also considered models in which nest initiation date relative to other clutches in the same year, clutch size relative to other clutches in the same year, and tarsus length were considered as explanatory variables for reporting rate and fidelity to TRC. Our rationale for these models was that individual quality is associated with nesting date, clutch size, and body size (Sedinger et al. 1995).

We did not include an estimate of  $c$  (overdispersion parameter,  $\hat{c}$ ) in our variance estimates or model selection because no

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Figure 1  
Cumulative return rates for adult female black brant nesting at the Tutakoke River Colony in which either 1) the male member of the pair was removed (dotted line) or 2) 18 cohorts of control individuals (shaded area). The shaded region depicts the range of cumulative return rates for females for which we have no record of mate loss; the thick black line is the mean estimate for this group. We provide predicted cumulative return rates based on our estimates of survival,  $\beta$ delity, and mean capture probability for the control and treatment groups.

and  $\beta$ delity to TRC to remain constant across years (Table 2). The overall best supported model allowed survival and reporting rate to differ in the year of mate loss (cov1) and constrained  $\beta$ delity to TRC to remain constant. We found substantial support for models containing cov1; sum of Akaike weights ( $\sum w_i$ ) = 0.83 and 0.55 for effects of cov1 on survival

Table 2  
Models of survival ( $S$ ), encounter probability ( $p$ ), reporting rate ( $r$ ), resighting probability ( $R$ ), and  $\beta$ delity ( $F$ ) for black brant nesting at the TRC, Alaska, 1987-2007

Model <sup>a</sup>	AICc	$\Delta$ AICc	Model weight	K
$S(\text{cov1}) p(t) r(\text{cov1}) R(t) F(.)$	24428.4	0.0	0.30	40
$S(\text{cov1}) p(t) r(.) R(t) F$				

and reporting rate, respectively. Overall, we found little support for annual variation in annual survival, reporting rate, and  $\beta$ delity to TRC:  $\sum w_i = 0.01, 0.00,$  and  $0.00,$  respectively. Model averaged estimates of annual survival in the year after treatment were lower for treated ( $0.716 \pm 0.081$ ) than control ( $0.856 \pm 0.004$ ) individuals (Figure 2). We found no support for lifelong effects (covF) on annual survival. Treated individuals experienced increased reporting rates ( $0.126 \pm 0.086$ ) compared with controls ( $0.066 \pm 0.006$ ) (Figure 2) in the year of mate loss (cov1). Because a model containing lifelong effects of mate loss (covF) on reporting rate had little support ( $w_i = 0.18$ ), we derived model-averaged parameter estimates for this model for the first year after treatment only. Converting reporting rates to ring recovery rates produced estimates of ring recovery rates of 0.03 and 0.01 for treated and control individuals, respectively. This allowed for a direct comparison with concurrent estimates of ring recovery rates for the same population (Sedinger et al. 2007). We found little support for treatment effects on  $\beta$ delity to TRC as estimates were nearly identical for the 2 groups ( $\sum w_i = 0.12; F = 0.976 \pm 0.013$  and  $0.976 \pm 0.004$ , for treatment and control females, respectively) (Figure 2), indicating that treatment and control females returned to breed at the same rates if they survived. We found no support for effects of relative clutch size before treatment, nest initiation date before treatment, or diagonal tarsus length on either reporting rate or  $\beta$ delity to TRC after mate loss ( $\Delta$ AICc  $> 10.0$ ; Nicolai 2010).

## DISCUSSION

Our results provide strong evidence that survival of female brant declines substantially when they lose their mates. Lower survival after mate loss might be expected in species where paired individuals enjoy higher social status (Black et al. 2007) and loss of a mate reduces access to food or other resources (Lamprecht 1987; Choudhury 1995). By not having a mate to provide vigilance during feeding bouts, body condition may be impacted and makes female brant more vulnerable to other mortality events such as predation and increased likelihood of disease or parasitism. Additionally, increased investment in rearing offspring after mate loss could also result in lower survival of the surviving mate (Daan et al. 1996). Lower survival of treatment females cannot be attributable

to harvest because: 1) we removed females from the analysis that were shot and reported within 1 day of the date their mate was reported and 2) the harvest rate we estimated is not sufficient even under a fully additive harvest model (Anderson and Burnham 1976) to account for the reduction in survival we observed.

Change or loss of mate is typically followed by lower reproductive investment or success (Ens et al. 1996; Catry et al. 1997; van de Pol et al. 2006). We found no support for reduced breeding performance for females that survived after the loss of a mate. Widowed females, if they survived, returned to breed at the same rate as control females and actually laid larger clutches than control females (Nicolai 2010). We interpret the latter result as an indication that only higher quality individuals survived, formed new pair bonds, and resumed breeding. That is, females who were of higher quality and laid larger clutches (e.g., Daan et al. 1990) before they lost their

- Ankney CD, MacInnes CD. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk*. 95:459-471.
- Barker RJ. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. *Biometrics*. 53:666-677.
- Black JM. 1996. Introduction: pair bonds and partnerships. In: Black JM, editor. *Partnerships in birds: the study of monogamy*. Oxford: Oxford University Press. p. 3-20.
- Black JM. 2001. Fitness consequences of long-term pair bonds in barnacle geese: monogamy in the extreme. *Behav Ecol*. 12:640-645.
- Black JM, Prop J, Larsson K. 2007. *Wild goose dilemmas*. Gröningen (the Netherlands): Branta Press.
- Bridge ES, Nisbet ICT. 2004. Wing molt and assertive mating in Common Terns: a test of the molt-signaling hypothesis. *Condor*. 106:336-343.