Should I stay or should I go? Fitness costs and benefits of prolonged parent–offspring and sibling–sibling associations in an Arctic-nesting goose population

Mitch D. Weegman1,2 · Stuart Bearhop1 · Geoff M. Hilton2 · Alyn J. Walsh3 · Kaitlin M. Weegman4 · David J. Hodgson1 · Anthony David Fox5

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Abstract Theory predicts persistence of long-term family relationships in vertebrates will occur until perceived fitness costs exceed benefits to either parents or offspring. We examined whether increased breeding probability and survival were associated with prolonged parent–offspring and sibling–sibling relationships in a long-lived Arctic migrant herbivore, the Greenland white-fronted goose (Anser albifrons flavirostris). Although offspring associated with parents for 1–13 years, 79 % of these associations lasted two or less years. Only 65 (9.9 %) of the 656 marked offspring bred once in their lifetime, and just 16 (2.4 %) bred twice or more. The probability of birds with siblings breeding successfully in a subsequent year was credibly greater than that of independent birds at all possible ages (i.e., ages 2–7+). A cost–benefit matrix model utilizing breeding and survival probabilities showed that staying with family groups was favored over leaving until age 3, after which there were no credible differences between staying and leaving strategies until the oldest ages, when leaving family groups was favored. Thus, most birds in this study either departed family groups early (e.g., at age 2, when the “stay” strategy was favored) or as predicted by our cost–benefit model (i.e., at age 3). Although extended family associations are a feature of this population, we contend that the survival benefits are not sufficient enough to yield clear fitness benefits, and associations only persist because parents and offspring mutually benefit from their persistence.

Keywords Bayesian multistate model · Cost–benefit model · Fitness · Greenland white-fronted goose · Breeding probability · Long-term family relationship

Introduction

Prolonged associations among kin (particularly between parents and offspring) are likely to be maintained only as long as fitness costs and benefits favor all parties. Generally, increased parental investment improves offspring fitness (Trivers 1972; Cam et al. 2003; Tinkler et al. 2007) because prolonged parent–offspring associations contribute to offspring learning foraging strategies, predator awareness, migratory routes, and potentially reproductive tactics from parents (Hochbaum 1955; Raveling 1970; Owen 1980; Warren et al. 1993; Slagsvold and Wiebe 2011). Parents may benefit from offspring associations through enhanced reproductive success (e.g., “helpers;” Skutch...
2. Is there a survival cost to independence, i.e., do off-

13 years) but highly variable kinship bonds (Warren et al.

1961), while extended parent–offspring bonds contribute
to mutual predator defense and/or greater foraging success,
for example amongst African elephants (Loxodonta afr-
cana; Moss and Poole 1983), killer whales (Orcinus orca;
Baird 2000), and sperm whales (Physeter macrocephalus;
Whitehead et al. 1991). Other family associations, such
as sibling–sibling associations, are less studied, but are
thought to persist in geese because extended family asso-
ciations increase group size, enhancing predator detection,
social dominance, and access to resources (Boyd 1953;
Raveling 1970; Black and Owen 1989a; Ely 1993; Warren
et al. 1993; Fox et al. 1995).

However, benefits from prolonged associations dimin-

increased age-specific breeding probability when inde-
dependent in subsequent years?

Materials and methods

Study area

Wexford Slobs (52°22′N, 6°24′W) in southeast Ireland
comprise intensively managed grassland and cropland that
constitute the single most important wintering area for
Greenland white-fronted geese, supporting over one-third
of the global population (Warren et al. 1992; Fox et al.
1998). From 1983 to 2003, 656 first-winter Greenland
white-fronted geese were caught at Wexford using tradi-
tional cannon-netting techniques. We truncated the data set
after the 2003 cohort to ensure adequate capture histories
(i.e., compiled up to 2009) for later cohorts. Caught birds
were individually marked with a white plastic leg band
and an orange neck collar (both inscribed with the identi-
cal alphanumeric code; see Warren et al. 1992) as well as
a standard numbered metal ring. Collar code combinations
were visible from up to 800 m using a 20–60× spotting
scope. Individual geese were aged on capture by plumage
characteristics (presence/absence of white frons on face
and black belly bars; Cramp and Simmons 1977) and sexed
by cloacal examination (Warren et al. 1992). AJW resighted
geese weekly during winter at Wexford from 1983 to 2010,
begining when birds arrived in autumn.

Parent–offspring and sibling–sibling observations

Parent–offspring and sibling–sibling associations were
determined by repeated observations (≥2) of collared
individuals together within and among winters. Temporary
relationships are hard to identify as some birds were
rarely seen; thus, single resightings of associations may be
unreliable and were not used (Owen 1984). Associations
of focal individuals with unmarked birds were not consid-
ered because unmarked individuals could not be consist-
ently identified within or between years. Breeding occurs
at a low density over large areas (>15,000 km2) of remote
west Greenland, so little research has been conducted on
the breeding biology of Greenland white-fronted geese.
Our winter observations of parent–offspring and sibling–
sibling associations are contingent on (1) juveniles sur-
viving as goslings, fledging, and migrating to wintering
areas, and (2) family members remaining together through
summer and autumn. Further, not all individuals of a fam-
ily unit were captured and marked; thus, our estimates of
family association duration are likely to be conservative
with respect to the “true” association duration. In families
comprising more than two adults, parents were identified
through repeated observations in association with marked first winter birds, and other marked adult family group members were assumed to be offspring from a previous year still associating with parents; this method for determining relatedness of closely associating individuals has recently been verified using molecular genetics in light-bellied brent geese (Branta bernicla hrota; see Harrison et al. 2010). When previously associated birds were not resighted together over the course of a subsequent winter, the relationship was considered terminated and a cause assigned (i.e., focal bird not resighted, associate not resighted, both not resighted, both resighted but no longer associating).

Adult paired geese resighted repeatedly (≥2 times) with juveniles within a winter were considered breeding parent birds. Twelve birds that paired with other collared birds were subsequently resighted with juveniles; in these cases, one bird of each pair was randomly removed from analyses.

### Statistical analyses

All birds were resighted in their first winter with at least one parent; the sum of years that a goose marked in their first winter associated with both parents and only one parent defined the duration of that parent–offspring association. Importantly, parents associating with adult offspring may breed in subsequent years, but associating offspring do not. Thus, only parents and independent offspring (i.e., not those associating with family) may accrue a direct reproductive benefit (through increased breeding probability) from familial association. We assumed offspring did not breed whilst associating with siblings, as we have no observations of this occurring.

To determine age-specific survival and breeding transition probabilities of birds with parents, siblings (post-parents), and those considered independent/nonbreeders and independent/breeders, we developed Bayesian multistate capture–recapture models using WinBUGS (http://www.mrc-bsu.cam.ac.uk/bugs), version 1.4.3, adapting examples outlined in Kéry and Schaub (2012) and Weegman et al. (2015, 2016). All models were run through the R2WinBUGS package (Gelman et al. 2013) in Program R, version 2.14.2 (R Development Core Team 2012). We assigned capture histories according to states: “1”—seen, with parents, “2”—seen, with ≥1 sibling, “3”—seen, independent/non-breeder, and “4”—seen, independent/breeder; only one state was assigned per year. In rare cases where states varied within year (i.e., multiple observations of birds with parents, siblings, and independent during the same winter), we used the modal state. All birds were resighted with at least one parent in their first year; thus, birds could not begin the capture history independent. Accordingly, survival probabilities of birds with a sibling, those that were independent/nonbreeder, and those that were independent/breeder were calculated from age 2, and the probability of transitioning from state “with parents” to all other states was calculated from age 1. Birds did not transition to previous states (e.g., from “independent/nonbreeder” to “with parents”). We limited multistate capture–recapture models to seven age classes, where ages of 7+ were combined into a single class due to small sample sizes. Previous age-specific survival analyses have indicated a linear relationship between age and survival (Weegman 2014); thus, to increase the precision of our estimates in the multistate framework, we modeled age as a linear trend on survival. We have no evidence to suggest a similar relationship between ages and transitions, so we modeled transitions with full age specificity (i.e., ages 1–7+). Nonetheless, we formed an additional multistate model with age-constant transitions, the results of which are presented in Figs. S1 and S2 in the Electronic supplementary material (ESM).

To estimate age- and state-specific survival and transition probabilities, we used normally distributed, noninformative priors with mean = 0 and variance = 0.001 with the multinomial logit link function for all but one transition parameter, constrained so that their sum was <1; the last transition was calculated as

\[ \beta_n = 1 - \sum_{i=1}^{n-1} \beta_i, \]

where \( \beta_n \) denotes the back-transformation of the final transition parameter \( n \), based on back-transformations of other transitions, \( \beta_i \). To estimate the state-specific resighting probabilities, we used uniformly distributed, noninformative priors with mean = 0 and variance = 1. Posterior summaries from three Markov chain Monte Carlo (MCMC) chains were based on 450,000 iterations after a burn-in of 90,000 and a thinning interval of 10. We confirmed chain convergence using the Gelman–Rubin statistic (see Gelman and Rubin 1992), and greater than 8000 samples were drawn from posterior distributions. Posterior means are presented with 95% credible intervals (CRI). Additional specification and code for the multistate model may be found in the ESM.

The multistate model produced posterior distributions of age- and state-specific probabilities of survival (modeled with age as a linear trend), and age-specific probabilities of moving between states (with parents, with siblings, independent/nonbreeder, independent/breeder). For each iteration of the model (i.e., each set of parameters in the posterior distribution), we populated an age- and state-transition matrix, where transitions to breeding were used as breeding probabilities. After transitioning into the breeding population, birds were subsequently lost to population growth in order to reflect the extreme rarity of multiple breeding attempts (this paper; Weegman 2014).
proxy for fitness of the “wild-type” life history was the dominant eigenvalue of this transition matrix ($\lambda_{\text{wt}}$), which gained its own posterior distribution via calculation across all iterations of the MCMC model. Hence, all projection matrices presented here are simplified versions of reality, in which “breeding” simply contributes a fecundity of 1, whereby $\lambda_{\text{wt}}$ (in this case) is a measure of relative fitness that assumes clutch size and fledging success are independent of parental age. We tested whether the distributions for age-specific survival of birds with parents or siblings and those independent were credibly different (i.e., whether the 95 % CRI of the difference overlapped zero). Likewise, we tested whether the transitions to breeding were credibly different between birds with siblings and those independent. We report approximate $P$-values for these tests, citing the proportion of posteriors lying below zero for independent birds. We claim “credibility” when this proportion is either <0.05 or >0.95.

Using age-specific breeding probabilities and survival estimates of birds with parents, siblings, and independents, we then formed a cost–benefit matrix model to examine optimal bond durations and determine how fitness depends on the tradeoff between survival benefits of staying with family, and the breeding benefits of independence. The structure of the model was based on the assumption that at each age, birds have the choice to remain another year with their parents or leave; once birds left their parents, they had a similar choice to remain with their siblings or leave. Thus, we simulated all combinations of potential family outcomes: birds could leave parents aged 1, 2, ..., 7+ years, then bond with siblings for 1, ..., 7+ years or enter the nonbreeding independent state. Independent birds then enjoyed the observed age-specific probability of entering the independent breeding state, at which point they contributed unit recruitment to the population. For each simulation, we forced all birds to transition into independence from parents, and independence from siblings, at a fixed age, but applied the observed probabilities of survival and breeding. Our proxy for fitness was the dominant eigenvalue ($\lambda_n$) of the age- and state-transition matrix formed by the simulated probabilities of state transitions and the observed probabilities of age- and state-specific survival. We used the posterior distributions of age- and state-specific survival to yield posterior distributions of simulated fitness. To determine the fitness costs or benefits associated with each simulated strategy, we calculated posterior distributions of the difference in fitness between wild-type and simulated strategies ($\omega = \lambda_{\text{wt}} - \lambda_n$). We also tested whether the simulated and wild-type distributions were credibly different (i.e., whether the 95 % CRI of $\omega$ overlapped zero). Similar to tests among survival and breeding transitions, we report approximate $P$-values for these tests, citing the proportion of wild-type posteriors lying below zero (claiming “credibility” when this proportion is either <0.05 or >0.95).

We monitored correlations among parameter estimates of subsequent ages for each state to ensure that negative correlations were not influencing year-on-year cost–benefit calculations. We predicted an “intersection” age where the advantage to the individual would switch between “stay” and “leave” strategies, whereby the stay strategy would be favored for a few years (i.e., simulated fitness distributions would be credibly less than wild-type fitness distributions) until declining survival and/or perceived fitness gains would favor adoption of the leave strategy (i.e., simulated and wild-type distributions would be similar).

Results

For marked first-winter individuals that hatched from 1983 to 2003, duration of parent–offspring association varied from 1 to 13 years, although most (89 %) associations lasted 3 years or less (Fig. 1). The majority of the birds (78 %) did not associate with siblings upon becoming independent from their parents. Among those that associated with at least one sibling post-parents, durations varied from 1 to 13 years, although most (91 %) were 3 years or less (Fig. S3 in the ESM). Of 656 life histories of geese marked in their first winter, only 65 birds (9.9 %) bred successfully (i.e., were observed with young on wintering areas) at least once in their lives, 13 (1.9 %) bred successfully twice, and just three bred successfully three times (Weegman 2014). Among breeders and nonbreeders, observed mean duration

![Figure 1](https://example.com/figure1.png)
of parent–offspring association was 2.31 (±SE 0.15) and 1.96 (±0.05) years, respectively. Mean observed duration of association with at least one sibling post-parents among breeders and non-breeders was 1.22 (±0.31) and 0.37 (±0.07) years, respectively. No geese were marked in 2000, and none bred from the 1996 (n = 22), 1997 (n = 13), 1999 (n = 13), and 2003 (n = 39) cohorts.

State-specific demography

Survival of birds that were associated with parents was credibly greater than that of same-aged independent birds at all ages (i.e., 95% credible intervals of birds with parents did not overlap means for birds considered independent/nonbreeders; Fig. 2). At ages 6 and 7, survival of birds with parents was also credibly greater than that of independent/breeder birds. In most cases, survival generally increased with age among all states, except for independent/breeder birds, whose age-specific survival was relatively stable across ages (Fig. 2). The probability of birds remaining with parents increased from age 2 (posterior mean = 0.60, 95% CRI = 0.52–0.66) to age 5 (posterior mean = 0.83, 95% CRI = 0.67–0.95), but decreased at age 6 (posterior mean = 0.61, 95% CRI = 0.42–0.80), and increased slightly at age 7 (posterior mean = 0.72, 95% CRI = 0.54–0.86; Fig. 3a). The probability of birds with siblings subsequently breeding successfully (i.e., skipping the independent/nonbreeder state) increased from age 3 (posterior mean = 0.03, 95% CRI = 0.002–0.08) to age 5 (posterior mean = 0.35, 95% CRI = 0.09–0.77), but decreased thereafter (Fig. 3b), and was credibly greater than the probability of independent birds subsequently breeding successfully at ages 5 (independent: posterior mean = 0.09, 95% CRI = 0.04–0.17; P = 0.99), 6 (siblings: posterior mean = 0.06, 95% CRI = 0.002–0.18; independent: posterior mean 0.0004, 95% CRI = 0.00001–0.01), and 7 (siblings: posterior mean 0.13, 95% CRI = 0.04–0.27; independent: posterior mean 0.06, 95% CRI = 0.03–0.10; see age-specific differences between open triangles in Fig. 3b, c). At all other ages, the probabilities of subsequently breeding successfully among individuals with siblings and those remain with parents (Remain with P: filled circles), move to siblings (To S, post-P: filled triangles), move to independent/nonbreeder (To I/NB: open circles), or move to independent/breeder (To I/B: open triangles).
that were independent were generally similar, and 95 %

CRI overlapped means. Resighting probability was the
greatest among breeding individuals (posterior mean 0.94,
95 % CRI 0.89–0.97) and the least among independent,
nonbreeding individuals (posterior mean 0.64, 95 % CRI
0.59–0.68).

Cost–benefit matrix model

The cost–benefit matrix model suggested that simulated fit-
ness was credibly lower than wild-type fitness for birds
that left parents and siblings at ages 1 ($P = 0.02$) and 2
($P = 0.007$), and that simulated fitness was marginally lower
than wild-type fitness for those that left parents and siblings
at age 3 ($P = 0.11$) and those that left parents at age 1 and
siblings at age 2 ($P = 0.12$; Fig. 4). These results suggest
that offspring maintain familial association through age 3.
At middle ages (i.e., ages 4–5), there were fewest differences
between the simulated and wild-type fitness distributions,
whilst at the oldest ages (i.e., ages 6–7+), simulated fitness
(i.e., leaving parents or siblings) was generally greater than
wild-type fitness among birds that remained with their par-
ents for 5–6 years and siblings for 1–2 years (i.e., right-hand
side of Fig. 4), which suggests that birds which remained
with family in old age suffered lower fitness (although our
sample sizes were small). A similar multistate model with
age as a linear trend on survival but age-constant transition
probabilities (Fig. S1 in the ESM) produced similar cost–
benefit model results (Fig. S2 in the ESM).

Discussion

This analysis shows that parent–offspring and sibling–sib-
ling associations are beneficial for the first 3 years of life
in Greenland white-fronted goose, whereby the fitness
(the composite of survival and eventual breeding prob-
ability) of the birds that maintained such associations was
credibly greater than the fitness of those that did not. Con-
versely, birds that maintained extended family associations
(>3 years) gained no credible fitness benefit over individ-
uals that left parents or siblings at the same age; further,
our cost–benefit model provided weak evidence suggesting
that fitness was actually lower among birds that remained
with their parents or siblings than among simulated birds
who were forced into independence at ages 6 and 7. These
findings support the departure of individuals from the fam-
ily unit at middle age (ages 4–5, where there were non-
credible fitness differences between birds with parents
or siblings and those that were independent) and old age.
Although subsequent breeding probability was greatest for
“older” individuals (those aged 5, as found in many other
bird and some mammal species; Dobson 1982; Greenberg
1986; Wallace and Temple 1987; Sherry and Holmes 1989;
Sedinger et al. 2001, 2008; Nichols et al. 2010) associat-
ing with siblings, these gains were offset by noncredible
survival differences between birds with siblings and those
that were independent, yielding lower overall fitness for
birds aged 5 than those aged 3. Independence after just 2
or 3 years may be especially important for species char-
acterized by very few breeders (such as Greenland white-
fronted goose), as it allows younger individuals inherently
more potential opportunities (than older birds who gain
independence at older ages, all else being equal) to experi-
ence “optimal” breeding conditions. In the case of Green-
land white-fronted goose, increased snowfall in Greenland
has contributed to poorer breeding conditions and limited
goose productivity there in recent years (Boyd and Fox
2008; Weegman 2014). These results are novel because
previous work on parent–offspring associations has focused
on the costs and benefits of shorter parental bonds (i.e., 1
or 2 years in duration; Cam et al. 2003; Nisbet et al. 1998;
Tarwater and Brawn 2010) or the short-term costs and ben-
efits of longer parental bonds (Inger et al. 2010), but very
few studies have examined the lifetime fitness implications
for offspring of long-term parental bonds in noncoopera-
tively breeding birds where offspring maintain such family
associations (with parents and siblings) into adulthood.

The cost–benefit model provides evidence for why most
Greenland white-fronted goose exhibit relatively short
family relationships (i.e., there is little fitness gained by
associating with parents or siblings for longer than 2 or
3 years), but also why such variability exists in the dura-
tion of parental and sibling bonds; the decision between

Fig. 4 Age-specific (1–7+) fitness differences between wild-type
(wt) and simulated (sim) distributions for birds leaving parents and
siblings, calculated using 656 known-age Greenland white-fronted
goose life histories. Ages at leaving siblings are represented by the
multiple estimates at each age at leaving parents.
staying and leaving is marginally balanced after age 3 and does not favor one payoff over the other. The cost–benefit model provides one example from which we might suggest hypotheses about strategies in other animal populations as a consequence of differing life histories. For instance, if fitness was not a strong positive function of family bonds for the first few years of life, leaving parents and/or siblings earlier would likely be a preferable strategy. A similar model examining “staying” and “leaving” strategies for birds that exhibit shorter parent–offspring associations would confirm whether Greenland white-fronted geese exhibit a stronger “stay” payoff than others. One would assume this to be the case, as few bird species exhibit longer associations with parents.

In many animal populations, independence from the family unit is one of the most risky decisions in the life history of an individual. That individuals with parents enjoyed greater survival than independent/nonbreeders suggests a hidden cost of independence. Moreover, such costs accrued at all ages and were thus long-lasting for individuals independent at early ages; indeed, survival of independent/nonbreeders was lower than that of individuals with parents at all ages. Our comparison between simulated and wild-type fitness distributions showed no clear optimal fitness strategy after age 3, which implies a high degree of individual variation in this system, whereby individual condition likely influences the balance between the risk of dying before breeding and the increase in lifespan (and subsequent breeding probability) achieved by remaining with the family group; such heterogeneity could result in differential “optimal” fitness strategies.

The variation in individual “staying” and “leaving” strategies may be explained by whether parents or offspring determine association termination. For parents and offspring, maintaining the family bond is beneficial because larger family units are better able to defend resources and detect predators (Jarman 1974; Black and Owen 1989a; Gregoire and Ankney 1990; Tanner 2006). For parents, an additional benefit of larger group size is potentially greater success in future reproductive attempts (i.e., encouraging the “stay” strategy; Black and Owen 1989b). Yet, in geese, offspring do not form pair bonds or breed whilst associating with the family unit. Thus, if offspring determine optimal association duration, they may terminate bonds sooner to advance their direct fitness through reproductive attempts. In these cases, we would expect the “leave” strategy (i.e., simulated fitness) to be favored at earlier ages. In 173 cases (26 %) of 656 known-age geese, offspring were precipitated into independence, as parents were not seen again (i.e., having likely died). Hence, the majority (74 %) of parent–offspring associations were terminated based on choice by parents, offspring, or a combination of both. There are likely commonalities in perceived optimal association durations for parents and offspring, which may be driven by inclusive fitness benefits (Hamilton 1964). Indeed, “helping” among individuals increased survival and future reproductive success of recipients in other birds, for example in the Florida scrub jay (Aphelocoma coerulescens), pied kingfisher (Ceryle rudis), and splendid fairy-wren (Malurus splendens); Mumme et al. (1989). Although we did not specifically evaluate inclusive fitness in this system, prolonged associations may be favorable in this respect for parents and offspring in populations where very few individuals ever successfully breed, and most of those that do breed do so only once.

In this study, we have shown that maintaining family bonds for up to 3 years increases Greenland white-fronted goose offspring fitness, but that very few geese ever breed successfully; indeed, more than 90 % of known-age marked individuals were never observed on wintering areas with young. Thus, for most individuals, the reproductive benefits of family association and independence are not realized. Nonetheless, the survival benefits for individuals with parents compared to independent/nonbreeders provides a potential explanation for such extended family associations. Remarkably, two unpaired birds (of 14) that remained with their family into old age (7+ years) eventually bred, despite our cost–benefit model results suggesting lower fitness for such a strategy. Although not explicitly tested in this analysis, poor-quality birds that are unlikely to ever reproduce might also maintain family associations at older ages. For both highest- and lowest-quality individuals, remaining with the family unit may be an optimal life strategy for group size benefits (i.e., greater access to resources; Boyd 1953) and increased inclusive fitness if parents or siblings later reproduce. Although extended family associations are a feature of this population, they are relatively uncommon, and the survival benefits of such associations are not sufficient to yield clear fitness benefits. Therefore, extended associations only persist because parents and offspring mutually benefit from their persistence.

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References

Baird RW (2000) The killer whale-foraging specializations and group hunting. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean societies. University of Chicago Press, Chicago, pp 127–153

Black JM, Owen M (1989a) Agonistic behaviour in goose flocks: assessment, investment and reproductive success. Anim Behav 37:199–209

Black JM, Owen M (1989b) Parent-offspring relationships in wintering barnacle goose. Anim Behav 37:187–198

Boyd H (1953) On encounters between wild white-fronted geese in winter flocks. Behaviour 5:85–129

Boyd H, Fox AD (2008) Effects of climate change on the breeding success of white-fronted geese Anser albifrons flavirostris in west Greenland. Wildfowl 58:55–70

Cam E, Monnat J-Y, Hines JE (2003) Long-term fitness consequences of early conditions in the kittiwake. J Anim Ecol 72:411–424

Cramp S, Simmons KEL (1977) Birds of the western Palearctic, vol 1. Oxford University Press, Oxford

Development Core Team R (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. Anim Behav 30:1183–1192

Ely CR (1993) Family stability in greater white-fronted goose. Auk 110:425–435

Fox AD, Boyd H, Bromley RG (1995) Mutual benefits of associations between breeding and non-breeding white-fronted goose, Anser albifrons. Ibis 137:151–156

Fox AD, Norriss DW, Stroud DA, Wilson HJ, Merne OJ (1998) The Greenland white-fronted goose in Ireland and Britain 1982/83-1994/95: population change under conservation legislation. Wild Biol 4:1–12

Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. Stat Sci 7:457–472

Gelman A, Sturtz S, Ligges U (2013) R2WinBUGS: running WinBUGS and OpenBUGS from R/S-PLUS. R package version 2.1-19. https://cran.r-project.org/web/packages/R2WinBUGS/

Greenberg PE, Ankney CD (1990) Agonistic behavior and dominance relationships among lesser snow goose during winter and spring migration. Auk 107:550–560

Hamilton WD (1964) The genetical evolution of social behaviour. J Theor Biol 7:1–52

Harrison JA, Tregenza T, Inger R, Colhoun K, Dawson DA, Gudmundsson GA, Hodgson DA, Horsburgh GJ, McElwain G, Bearhop S (2010) Cultural inheritance drives site fidelity and migratory connectivity in a long-distance migrant. Mol Ecol 19:5484–5496

Hochbaum HA (1955) Travels and traditions of waterfowl. University of Minnesota Press, Minneapolis

Inger R, Harrison JA, Ruxton GD, Newton J, Colhoun K, Gudmundsson GA, McElwain G, Pickford M, Hodgson D, Bearhop S (2010) Carry-over effects reveal reproductive costs in a long-distance migrant. J Anim Ecol 79:974–982

Jarman PJ (1974) The social organisation of antelope in relation to their ecology. Behaviour 48:215–267

Kéry M, Schaub M (2012) Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic, Waltham

Moss CI, Poole JH (1983) Relationships and social structure in African elephants. In: Kinde RA (ed) Primate social relationships: an integrated approach. Blackwell, Oxford, pp 315–325

Mumme RL, Koenig WD, Ratnieks FLW (1989) Helping behaviour, reproductive value, and the future component of indirect fitness. Anim Behav 38:331–343

Nichols HJ, Amos W, Cant MA, Bell MBV, Hodge SJ (2010) Top males gain high reproductive success by guarding more successful females in a cooperatively breeding mongoose. Anim Behav 80:649–657

Nisbet ICT, Spendelow JA, Hatfield JS, Zingo JM, Gough GA (1998) Variation in growth of roseate tern chicks: II. Early growth as an index of parental quality. Condor 100:305–315

Owen M (1980) Wild geese of the world: their life history and ecology. Batsford, London

Owen M (1984) Dynamics and age structure of an increasing goose population: the Svalbard barnacle goose Branta leucopsis. Nor Polarinst Skr 181:37–47

Raveling DG (1970) Dominance relationships and agonistic behaviour of Canada goose in winter. Behaviour 37:291–319

Sedinger JS, Lindberg MS, Chelgren ND (2001) Age-specific breeding probability in black brants: effects of population density. J Anim Ecol 70:798–807

Sedinger JS, Chelgren ND, Ward DH, Lindberg MS (2008) Fidelity and breeding probability related to population density and individual quality in black brent geese Branta bernicla nigricans. J Anim Ecol 77:702–712

Sherry TW, Holmes RT (1989) Age-specific social dominance affects habitat use by breeding American redstarts Setophaga ruticilla: a removal experiment. Behav Ecol Sociobiol 25:327–333

Skutch AF (1961) Helpers among birds. Condor 63:198–226

Slagsvold T, Wiebe KL (2011) Social learning in birds and its role in shaping a foraging niche. Phil Trans R Soc B 366:969–977

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Tanner CJ (2006) Numerical assessment affect aggression and competitive ability: a team-fighting strategy for the ant Formica xerophila. Proc R Soc B 273:2737–2742

Tarwater CE, Brawn JD (2010) The post-fledging period in a tropical bird: patterns of parental care and survival. J Avian Biol 41:479–487

Tinkler E, Montgomery WI, Elwood RW (2007) Parent-offspring associations in wintering brent goose: parental investment or mutual assistance? J Zool 4:398–405

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man. Heine- mann, London, pp 136–179

Trivers RL (1974) Parent-offspring conflict. Am Zool 14:249–264

Wallace MP, Temple SA (1987) Competitive interactions within and between species in a guild of avian scavengers. Auk 104:290–295

Warren SM, Fox AD, Walsh A, O’Sullivan P (1992) Age of first pairing and breeding among Greenland white-fronted geese. Condor 94:791–793

Warren SM, Fox AD, Walsh A, O’Sullivan P (1993) Extended parent-offspring relationships in Greenland white-fronted geese (Anser albifrons flavirostris). Auk 110:145–148

Weegman MD (2014) The demography of the Greenland white-fronted goose. PhD dissertation. Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, Penryn
Weegman MD, Fox AD, Bearhop S, Hilton GM, Walsh AJ, Cleasby IR, Hodgson DJ (2015) No evidence for sex bias in winter intersite movements in an Arctic-nesting goose population. Ibis 157:401–405

Weegman MD, Bearhop S, Fox AD, Hilton GM, Walsh AJ, McDonald JL, Hodgson DJ (2016) Integrated population modelling reveals a perceived source to be a cryptic sink. J Anim Ecol 85:467–475

Whitehead H, Waters S, Lyrholm T (1991) Social organization in female sperm whales and their offspring: constant companions and casual acquaintances. Behav Ecol Sociobiol 29:385–389