Movements and survival of Lesser Snow Geese *Chen caerulescens caerulescens* wintering in two habitats along the Gulf Coast, Louisiana

JÓN EINAR JÓNSSON[1]*, MORTEN FREDERIKSEN[2] &
ALAN D. AFTON[3]

[1]University of Iceland, Research Centre at Snæfellsnes, Hafnargata 3, Stykkishólmur 340, Iceland.
[2]Department of Bioscience, Aarhus University, Frederiksborgvej 399, DK-4000 Roskilde, Denmark.
[3]U. S. Geological Survey, Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana State University, Baton Rouge, Louisiana 70803, USA.
*Correspondence author. E-mail: joneinar@hi.is

Abstract

Lesser Snow Geese *Chen caerulescens caerulescens* (hereafter Snow Geese) use two wintering habitats in southwest Louisiana. Snow Geese in coastal marshes generally have larger bodies and proportionally thicker bills, longer skulls and longer culmen lengths than do those in adjacent rice-prairies. An important question is whether or not these morphs are sub-populations that segregate during winter. Using a mark-resightings analysis of observations of neck-collared birds, annual apparent survival (Φ) and movement probabilities (Ψ) of Snow Geese were compared between habitats during winters 2001/02–2003/04. The analysis tested the hypothesis of Alisauskas (1998), based on his data collected in winter 1983/84, that larger bill size would increase Φ and decrease Ψ in coastal marshes. Specific predictions were that: 1) larger-billed Snow Geese would be relatively more likely to move from rice-prairies to coastal marshes, or have higher Φ within coastal marshes; and 2) smaller-billed Snow Geese would be relatively more likely to move from coastal marshes to rice-prairies, or have lower Φ within coastal marshes. Estimated annual Φ (± s.e.) was 0.601 ± 0.082, independent of both habitat and time interval. A body size covariate, used to index the morphs, did not improve model fit, indicating that Φ was unrelated to body size after accounting for habitat effects. Estimates of Ψ differed widely between intervals (November–December inclusive, *versus* the rest of the year) and habitats; they averaged 0.18 (range: 0.00–0.56) for birds moving from rice-prairies to coastal marshes and 0.57 (0.00–0.98) on moving from coastal marshes to rice-prairies. Movements of marked individuals were frequent from marshes to rice-prairies, and Ψ was independent of body size. However, movement probabilities were dependent on time intervals and we interpret such interval-specific movement probabilities as responses to shifts in environmental conditions. Thus, the two groups differ in morphology and generally remain segregated except that they mix during intervals of high movements, which occur every 1–3 years.

Key words: ecological segregation, geese, habitat selection, Louisiana, morphology, phenotype.

The total estimated population of Lesser Snow Goose *Chen caerulescens caerulescens* (hereafter Snow Goose) increased from approximately 1 million adult birds in 1970 to 13–15 million in 2000–2005 (Alisauskas *et al.* 2011). The population increase caused high grazing pressure that had negative ecological consequences for plants and other herbivores on Arctic breeding areas of Snow Geese (Samelius & Alisauskas 2009). Thus, a special hunting season (officially termed the special conservation order) was implemented in 1998 in an attempt to counteract this population increase (Alisauskas *et al.* 2011). Once the conservation order was in place, local concerns were raised for the declining numbers of Snow Geese using coastal marshes in southwest Louisiana and whether those birds would be negatively affected by the conservation order (Wilson 2002).

Historically, Snow Geese wintered in coastal marshes along the Gulf of Mexico coast; however, they began using rice-prairies within the last 80 years (Bateman *et al.* 1988). An important question is whether or not Snow Geese in coastal marsh habitats comprised a segregated sub-population, perhaps requiring population-specific habitat management actions (Wilson 2002). Specific threats for Snow Geese in coastal marshes include continued coastal erosion, increased disturbance and habitat alteration from oil exploration and extraction activities, droughts, salt water intrusion following hurricanes (such as Rita in 2005 and Ike in 2008), or other natural or human-related disasters which potentially will affect habitat use and availability for Snow Geese in the future (Jónsson & Afton 2006).

Variation in bill size and shape can result in adaptations to changes in food availability that eventually lead to divergent selection towards morphs that are specialised for different food types (Smith 1990; Grant & Grant 2002; Scott *et al.* 2003). Intraspecific bill size variation commonly is associated with differences in habitat use in geese (Larsson & Forslund 1991, Alisauskas 1998, Williams *et al.* 2008). Snow Geese collected from marsh habitats have larger bodies and proportionally thicker bills, longer skulls and longer culmen lengths than do those collected from adjacent rice-prairie habitats (Alisauskas 1998; Jónsson 2005).

Individual geese with larger bills attain larger bite sizes (Durant *et al.* 2003; Cope *et al.* 2005; van der Graaf *et al.* 2006). Morphometric differences correspond to differing foraging behaviours: Snow Geese in coastal marshes forage primarily by grubbing for below-ground vegetation, whereas those in rice-prairies mostly graze on agricultural plants and consume above-ground vegetation (Alisauskas *et al.* 1988; Alisauskas 1998). Snow Geese from these habitats differ markedly in time budgets and food intake rates (Jónsson & Afton 2006), indicating that different feeding adaptations may be beneficial within each habitat as suggested by Alisauskas (1998). These combined differences in morphology and foraging behaviour may be explained by ecological segregation by two separate morphs (Phenotypic Selection Hypothesis; Alisauskas 1998) or individual differences in habitat selection based on bill size and associated foraging efficiency (Habitat Selection Hypothesis; Alisauskas 1998).

Alisauskas' (1998) hypothesis of two separate morphs is consistent with the idea that Snow Geese in coastal marshes are a segregated sub-population (see Wilson 2002). Mark-resighting methodology was used to estimate annual apparent survival of Snow Geese and probabilities of movement between habitats, to inform waterfowl managers regarding the possible need for sub-population specific habitat management. Sub-populations were defined in the classical sense; *i.e.* as a group of conspecific individuals that is demographically, genetically or spatially separated from other groups of individuals. It was assumed that if the two groups were demonstrated to be spatially separated, such results would support a conclusion that the two groups of Snow Geese constituted sub-populations that segregate during winter. Pair bonds are formed on the wintering grounds in Snow Geese (Ganter *et al.* 2005); thus, winter pairing provides opportunities for genetic differentiation between winter habitats.

The main objective was to refute a working hypothesis of limited exchange of individual Snow Geese between habitats during winter. Movement probability (Ψ), estimated after model selection based on banding data, was used to determine whether or not Snow Geese moved between habitats and, if so, with what movement probabilities. The analysis also tested the hypothesis of Alisauskas (1998) that larger bill size would increase annual apparent survival (Φ) in coastal marshes because of a larger bite size, essential to successfully excavate marsh plants. Specific predictions were as follows: 1) larger-billed Snow Geese would be more likely to move from rice-prairies to coastal marshes, or have higher Φ within coastal marshes, than smaller-billed Snow Geese; and 2) smaller-billed Snow Geese would be more likely to move from coastal marshes to rice-prairies, or have lower Φ within coastal marshes, than larger-billed Snow Geese.

Methods

Study area

The study area comprised a 10,764 km^2 area in southwest Louisiana, where the Intracoastal Canal separates coastal marshes and rice-prairies (Fig. 1). Coastal marshes are comprised of fresh, intermediate, brackish and saline wetlands; however, fresh and intermediate marshes are not used regularly by Snow Geese (Bateman *et al.* 1988). Brackish marshes are separated from rice-prairies by a 30 km wide area of fresh and intermediate marshes (Bateman *et al.* 1988). The study area was described in detail by Alisauskas *et al.* (1988) and Bateman *et al.* (1988).

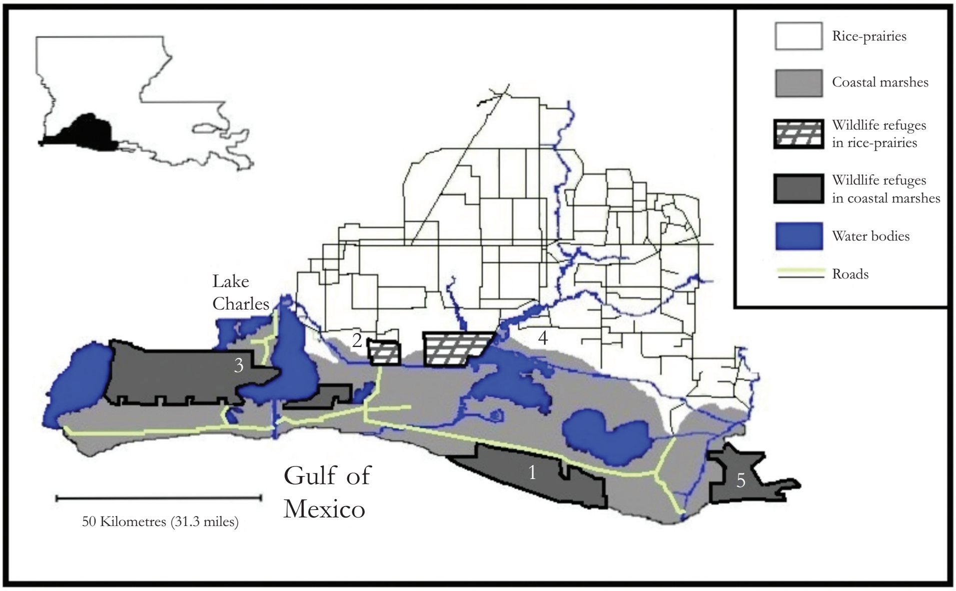


Figure 1. Map of the study area in southwest Louisiana during winters 2001/02, 2002/03, and 2003/04. Snow Geese were captured and marked at 1: Rockefeller State Wildlife Refuge; 2: Cameron Prairie National Wildlife Refuge (NWR); 3: Sabine NWR; and 4: Oak Island (private ownership). Also shown is 5: State Wildlife Refuge.

Estimated numbers of Snow Geese using the study area during the mid-winter waterfowl survey (conducted during the first week of January) were 278,833, 263,737 and 363,420 during winters 2001/02, 2002/03 and 2003/04, respectively (Fronczak 2004). Annual waterfowl surveys, conducted concurrently with our study (in winters 2001/02–2003/04), indicated that 65–70% of all Snow Geese were found in the rice-prairies and 60–77% of all Snow Geese in coastal marshes were sighted at State Wildlife Refuge and/or Marsh Island State Wildlife Refuge (SWR) (Fronczak 2004). Snow Geese arrived in mid-November and began to migrate north in late January – early February (Jónsson 2005). Snow Geese in rice-prairies formed mixed flocks with Ross's Geese *Chen rossii*, but Ross's Geese rarely are observed in coastal marshes (Alisauskas 1998; Jónsson & Afton 2006, 2008, 2009).

Capture and sighting effort

Snow Geese were captured using rocket nets on grit sites (patches of sand and gravel, created for gizzard-grit consumption by waterfowl), which they visit daily to ingest grit to grind their food (Harris 1990; Amat & Varo 2008). Grit sites were located at Cameron Prairie National Wildlife Refuge (NWR) and Oak Island within rice-prairies, and at Sabine NWR and Rockefeller SWR in coastal marshes (Fig. 1). Snow Geese were captured and marked under the following permits: banding permit 08810 from the U.S. Geological Survey-Bird Banding Lab; U.S. Fish and Wildlife Service special use permits 43612-03004 (Cameron Prairie NWR) and 43640-02028 (Sabine NWR); and the Louisiana State University Agricultural Center Institutional Animal Care and Use Committee (LSU AgCenter IACUC) permit number A01-09.

Snow Geese were caught and marked at all locations in all three winters but capture efforts in coastal marshes were more restricted in time than those in rice-prairies, especially in the first winter 2001/02. Snow Geese were catchable in rice-prairies from 20 November to 10 February, whereas this period was 17 December to 20 January in coastal marshes. Marking events were subsequently treated as the first sighting in each sighting history. Marking efforts began in November 2001 and ended in January 2004. In the rice-prairies, Snow Geese were generally marked at Cameron Prairie NWR in November or December 2001–2003. Oak Ridge was added as a rice-prairie marking site in the second winter, and was used on three occasions (2 February 2003, 6 December 2003 and 15 December 2003). In the coastal marshes, Snow Geese were marked in December or January. Observation efforts began 10 November and lasted until 10 February (give or take 2–5 days) each winter.

Captured Snow Geese were individually marked with black neck-collars that had white, three-digit alpha numeric codes and aged by plumage colour (Mowbray *et al.* 2000). We assumed that the sample of Snow Geese was unbiased with respect to body condition (*cf.* Weatherhead & Ankney 1984) because Snow Geese were caught at sites they used regularly and bait or foods were not added to grit sites. Moreover, an experimental study on Greater Snow Geese *C. caerulescens atlanticus* found no evidence of condition-bias for those captured using bait (Morez *et al.* 2000). A subsample of captured adults was measured with callipers (± 0.1 mm): total tarsus, head length, bill nares, bill thickness, culmen length, gape length, skull width, skull height and wing length (see Dzubin & Cooch 1992; Alisauskas 1998). Hereafter, marked Snow Geese in the study are referred to as "marsh Snow Geese" and "rice Snow Geese", according to their capture sites; however, the use of these terms is not meant to imply two separate morphs or sub-populations.

Observers used spotting scopes (20–60×) and recorded locations of sightings with aide of GPS units. In winter 2001/02, one observer scanned goose flocks for neck-bands four days each week with an additional observer for two of those days. In winters 2002/03 and 2003/04, two observers scanned goose flocks for neck-bands for four days each week with an additional observer for two of those days. Goose flocks generally were too dense to quickly infer social or family status of individuals during scans for neck-collars, although pair status was obvious if both members were neck-collared. Occasional collar-readings were recorded during separate time-budget observations for another study (Jónsson & Afton 2006, 2008, 2009).

Observers scanned goose flocks less frequently in coastal marshes than in rice-prairies because of logistical constraints and lower numbers of geese in the former habitat during 2001–2004 (Jónsson 2005; see also Prevett & MacInnes 1980). Road access was good in the rice-prairies (Fig. 1), whereas vast areas of coastal marshes are accessible only by airboat or aircraft, which flush geese on approach. These logistical constraints meant that marked geese were observed more frequently in the rice-prairies. Thus, we included a habitat effect on resighting probability (p) in all models in subsequent mark-resighting analyses. Hereafter, rice-prairies and coastal marshes are collectively termed *habitats* (equivalently termed landscapes; Alisauskas 1998) and their "site" effect in the models (Lebreton *et al.* 2002) is termed *habitat effect*.

Mark-resighting analysis

Multi-state models for live recaptures (hereafter sightings) were implemented in Program MARK (White & Burnham 1999; White *et al.* 2006; Cooch & White 2010) to estimate probabilities of Snow Geese surviving and moving between two habitats, *i.e.* rice-prairies and marshes. Observation histories were collated for Snow Geese caught and released in either rice-prairies or coastal marshes (Jónsson 2005). Model parameters were defined as follows (Lebreton *et al.* 2002):

Annual apparent survival ($\Phi_{t,j}$) = the probability that a bird survives from i to $i + 1$ and remains within the overall study area, given that it was in habitat j at occasion i;

Movement probability ($\Psi^{j \rightarrow k}{}_{t,j}$) = the probability of being in habitat k at occasion $i + 1$, given that the bird was alive and in the overall study area at occasion $i + 1$ and in habitat j at occasion i;

and

Sighting probability ($\mathbf{p}_{i,j}$) = the probability that a bird alive in habitat j during occasion i is sighted during that occasion.

As is general for restricted-area capture-mark-resighting studies based on live encounters only, the estimates of survival ignore potential permanent emigration from the study area and therefore were likely biased low. Although we tested for movements between two habitats, our birds could still be alive but move out of our study area that covered both habitats.

This modelling approach is well suited for our dataset, which is limited to six occasions (the periods when birds are sighted) and five intervals with the main objective to evaluate movements between two habitats. The study spanned three winters (2001/02, 2002/03, and 2003/04) and each winter was divided into two occasions: 1) early winter, from 1 November–31 December; and 2) late winter, from 1 January–28 February. We split each winter into two occasions because: 1) Snow Geese arrived from mid-November through December and began to leave in mid-January through February (Jónsson 2005); and 2) the analysis needed to allow for movements within winter because if Snow Geese in the two habitats were one population, we assumed they would use both habitats within each winter. During field observations, occasions within each of the three winters were defined as: 1) early winter, from 1 November–31 December; and 2) late winter, from

1 January–28 February. The survival intervals thus lasted respectively 2 months (1 November–31 December) and 10 months (1 January to 1 November). The estimates of **Φ** were scaled to the estimated annual apparent survival (by adjusting interval length values so they added up to 1.0, *i.e.* 0.167 (2 months) and 0.833 (10 months)), whereas **Ψ** measured the probability of moving from one habitat to the other between successive occasions and **p** measured the probability of encounter on each occasion.

Minimising possible violations of independence

When individuals were sighted more than once (range = 2–4 times) for a given occasion (within early or late winter), we coded it as one sighting event. With three exceptions, all such multiple sightings occurred within the same habitat; habitats were assigned to the three exceptions using random numbers, with even numbers being assigned to rice-prairies and odd numbers to coastal marshes.

The analyses were restricted to adults because: 1) only 28 sightings were obtained of juveniles (141 were banded, Jónsson 2005); and 2) juveniles do not behave independently of their parents (Lebreton *et al.* 2002). Including both members of a marked pair would cause their respective observation history to be over-represented by the frequency of one (Schmutz *et al.* 1995), and paired birds where both individuals were marked comprised 8.5% (25 pairs in total) of resighted neck-collared Snow Geese (see Jónsson & Afton 2008 for frequencies of pairs and families in this population). Thus, one observation history representing one member of each pair from the distribution of observation histories was removed by: 1) assigning random numbers from a set of 100 numbers to each pair; 2) then deleting male data from pairs with odd random numbers; and 3) deleting female data from pairs with even random numbers.

Sex effects frequently are analysed in mark-recapture studies of birds; however, our preliminary analyses indicated that models with sex effects performed poorly (see Jónsson 2005). Thus, we pooled the sexes in the analysis.

Two rounds of model selection

Currently, we are not aware of methods for directly testing for population segregation using mark-resightings data. We therefore followed conventional model selection (Cooch & White 2010), where effects of site (habitat) and time, and their interaction were included and evaluated. Our research question focused on whether Snow Geese moved between rice-prairies and coastal marshes, *i.e.* the value of **Ψ** that would eventually be estimated by the final model determined by AIC model selection. Assuming no interval variation in **Ψ**, no movements detected between habitats (**Ψ** = 0) could be inferred, as there were two, segregated sub-populations, despite there being insufficient time for the evolution of genetic differentiation. Conversely, under the same assumption of no interval variation, if movements (**Ψ** notably higher than 0) were detected, we could conclude that marked Snow Geese comprised one population. However, the situation may not represent such polar opposites if there is substantial variation in movement probabilities between intervals. In fact, a finding of substantial interval variation would indicate a more dynamic situation than that predicted by either liberal habitat selection or strict population segregation.

To obtain estimates of **Ψ**, we selected the best model using conventional multi-state model selection in MARK (Cooch & White 2010). The model selection process determined only the most parsimonious models on the basis of the data available, however, and estimated whether parameters differed or were similar between intervals. We tested for habitat effects on **Φ**, but for **Ψ** and **p** we kept habitat effects in all models due to design considerations. For example: 1) removing habitat from **p** would have ignored obvious differences in sighting probabilities between habitats; and 2) there is no real biological reason to expect **Ψ** to be the same for each habitat, especially since Snow Geese arrive later at the coastal marshes (December) than at the rice-prairies (November; Jónsson 2005). A previous study reported that marsh Snow Geese were larger but also displayed less variation in body size measurements than rice-prairie Snow Geese, indicating more restrictive selection on bill size in marshes than in rice-prairies (Alisauskas 1998). This knowledge, which is confirmed by the data (Jónsson 2005), further contributed to the view that models without a habitat effect on **Ψ** made no biological sense.

We had *a priori* reasons to expect stronger habitat effects on **Ψ** in marshes, which was accounted for by comparing interactive (h*t) models to additive (h + t) models, with t being the time interval in each case. For **Ψ**, interactions might be expected where the parameters could be positively related to conditions in the marsh, but not the rice-prairies. This led to the inclusion of additive models, *i.e.* comparing h + t *versus* h*t for **Ψ**. The additive models (habitat + interval) tested if habitat differences in **Ψ** were constant over all the 5 intervals, whereas the interactive models (habitat*interval) allowed habitat differences in **Ψ** to differ among the 5 intervals.

Two multi-state analyses were conducted. Firstly, **Φ** and **Ψ** were estimated for all observation histories (hereafter full dataset analysis). A second analysis was restricted to the subsample of 388 adults for which morphometrics data were available, to examine whether body size, an index of the morphs based on principal components analysis (following Alisauskas 1998), was related to **Φ** or **Ψ** (hereafter covariate analysis).

Model selection one: full dataset

Given that we pooled the sexes, the most general model (hereafter global model) was **Φ**(habitat*interval) **p**(habitat*interval) **Ψ**(habitat*interval), with 30 structural parameters. In this global model, effects of habitat and the time interval were interactive, *i.e.* effects of one variable were dependent on the level of the other for all three parameters. This model had 28 estimable parameters of 30 possible parameters, which was expected given that one combination of the final **Φ**, **p** and **Ψ** was unidentifiable for each site. Model selection began with the global model and created the subsequent models considered by removing the time effect from one, two or all parameters: **Φ**, **p** or **Ψ**. The relevant models were then added without habitat effect (**Φ**. models) on annual apparent survival. Finally, additive models (main effects models) were considered, *i.e.* the habitat + interval (main effects) models that corresponded to the habitat*time models (interactive models) for **Ψ** because of the biological interest in movements between habitats. Thus, 17 models in total were considered in the analysis of the full dataset.

U-Care (Pradel *et al.* 2003) was used to examine models for structural integrity (goodness-of-fit, hereafter GOF). U-Care was also used to calculate $\hat{c}$ to adjust model selection for overdispersion. When needed, Quasi-likelihood adjusted Akaike's Information Criterion ($QAIC_c$) was used to rank models according to $QAIC_c$ differences between models ($\Delta QAIC_c$; Burnham & Anderson 2002); otherwise, we present AIC_c.

Model selection two: covariate analysis

As observed in 1983 and 1984 by Alisauskas (1998), marsh Snow Geese in our study (from winters 2001/02–2003/04), had proportionally thicker bills and wider skulls than did rice Snow Geese (see Jónsson 2005), which may affect their habitat selection, movement probability and survival rates. The effects of body size therefore were evaluated by their inclusion as a covariate in the mark-resighting analyses. Prior to the covariate analysis, morphometrics were chosen by comparing the morphology of rice and marsh Snow Geese using principal components analysis (PCA; body size measures assessed are listed in Appendix 1). The highest ranked model from the full dataset analysis was used as starting models in the covariate analysis (see results). Based on the findings of Alisauskas (1998), we expected *a priori* that the first principal score (PC1), which has similar loadings for all variables and thus represents overall body size, would represent the bulk of the variation in morphometrics (≥ 50%) and this proved to be the case (Appendix 1). PC1 therefore was added to the highest-ranked model from the first analysis to examine if overall body size affected **Φ**, **Ψ**, or both. Other PC scores each represented < 10% of the overall variation, and thus, are not included here. The covariate analysis had an effective sample size of 525, whereas the analysis of the full dataset had an effective sample size of 1,190. Basically, if parameters **Φ** or **Ψ** were influenced by body size, the respective covariate model(s) would: 1) have lower AIC values than the model used as a starting point in the covariate analysis; 2) contain a significant relationship between PC1 and individual **Ψ** or **Φ**, with a slope (β) significantly different from zero.

If larger bill size or body size improved survival within coastal marshes or rice-prairies, models which included them as covariates on annual apparent survival would represent improvements over models without covariates. If bill size or body size were related to habitat choice, models which included them as covariates on movement probability would represent improvements over models without covariates.

Results

A total of 993 adult Snow Geese were captured and marked with neck-collars. In the field, 906 sightings were recorded (not counting initial marking) of 295 adults during the study and used for the full analysis. We recorded morphometrics for a subsample of 388 adult Snow Geese and obtained 180 sightings (not counting initial marking) of 120 individuals for the covariate analysis.

Full dataset analysis

For the full data set, results from GOF analysis were as follows: 1) Test WBWA: $\chi^2_5 = 6.8$, $P = 0.236$, n.s., indicated no memory effect. 2) Test 3G.SR: $\chi^2_6 = 22.5$, $P = 0.001$ indicated a transience, *i.e.* higher probability of mortality or higher permanent emigration after first capture. 3) Test 3G.Sm: $\chi^2_{15} = 29.6$, $P = 0.013$, indicated further heterogeneity related to time since marking. 4) Test M.ITEC: $\chi^2_4 = 8.7$, $P = 0.069$, n.s., indicated no immediate trap-dependence. 5) Test M.LTEC: $\chi^2_2 = 0.8$, $P = 0.683$, n.s., indicated no long-term trap-dependence. 6) Total: $\chi^2_{32} = 68.4$, $P < 0.0001$, indicated an overall lack of fit. Thus, there was some heterogeneity in survival in the full dataset, related to time since marking, and a variance inflation factor ($\hat{c}$) therefore was calculated and used to adjust the fit of the data (68.4/32 = 2.14).

Based on $\mathrm{QAIC_c}$ values < 2, the model $\mathbf{\Phi}$(.) $\mathbf{p}$(h*t) $\mathbf{\Psi}$(h*t) was the preferred model (Table 1). This model estimated annual apparent $\mathbf{\Phi}$ ($\mathbf{\Phi} \pm$ s.e.) as 0.601 ± 0.082, independent of both habitat and interval (Table 2). Estimated sighting probabilities were much higher for rice-prairies (range: 0.287–0.534 for 5 time intervals) than coastal marshes (0.020–0.072, for 3 of 5 intervals; Table 2). Two **p** estimates were reported as 1.000 for intervals 1 and 2 in coastal marshes, which corresponds to the model inferring that all marked geese were seen alive and present in the marsh habitat on these first two occasions. We believe that these two estimates of **p** are overestimates, caused by sparse data for these two intervals within the coastal marshes within the first winter 2001/02. Estimates of **p** improved as the study progressed with improved observation efforts and more bandings. Estimated probabilities of moving from coastal marshes to rice prairies were higher (range: 0.000–0.981) than the probabilities of moving from rice prairies to marshes (range: 0.000–0.564) (Table 2). The $\mathbf{\Psi}$ for intervals 1 and 5 in rice-prairies and interval 5 in coastal marshes were estimated as 0 (with s.e. > 0), indicating that any movements between these habitats during these within-winter time periods were rarely observed.

Covariate analysis

For the covariate data set, the GOF results were as follows: 1) Test WBWA: $\chi^2_2 = 0.6$, $P = 0.746$, n.s., indicated no memory effect; 2) Test 3G.SR: $\chi^2_7 = 6.3$, $P = 0.505$, n.s., indicated that there was no transience effect; 3) Test 3G.Sm: $\chi^2_{14} = 14.5$, $P = 0.416$, n.s., indicated no further heterogeneity related to time since marking; 4) Test M.ITEC: $\chi^2_3 = 1.5$, $P = 0.685$, n.s., indicated no immediate trap-dependence; 5) Test M.LTEC: $\chi^2_2 = 0.5$, $P = 0.792$, n.s., indicated no long-term trap-dependence; and 6) Total: $\chi^2_{28} = 23.3$, $P = 0.718$, n.s., indicated no lack of fit. Thus, we did not calculate a $\hat{c}$ to adjust the covariate analysis (see Cooch & White 2010) and present $\mathrm{AIC_c}$ instead of $\mathrm{QAIC_c}$. We suspect the

Table 1. Model selection for obtaining parameter estimates of annual apparent survival (**Φ**), sighting probability (**p**), and movement probability (**Ψ**) for Lesser Snow Geese neck-collared in southwest Louisiana in winters 2001/02, 2002/03, and 2003/04. Models with $\Delta QAIC_c > 2$ essentially have little or no support. *K* = the number of parameters in each model; Qdev = deviance. Model used for inference is indicated in bold.

Rank	**Model**	**$\Delta QAIC_c$**	**$\Delta QAIC_c$ weight**	**Model likelihood**	***K***	**Qdev**
1	**Φ**(.) **p**(h*t) **Ψ**(h*t)	0.0	0.428	1.0000	21	123.1
2	**Φ**(h) **p**(h*t) **Ψ**(h*t)	1.7	0.182	0.4244	22	122.7
3	**Φ**(.) **p**(h*t) **Ψ**(h+t)	2.3	0.134	0.3129	17	133.7
4	**Φ**(h) **p**(h*t) **Ψ**(h+t)	3.8	0.065	0.1517	18	133.0
5	**Φ**(h*t) **p**(h*t) **Ψ**(h+t)	3.8	0.065	0.1515	23	122.7
6	**Φ**(h) **p**(h) **Ψ**(h*t)	4.0	0.059	0.1376	14	141.5
7	**Φ**(.) **p**(h) **Ψ**(h*t)	4.3	0.051	0.1194	13	143.8
8	**Φ**(h*t) **p**(h*t) **Ψ**(h)	9.5	0.004	0.0087	22	130.5
9	**Φ**(h*t) **p**(h) **Ψ**(h*t)	9.6	0.004	0.0084	22	130.6
10	**Φ**(h*t) **p**(h*t) **Ψ**(h*t)	9.6	0.004	0.0084	28	118.0
11	**Φ**(.) **p**(h*t) **Ψ**(h)	10.1	0.003	0.0063	13	149.7
12	**Φ**(.) **p**(h) **Ψ**(h+t)	11.4	0.001	0.0033	9	159.2
13	**Φ**(h) **p**(h*t) **Ψ**(h)	12.0	0.001	0.0025	14	149.5
14	**Φ**(h) **p**(h) **Ψ**(h+t)	12.1	0.001	0.0023	10	157.8
15	**Φ**(h*t) **p**(h) **Ψ**(h)	15.8	0.000	0.0004	14	153.3
16	**Φ**(h) **p**(h) **Ψ**(h)	26.0	0.000	0.0000	6	179.8
17	**Φ**(.) **p**(h) **Ψ**(h)	26.3	0.000	0.0000	5	182.2

habitat (h): rice-prairies or coastal marshes.
time (t): temporal variation, *i.e.* early or late winter, specific for each winter (2001/02, 2002/03, and 2003/04).
(.) with a variable means it was independent of habitat and time, *i.e.* held constant.
* indicates an interaction between variables.
+ indicates that effects of variables were additive.

morphometric sub-sample may have become more balanced with respect to movements than the full dataset (possibly by chance or an inherent randomness of the sub-sample), and thus, not requiring an $\hat{c}$ adjustment.

Table 2. Parameter estimates for annual apparent survival (Φ), sighting probability (**p**) and movement probability (Ψ) for Lesser Snow Geese neck-collared in southwest Louisiana during winters 2001/02–2003/04, based on the highest ranked model in Table 1. The model indicated that Φ was constant (no interval effect) and the same for both habitats, whereas **p** and Ψ differed between habitats and were time-dependent (had an interval effect).

		Rice-prairies		**Coastal marshes**	
Parameter	**Interval**	**Estimate**	**s.e.**	**Estimate**	**s.e.**
Annual apparent survival (Φ)	Constant	0.601	0.082	0.601	0.082
Sighting probability (**p**)	1	0.299	0.071	1.000	0.000
	2	0.287	0.063	1.000	0.000
	3	0.489	0.118	0.033	0.021
	4	0.534	0.082	0.020	0.014
	5	0.343	0.087	0.072	0.028
Movement probability (Ψ)	1	0.000	0.000	0.797	0.085
	2	0.017	0.024	0.981	0.019
	3	0.564	0.129	0.845	0.119
	4	0.000	0.000	0.220	0.068
	5	0.148	0.165	0.000	0.000

Intervals: 1 = observations made in 1 Nov–31 Dec 2001 compared with those in 1 Jan–28 Feb 2002; 2 = from 1 Jan–28 Feb 2002 to 1 Nov–31 Dec 2002; 3 = from 1 Nov–31 Dec 2002 to 1 Jan–28 Feb 2003; 4 = from 1 Jan–28 Feb 2003 to 1 Nov–31 Dec 2003; 5 = from 1 Nov–31 Dec 2003 to 1 Jan–28 Feb 2004. s.e. = standard error.

We began the covariate model selection with the most parsimonious and best supported model from Table 1. We then proceeded to add our index of overall body size, PC1, as a covariate to this starting model, as follows: 1) PC1 was added to Ψ for all intervals; 2) PC1 was added to Ψ for all intervals but only for coastal marshes and not rice-prairies; 3) PC1 was added to the Φ parameter; 4) PC1 was added to the Φ parameter but only for coastal marshes and not for rice-prairies; 5) PC1 was added to Φ and Ψ parameters simultaneously; 6) PC1 was added to Φ but only for the interval November–February (within winter) and not the March–October interval; and 7) PC1 was added to a habitat effect on Ψ, testing an interaction between habitat and body size. All these covariate models failed to outperform the starting model (see Appendix 2), and thus, we concluded that there was no effect of body size on annual apparent survival or movement probabilities.

Adding PC1 (Appendix 1 for PCA results) as a continuous covariate did not improve the best model, nor did it improve any of the 17 models in Table 1; it generally increased AIC values by 1–3.2, despite adding only 1 or 2 parameters to each model (Appendix 2). Since all of the covariate models failed to out-perform the starting model, they cannot be considered equally plausible despite some of them having a ΔAIC < 2.0. The starting model was the best supported model in this analysis. The second-best model, *i.e.* relatively the best of the covariate models, which included an effect of PC1 on movement probability for all intervals and both habitats, was poorly supported (ΔAIC_c = 1.0 (Appendix 2), and the estimated slope was negative (β = –0.127, 95% C.I. = –0.327–0.073). The third-best model, (*i.e.* second best of the covariate models), which included an effect of PC1 on movement probability for all intervals but only in the coastal marshes, was likewise poorly supported (ΔAICc = 1.2 (Appendix 2), and the estimated slope was negative again, opposite to expectations that the larger marsh birds would be less likely to move to the rice fields (β = –0.121, 95% C.I. = –0.324–0.083). All the covariate models had β that did not differ from 0; *i.e.* had 95% C.I. that surrounded 0. Thus, we concluded on the basis of the current dataset that PC1 did not affect Φ or Ψ for candidate models that included body size as a covariate.

Discussion

We frequently observed Snow Geese moving between coastal marshes and rice-prairies. Admittedly, the sample power is low, study duration was short and **p** for two intervals were non-estimable; nevertheless, we believe the analysis is valid for addressing the main question regarding the presence of movements between habitats in Louisiana. The dataset shows that such movements can be common, at least from coastal marshes to the rice-prairies, and that there is temporal variation in movement probabilities. We suspect that certain groups of Snow Geese are more likely to use the marshes and that Snow Geese are somewhat site-faithful, but as indicated by the interval effect on movement probability, this may depend on temporal variation in weather conditions or perhaps local depletion of food. The addition of a body size covariate did not improve any of the models considered. There was no reason to doubt a habitat effect (h*t or h) on movement probability (Ψ) but there was little support for a habitat effect on annual apparent survival (Φ). Thus, although Snow Geese that frequent marsh habitats in winter are generally larger in size than those from adjacent rice-prairies (Alisauskas 1998; Jónsson 2005), there was little evidence from our study to suggest that bill size influences annual apparent survival or movement probabilities across these two habitats.

Our findings also indicate that movement probabilities were highly variable between intervals, as indicated by models with only habitat effects on Ψ performing poorly in the model selection. For birds marked in the rice-prairies, movements to the coastal marshes were extremely rare in three intervals, but during two of them, movements were at least notable (interval 5, within the 2003/04 winter) and common (interval 3, within the 2002/03 winter). For birds marked in the coastal marshes, movements to the rice-prairies were very common during the first three intervals, notable in interval 4 but extremely rare in the fifth interval. We interpret these interval-specific movement probabilities as responses to shifts in environmental conditions. Although Snow Geese banded in coastal marshes moved into rice-prairies and *vice versa*, the banded birds still differed in morphological size between the habitats (Jónsson 2005). The morphometric differentiation varied annually between habitats in the study area (Jónsson 2005), as reported by Alisauskas (1998). Morphology and associated niche selection may vary annually in relation to alternation of wet and dry years, or frequencies of storm fronts, which potentially affect food resources (Alisauskas *et al.* 1988, 1998). For example, wet years may favour one bill morph type whereas drier years favour the other (Grant & Grant 2002). The predicted relationships, based on the hypotheses, presumed constant environmental conditions, but once environmental variation (weather, food depletion) alters the habitat conditions for Snow Geese, then further interactions between rice-prairies and coastal marshes are expected.

Mid-winter survey numbers of Snow Geese, averaged for the three winters of the study, were 213,954 and 88,042 for rice-prairies and coastal marshes, respectively (Fronczak 2004). If these numbers are multiplied with movement probabilities in Table 2, up to 120,000 Snow Geese moved between the two habitats, during the intervals with the highest movement probabilities, which in turn represents 40–50% of the Snow Geese observed within winter surveys 2001/02–2003/04 (Fronczak 2004). Conversely, there were 3–4 intervals where hardly any movements were observed from either habitat. Thus, the two groups of banded birds can interact, at least once every 1–3 years, suggesting that they do not represent segregated sub-populations, and that population-specific habitat management may not be necessary. Humphries *et al.* 2009 found no differentiation in mitochondrial DNA between Snow Geese from these two habitats, although they urged further work with nuclear DNA to better understand population connectivity and structuring. However, a genetic component to the population structure may be unlikely, given that our findings suggest that movements can be substantial between habitats in 1–2 out of every five intervals. Despite the winter pair formation in Snow Geese (Ganter *et al.* 2005), we suspect that some mixing of the two groups may also occur on the breeding grounds.

Annual apparent survival estimates were similar between habitats. Our estimate of apparent annual survival (0.601) was within the lower range of those reported for other Snow Goose populations (0.6 and 0.9, depending on location and year; Mowbray *et al.* 2000; Calvert & Gauthier 2005; Table 4 in McWilliams *et al.* 2008; Fig. 9 in Alisauskas *et al.* 2011). These estimates are also slightly lower than those reported for Ross's Geese (Drake & Alisauskas 2004; Alisauskas *et al.* 2006) and for Black Brant *Branta bernicla nigricans* within certain years (Lindberg *et al.* 1998). As mentioned above, our survival estimates are likely to be biased low due to permanent emigration from the overall study area. Contrary to that for movement probabilities, there was no evidence to suggest that survival rates differed between the time intervals, similar to results reported for other large waterfowl (Varner & Eichholz 2012).

Neck-collars have been reported to reduce body condition and survival of Snow Geese (Legagneux *et al.* 2013) and the closely related Ross's Geese (Caswell *et al.* 2012). A suspected effect on body condition is that neck-collars increase energy expenditure (due to elevated drag during flight or to stress) or reduce their foraging efficiency (Legagneux *et al.* 2013). While we acknowledge that such effects probably were present in our study, predicting any directional or behavioural effects on movement probabilities, or habitat choices, is difficult without further empirical data. Apparently, breeding propensity is reduced in neck-collared Snow Geese (Legagneux *et al.* 2013) and we noted that although we frequently caught pairs and observed them together, these birds were only twice reliably seen accompanied by juvenile geese. Thus, our collared birds could have been of mid- or lower social status (Jónsson & Afton 2008) and such birds may be more exploratory or more easily displaced from favourable feeding locations.

Annual apparent survival estimates from our dataset possibly were confounded by differing emigration rates (Williams *et al.* 2008). Coastal marshes are the southernmost part of the mid-continental population's winter range. The geographical distribution of marshes is restricted to the Gulf Coast, whereas that of rice-prairies includes all inland agricultural habitats in general, from southwest Louisiana northwards and even into Arkansas or Missouri.

Snow Geese are hunted on most days within the sighting periods, both during regular season and during the special hunting season. Hunting pressure may be variable within rice-prairies or coastal marshes from year to year, and potentially differs between habitats, at least in some years. We suspect that hunting opportunities in coastal marshes have a more clumped distribution than those in the rice-prairies. Most Snow Geese in the coastal marshes are found at State Wildlife Refuge or the Marsh-Island NWR, where hunting is not allowed. Thus, we suspect that some Snow Geese may use the marshes as refuge from the hunter pressure in the rice-prairies, and return to the rice-prairies on days when hunting pressure declines.

In recent decades, environmental conditions generally have been favourable on the wintering grounds of Snow Geese (Abraham *et al.* 2005). The acreage of wildlife refuges or semi-natural wetlands in the vicinity of feeding habitats positively influences the survival of wintering geese (Gauthier *et al.* 2005; Elphick 2008). The combination of refuges and rice-farming may explain why Snow Geese continue to use both habitats, despite the population increase in agricultural habitats and the higher intake rates in rice-prairies (Jónsson

& Afton 2006). Movements between these habitats may be diurnal movements or restricted to certain time-periods within winter. Subsequent research using telemetry could determine the exact nature of these movements. Our study spanned winters 2001/02–2003/04. Hunter recoveries of these banded birds from 2001/02–2012/13 (Jónsson & Afton, unpubl. data) have shown that the timing of sampling and the earliest migratory movements by Snow Geese coincide with one another. In fact, data from 2001/02–2012/13 have shown that our marked Snow Geese can be recovered in Louisiana, Arkansas or Missouri in late January or early February. We suspect that such early, northwards migratory movements may partly explain the asymmetry in movements from coastal marshes to rice-prairies. This stems partly from logistical restraints on the sampling design, as well as the ability of Snow Geese to alter migratory patterns in response to early or late onsets of spring at locations throughout their midcontinent flyways.

We conclude, based on our data, that Snow Geese in coastal marshes do not comprise a segregated sub-population. Annual apparent survival does not differ appreciably from that of Snow Geese in the rice-prairies or other parts of their wintering range. Snow Geese select and use both habitats, but the general importance of each habitat may differ between years. Although Snow Geese can display strong fidelity to winter locations (Johnson 1996; Williams *et al.* 2008), they also change diets or habitats within a given winter, and during migration through adjacent habitats. These changes may be influenced by weather or hunting pressure as well as resource availability (Hill & Frederick 1997; Hénaux *et al.* 2012). In Louisiana, combinations of frost and drought can kill emerging green vegetation in some years and such events can impact food availabilities differently in rice-prairies and coastal marshes (Alisauskas 1998). In certain years, Gulf Coast marshes may be important habitats, even to Snow Geese that normally would not winter there (Alisauskas *et al.* 1998). Furthermore, if rice acreage decreases in the future, or vast areas of rice-fields are destroyed by salt-water intrusion, increased use of the coastal marshes by Snow Geese may occur. Notably, rice acreage in the state of Louisiana averaged 520,600 acres/year during 2001–2005, but declined to an average of 428,150 acres/year in 2006–2013 (U.S. Department of Agriculture 2014). Annual variation in food availability and concomitant variation in movement patterns may also be affected by variation in rice production or the timing of rice harvesting.

Rainfall affects water levels in rice-fields and coastal impoundments and can interfere with beneficial marsh burns in coastal marshes; lack of successful marsh burns reduce the attractiveness of coastal marshes to Snow Geese (Gabrey & Afton 2004). Climate events such as hurricanes can alter water levels or other factors that affect access to feeding grounds or interfere with marsh burns or rice plantings. All these variations probably favour some movements between habitats, which are adaptive for the long-term future of Snow Geese.

The movements documented here and the observed differences between habitats by bill size may be more congruent with habitat selection than with phenotypic selection (both scenarios were hypotheses of Alisauskas 1998) because the phenotypic selection hypothesis posits natural selection within habitats, which leads to different bill morphologies, which ultimately must assume limited exchange of Snow Geese between habitats. Resource availability probably affects use of these two habitats by wintering Snow Geese. New research to assess relative values of rice-prairies and coastal marshes under different conditions across the size spectrum of Snow Geese would be useful to inform wildlife managers. However, such a study would take many years, and need to account for annual variation due to weather (particularly precipitation) and the resulting availability of standing water, frequency of marsh burns and Snow Goose numbers present. Such a study should also quantify hunter activity or hunting pressure, collect data on movements of Snow Geese using radio telemetry, and lastly, consider annual variation in morphological measurements (Alisauskas 1998; Jónsson 2005).

Acknowledgements

Our study was funded by the Canadian Wildlife Service, Louisiana Department of Wildlife and Fisheries (LDWF), Delta Waterfowl Foundation, Rockefeller Scholarship program, and the USGS-Louisiana Cooperative Fish and Wildlife Research Unit, Graduate School, Agricultural Center, and School of Renewable Natural Resources at Louisiana State University. We thank D. Blouin, B. Barbe, M. Chamberlain, W. Henk, D. Homberger, R.N. Helm (deceased), D. Caswell, R. Elsey, G. Perrie, C. Jeske (deceased), J. Linscombe, T. Hess (deceased), M. Hoff, W. Norling and S. Lariviere for their valuable input and support. R. Choquet and C. Nicolai advised on the use of MARK and U-Care. We especially thank the staff of Rockefeller SWR, Cameron Prairie NWR, Sabine NWR, Sweet Lake Land and Oil Co. and LDWF, who kindly provided housing and logistical support. C.J. Michie, B. Meixell, M. Pollock, T. Blair, J. Yurek, and P. Becnel read neck-collars. We thank all those who volunteered to assist with capture and neck-collaring of Snow Geese (see list in Jónsson 2005). R. Alisauskas, B. Clark, J.-F. Giroux, T.G. Gunnarsson and an anonymous reviewer provided helpful comments on earlier drafts of the manuscript.

References

Amat, J.A. & Varo, N. 2008. Grit ingestion and size-related consumption of tubers by Graylag Geese. *Waterbirds* 31: 133–137.

Abraham, K.F., Jefferies, R.L. & Alisauskas, R.T. 2005. The dynamics of landscape change and Snow Geese in mid-continent North America. *Global Change Biology* 11: 845–855.

Alisauskas, R.T. 1998. Winter range expansion and relationships between landscape and morphometrics of midcontinent Lesser Snow Geese. *Auk* 115: 851–862.

Alisauskas, R.T., Drake, K.L., Slattery, S.M. & Kellett, D.K. 2006. Neckbands, harvest and survival of Ross's Geese from Canada's Central Arctic. *Journal of Wildlife Management* 70: 89–100.

Alisauskas, R.T., Ankney, C.D. & Klaas, E.E. 1988. Winter diets and nutrition of midcontinental Lesser Snow Geese. *Journal of Wildlife Management* 52: 403–414.

Alisauskas, R.T., Klaas, E.E., Hobson, K.A. & Ankney, C.D. 1998. Stable-carbon isotopes support use of adventitious color to discern winter origins of Lesser Snow Geese. *Journal of Field Ornithology* 69: 262–268.

Alisauskas, R.T., Rockwell, R.F., Dufour, K.W., Cooch, E.G., Zimmerman, G., Drake, K.L, Leafloor, J.O., Moser, T.J. & Reed, E.T. 2011. Harvest, survival and abundance of midcontinent Lesser Snow Geese relative to population reduction efforts. *Wildlife Monographs* 179: 1–42.

Bateman, H.A., Joanen, T. & Stutzenbaker, C.D. 1988. History and status of midcontinent Snow Geese on their Gulf Coast winter range. *In* M.W. Weller (ed.), *Waterfowl in Winter*, pp. 495–515. University of Minnesota Press, Minneapolis, Minnesota, USA.

Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multi-model Inference*. Springer-Verlag Telos, Berlin, Germany.

Calvert, A.M. & Gauthier, G. 2005. Effects of exceptional conservation measures on survival and seasonal hunting mortality in Greater Snow Geese. *Journal of Applied Ecology* 42: 442–452.

Caswell, J.H., Alisauskas, R.T. & Leafloor, J.O. 2012. Effect of neckband color on survival and recovery rates of Ross's Geese. *Journal of Wildlife Management* 76: 1456–1461.

Cooch, E.G. & White, G.C. 2010. Program MARK – a gentle introduction. Accessible at http://www.phidot.org/software/mark/docs/book/ (last accessed 7 April 2014).

Cope, D.R., Loonen, M.J.J.E., Rowcliffe J.M. & Pettifor, R.A. 2005. Larger Barnacle Geese (*Branta leucopsis*) are more efficient feeders: a possible mechanism for observed body size-fitness relationships. *Journal of Zoology, London* 265: 37–42.

Durant, D., Fritz, H., Blais, S. & Duncan, P. 2003. The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size. *Journal Animal Ecology* 72: 220–231.

Drake, K.L. & Alisauskas, R.T. 2004. Breeding dispersal by Ross's Geese in the Queen Maud Gulf metapopulation. *Animal Biodiversity and Conservation* 27: 331–341.

Dzubin, A. & Cooch, E.G. 1992. *Measurements of Geese: General Field Methods*. California Waterfowl Association, Sacramento, California, USA.

Elphick, C. 2008. Landscape effects on waterbird densities in California rice fields: taxonomic differences, scale-dependence, and conservation implications. *Waterbirds* 31: 62–69.

Fronczak, D. 2004. *Waterfowl Harvest and Population Survey Data*. U.S. Fish and Wildlife Service, Division of Migratory Bird Management, Columbia, Missouri, USA.

Gabrey, S.W. & Afton, A.D. 2004. Composition of breeding bird communities of Gulf Coast Chenier Plain marshes: effects of winter burning. *Southeastern Naturalist* 3: 173–185.

Ganter, B., Boyd, W.S., Baranyuk, V.V. & Cooke, F. 2005. First pairing in Snow Geese *Anser caerulescens*: at what age and at what time of year does it occur? *Ibis* 147: 57–66.

Gauthier G., Giroux, J.-F., Reed, A., Bechet, A. & Belanger, L. 2005. Interactions between land use, habitat use and population increase in Greater Snow Geese: what are the consequences for natural wetlands? *Global Change Biology* 11: 856–868.

Grant, P.R. & Grant, B.R. 2002. Unpredictable evolution in a 30-year study of Darwin's Finches. *Science* 296: 707–711.

Harris, G.A. 1990. Grit site use by wildlife in southwestern Louisiana and southeastern Texas. M.Sc. thesis, Louisiana State University, Baton Rouge, Louisiana, USA.

Hénaux V., Powell, L.A., Vrtiska, M.P. & Hobson, K.A. 2012. Establishing winter origins of migrating Lesser Snow Geese using stable isotopes. *Avian Conservation and Ecology* 7(1): 5.

Hill, M.R.J., & Frederick, R.B. 1997. Winter movements and habitat use by Greater Snow Geese. *Journal of Wildlife Management* 61: 1213–1221.

Humphries, E.M., Peters, J.L., Jónsson, J.E., Stone, R., Afton, A.D. & Omland, K.E. 2009. Genetic differentiation between sympatric and allopatric wintering populations of Snow Geese. *Wilson Journal of Ornithology* 21: 730–738.

Johnson, S.R. 1996. Staging and wintering areas of Snow Geese nesting on Howe Island, Alaska. *Arctic* 49: 86–93.

Jónsson, J.E. 2005. Effects of body size and habitat use on goose behavior: Lesser Snow Goose and Ross's Goose. Ph.D. thesis, School of Renewable Natural Resources, Louisiana State University, Baton Rouge, Louisiana, USA.

Jónsson, J.E. & Afton, A.D. 2006. Differing time and energy budgets of Lesser Snow Geese in rice-prairies and coastal marshes in southwest Louisiana. *Waterbirds* 29: 451–458.

Jónsson, J.E. & Afton, A.D. 2008. Lesser Snow Geese and Ross's Geese form mixed flocks during winter but differ in family cohesiveness and social status. *Wilson Journal of Ornithology* 120: 725–731.

Jónsson, J.E. & Afton, A.D. 2009. Time budgets of Snow Geese and Ross's Geese in mixed flocks: implications of body size, ambient temperature and family associations. *Ibis* 151: 134–144.

Larsson, K. & Forslund, P. 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. *Journal of Evolutionary Biology* 4: 619–636.

Lebreton, J.D. & Pradel, R. 2002. Multistate recapture models: Modeling incomplete individual histories. *Journal of Applied Statistics* 29: 353–369.

Legagneux, P., Simard, A.A., Gauthier, G. & Bety, J. 2013. Effect of neck collars on the body condition of migrating Greater Snow Geese. *Journal of Field Ornithology* 84: 201–209.

Lindberg, M.S., Sedinger, J.S., Derksen, D.V. & Rockwell, R.F. 1998. Natal and breeding philopatry in a Black Brant, *Branta bernicla nigricans*, metapopulation. *Ecology* 79: 1893–1904.

Morez, V., Gauthier, G. & Reed, A. 2000. Effect of body condition on vulnerability of Greater Snow Geese to hunting and capture. *Journal Wildlife Management* 64: 875–886.

Mowbray, T.B., Cooke, F. & Ganter, B. 2000. Snow Goose (*Chen caerulescens*). *In* A. Poole & F. Gill (eds.), The Birds of North America, No. 514. The Academy of Natural Sciences, Philadelphia, PA, USA, and The American Ornithologists' Union, Washington D.C., USA. Accessible at http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/514 (last accessed 7 Apr 2014).

Pradel, R., Wintrebert, C.M.A. & Gimenez, O. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwartz multisite capture-recapture model. *Biometrics* 59: 43–53.

Prevett, J.P. & MacInnes, C.D. 1980. Family and other social groups in Snow Geese. *Wildlife Monographs* 71: 6–46.

Samelius, G. & Alisauskas, R.T. 2009. Habitat alteration by geese at a large arctic goose colony: consequences for lemmings and voles. *Canadian Journal of Zoology* 87: 95–101.

Schmutz, J.A., Ward, D.H., Sedinger J.S. & Rexstad, E.A. 1995. Survival estimation and the effects of dependency among animals. *Journal of Applied Statistics* 22: 673–681.

Scott, S.N., Clegg, S.M., Blomberg, S.P., Kikkawa, J. & Owens, I.P.F. 2003. Morphological shifts in island-dwelling birds: the roles of generalist foraging and niche expansion. *Evolution* 57: 2147–2156.

Smith, T.B. 1990. Resource use by bill morphs of an African finch: evidence for intraspecific competition. *Ecology* 71: 1246–1257.

U.S. Department of Agriculture. 2014. Rice online. Rice industry news from around the world. Rice Acreage. Accessible at https://www.riceonline.com/usda_information (last accessed 7 April 2014).

van der Graaf, A.J., Coehoorn, P. & Stahl, J. 2006. Sward height and bite size affect the functional response of Barnacle Geese *Branta leucopsis*. *Journal of Ornithology* 147: 479–484.

Varner, D.M. & Eichholz, M.W. 2012. Annual and seasonal survival of trumpeter swans in the upper Midwest. *Journal of Wildlife Management* 76: 129–135.

Weatherhead, P.J. & Ankney, C.D. 1984. A critical assumption of band-recovery models may often be violated. *Wildlife Society Bulletin* 12: 198–199.

White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Suppl.): 120–139.

White, G.C., Kendall, W.L. & Barker, R.J. 2006. Multistate survival models and their extensions in program MARK. *Journal of Wildlife Management* 70: 1521–1529.

Williams, C.K., Samuel, M.D., Baranyuk, V.V., Cooch, E.G. & Kraege, D. 2008. Winter fidelity and apparent survival of Lesser Snow Goose populations in the Pacific Flyway. *Journal of Wildlife Management* 72: 159–167.

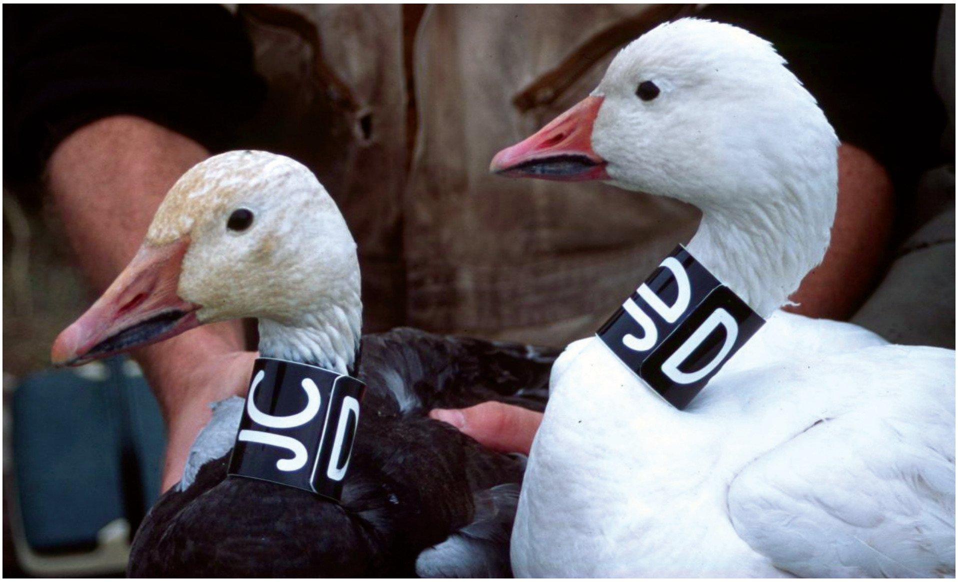
Wilson, B.C. 2002. *North American Waterfowl Management Plan, Gulf Coast Joint Venture: Evaluation Plan*. North American Waterfowl Management Plan, Albuquerque, New Mexico, USA. Accessible at http://www.gcjv.org/docs/Waterfowl Evaluation Plan Oct 29, 2002.doc (last accessed 26 July 2014).

Appendix 1. Principal components analysis of morphological measurements of 388 adult Lesser Snow Geese caught in southwest Louisiana in winters 2001/02, 2002/03 and 2003/04. Numbers in bold correspond to variables that covaried the strongest with each PC score (*i.e.* had the highest loadings).

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**
Wing length	**0.30**	0.28	**–0.42**	**–0.58**	0.28	**0.41**	0.27	–0.05	0.04
Culmen length	**0.37**	–0.33	0.01	–0.05	–0.17	0.13	–0.35	**–0.63**	**0.42**
Bill nares	**0.30**	**–0.52**	**0.45**	–0.37	–0.04	0.08	0.10	**0.53**	0.09
Bill thickness	**0.32**	0.10	–0.34	0.14	**–0.82**	0.01	0.16	0.21	–0.04
Gape length	**0.30**	–0.36	**–0.27**	**0.64**	0.37	0.16	0.36	0.06	0.04
Head length	**0.40**	–0.08	0.02	–0.02	0.08	–0.01	–0.35	–0.10	**–0.83**
Total tarsus	**0.35**	0.08	–0.04	–0.15	0.15	**–0.86**	0.25	–0.11	0.10
Skull width	**0.28**	**0.45**	**0.66**	0.20	–0.06	0.21	0.37	–0.25	–0.03
Skull height	**0.35**	**0.43**	0.01	0.21	0.21	0.00	**–0.56**	**0.43**	0.33
% variance explained	55.5	9.5	8.5	6.7	5.8	4.8	4.1	3.1	2.2

Appendix 2. Model selection ranks, ΔAICc, ΔAICc weights, model likelihoods, and number of parameters (K) for the covariate size analysis of movements of Lesser Snow Geese collared in southwest Louisiana in winters 2001/02, 2002/03 and 2003/04. Model $\mathbf{\Phi}_{.}$; $\mathbf{p}_{h*t}$; $\mathbf{\Psi}_{h*t}$ was the starting model in this analysis, and covariates were only added to **Φ** and **Ψ**.

Rank	Model	ΔAIC_c	AIC_c weight	Model likelihood	*K*	Deviance
1	**Φ**(.) **p**(h*t) **Ψ**(h*t)	0.0	0.259	1.000	21	1036.0
2	**Φ**(.) **p**(h*t) **Ψ**(h*t-PC1)	1.0	0.156	0.602	22	1034.9
3	**Φ**(.) **p**(h*t) **Ψ**(h*t-PC1-marsh only)	1.2	0.140	0.540	22	1035.1
4	**Φ**(.PC1) **p**(h*t) **Ψ**(h*t)	1.5	0.122	0.470	22	1035.3
5	**Φ**(.PC1-marsh only) **p**(h*t) **Ψ**(h*t)	2.1	0.093	0.358	22	1035.9
6	**Φ**(.PC1) **p**(h*t) **Ψ**(h*t-PC1)	2.1	0.090	0.345	23	1033.8
7	**Φ**(.PC1 within winter only) **p**(h*t) **Ψ**(h*t)	2.2	0.087	0.337	22	1036.0
8	**Φ**(.) **p**(h*t) **Ψ**(h*t-habitat*PC1 interaction)	3.2	0.052	0.202	23	1034.8



Photograph: Lesser Snow Geese caught at Cameron Prairie National Wildlife Refuge, Calcasieu Parish, Louisiana, USA in November 2001, by Jón Einar Jónsson. The Snow Goose on the left (blue colour phase) is representative of geese from coastal-marsh habitat whereas the Snow Goose on the right (white colour phase) is representative of those from rice-prairie habitat.