

Spring hunting changes the regional movements of migrating greater snow geese

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Summary

1. Human-induced disturbance such as hunting may influence the migratory behaviour of long-distance migrants. In 1999 and 2000 a spring hunt of greater snow geese *Anser caerulescens atlanticus* occurred for the first time in North America since 1916, aimed at stopping population growth to protect natural habitats.
2. We evaluated the impact of this hunt on the staging movements of geese along a 600-km stretch of the St Lawrence River in southern Quebec, Canada.
3. We tracked radio-tagged female geese in three contiguous regions of the staging area from the south-west to the north-east: Lake St Pierre, Upper Estuary and Lower Estuary, in spring 1997 ($n = 37$) and 1998 ($n = 70$) before the establishment of hunting, and in 1999 ($n = 60$) and 2000 ($n = 59$) during hunting.
4. We used multi-state capture–recapture models to estimate the movement probabilities of radio-tagged females among these regions. To assess disturbance level, we tracked geese during their feeding trips and estimated the probability of completing a foraging bout without being disturbed.
5. In the 2 years without hunting, migration was strongly unidirectional from the south-west to the north-east, with very low westward movement probabilities. Geese gradually moved from Lake St Pierre to Upper Estuary and then from Upper Estuary to Lower Estuary.
6. In contrast, during the 2 years with hunting westward movement was more than four times more likely than in preceding years. Most of these backward movements occurred shortly after the beginning of the hunt, indicating that geese moved back to regions where they had not previously experienced hunting.
7. Overall disturbance level increased in all regions in years with hunting relative to years without hunting.
8. *Synthesis and applications.* We conclude that spring hunting changed the stopover scheduling of this long-distance migrant and might further impact population dynamics by reducing pre-nuptial fattening. The spring hunt may also have increased crop damage. We propose that staggered hunt opening dates could attenuate secondary effects of such management actions.

Key-words: agriculture, *Anser caerulescens atlanticus*, capture–recapture models, disturbance, migration, stopover

Journal of Applied Ecology (2003) **40**, 553–564

Introduction

Animals rely upon nutrients and energy either directly ingested at the time of breeding (income breeders) or extracted from stored reserves (capital breeders) for their reproduction (Drent & Daan 1980; Jönsson 1997). Whereas wintering birds generally maintain a moderate body condition to escape predation (Witter & Cuthill 1993), a bird's priority changes to one of accumulation of fat and protein reserves during pre-nuptial migration (Metcalf & Furness 1984; Lindström & Piersma 1993). In capital breeders these critical reserves are required to complete migration and contribute to breeding success (Ankney & MacInnes 1978; Gauthier, Giroux & Bédard 1992; Bêty, Gauthier & Giroux 2003). Therefore, the availability and timing of stopovers influence forthcoming reproduction (Weber, Ens & Houston 1998).

Disturbance has considerable effects on the large-scale distribution of waterfowl during migration (Fox & Madsen 1997; Percival, Halpin & Houston 1997) but few studies have quantitatively addressed consequences for stopover scheduling and reserve accumulation. Hunting is an important cause of disturbance for waterfowl and a potentially important source of mortality that has been regulated carefully (Tamisier 1985; Harradine 1991). Since 1916, the hunting season for waterfowl in North America has been restricted to autumn and winter by the Migratory Bird Treaty Act, and similar regulations were recently implemented in Europe (Anonymous 1979). Specifically, hunting during the pre-nuptial migration was prohibited because of fear of interfering with reproduction. Efforts were also directed towards the creation of refuges with intensive management to reduce disturbance and increase resource availability (Burgess 1969; Madsen 1998; Vickery & Gill 1999). Concurrently, several goose species have increasingly used agricultural habitats for feeding, which often improved the overall quality of their wintering and stopover areas (Gill, Watkinson & Sutherland 1996; Van Eerden *et al.* 1996). The combined effects of restrictive harvest regulations, creation of refuges and increased use of agricultural resources are generally thought to be responsible for the dramatic increase in several goose populations over recent years (Owen 1990; Madsen 1991; Menu, Gauthier & Reed 2002).

In North America, concerns have been expressed regarding the ecological consequences of the large increase of white goose populations. Degradation of the arctic tundra due to overgrazing by lesser snow geese *Anser caerulescens caerulescens* L. (Jano, Jefferies & Rockwell 1998) and concern about similar effects on the greater snow goose *A. c. atlanticus* K. breeding habitat led Johnson (1997) and Giroux *et al.* (1998) to, respectively, recommend reduction of the mid-continent lesser snow goose population and stabilization of the greater snow goose population. In an attempt to control the greater snow goose population, a spring hunt has been implemented since 1999 over all the agricultural habitats

of southern Quebec, Canada. A secondary aim of the hunt was to reduce field use by geese to minimize crop depredation.

This hunt may have strong impacts on the population dynamics that require evaluation by long-term monitoring. However, we were able to investigate the immediate effects of hunting disturbance on the inter-regional movements of greater snow geese during their spring migration in southern Quebec through daily tracking of radio-tagged individuals. We compared movements in 2 years of monitoring without hunting (1997–98) and 2 years with hunting (1999–2000) involving more than 9000 hunters distributed throughout southern Quebec (H. Lévesque, Canadian Wildlife Service, personal communication).

In the absence of hunting, the goose migration along the St Lawrence River is thought to be directional, i.e. geese first arrive in south-western Quebec and later move north-eastwards (Reed, Giroux & Gauthier 1998). We hypothesized that the spring hunt would induce more regional movements than usual, including reverse migration movements, as geese sought less disturbed places to forage. Therefore we made five predictions. (i) In years without hunting, movements of geese in southern Quebec would be unidirectional, the probabilities of north-eastward movements being much higher than the probabilities of south-westward movements. (ii) The probabilities of south-westward movements would be higher in years with hunting than in those without. (iii) In years with hunting, the overall disturbance level would increase relative to years without. (iv) Probabilities of staying in a region would be inversely related to hunting disturbance. (v) In years with hunting, westward movements would correspond to movements from regions with high disturbance towards regions with low disturbance.

Methods

STUDY SPECIES

Greater snow geese breed in the eastern high Arctic of Canada, winter along the Atlantic coast of the USA, from New Jersey to South Carolina, and stage along the St Lawrence River in Quebec, Canada, during their autumn and spring migration (Fig. 1). The entire population stops in Quebec in spring. The first geese arrive by mid-March and the last ones leave for the Arctic in the last week of May (Reed, Giroux & Gauthier 1998).

STUDY AREA

The spring staging area extends over 600 km along the St Lawrence River (Fig. 1). We divided this area into three contiguous regions, the Lake St Pierre (LSP), the Upper Estuary (UEST) and the Lower Estuary (LEST), each characterized by different agricultural and natural habitats used by geese. In the LSP region cornfields are abundant and waste corn is the main food resource for

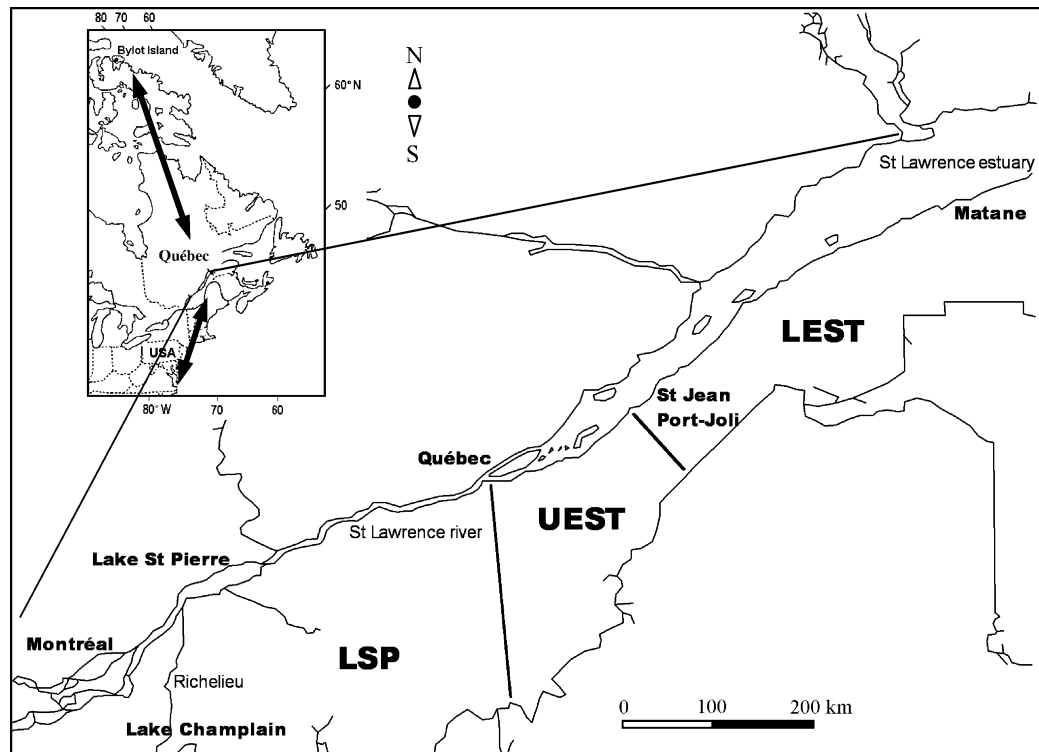


Fig. 1. The St Lawrence River Valley in southern Quebec (Canada) with the three regions used by greater snow geese during their spring stopover: the Lake St Pierre region (LSP), the Upper Estuary (UEST) and the Lower Estuary (LEST). Arrows in the inset map represent the general migration routes.

geese (Giroux & Bergeron 1996). Roosts consist of managed flooded fields, rivers (Richelieu and St Lawrence River) and some reservoirs. In the UEST, *Scirpus* marshes are used as roosts and feeding sites (Giroux & Bédard 1988). Geese also feed on mixtures of grasses and legumes in adjacent hayfields (Bédard & Gauthier 1989) and to a lesser extent on some cornfields that recently appeared in the south-west of the region. Finally, *Spartina* marshes are used for roosting in the LEST while feeding occurs in both marshes and adjacent hayfields (Gauthier, Bédard & Bédard 1988).

In 1999 and 2000 hunting was open on all agricultural lands from 15 April to 31 May. Hunting-free areas were limited to roosts, marshes and a few fields managed as alternative feeding areas (550 ha) in the UEST. Outside these refuges, farmers scared the geese from their fields by chasing them on foot and with all-terrain vehicles in order to reduce crop depredation.

RADIO-TAGGING AND TRACKING

A total of 310 adult female greater snow geese were fitted with radio-collars on their breeding area at the Bylot Island bird sanctuary, Nunavut (73°00'N, 80°00'W), in August between 1996 and 1999. We captured small family groups (< 30 geese) of moulting adults with their 25–35-day-old young using corral traps (Demers *et al.* 2003). All geese received US Fish and Wildlife Service aluminium rings, and males were fitted with coded yellow plastic collars. Radios weighed

59 ± 9 g (SE) (i.e. $2.5 \pm 0.02\%$ of the female body mass) and lasted for 16–24 months with a signal range of 1–2 km on the ground and 5–6 km from the air or when the geese were flying.

Each spring from 1997 to 2000, radio-tagged geese were tracked daily from the beginning of the staging period until departure of the last geese. Six crews with vehicles covered the entire staging area (Fig. 1). Ground counts of the geese were performed daily at dawn at the most important roosts and once every 2 or 3 days in the others. Every week, the same observer flew the area with an aircraft to locate missing radio-tagged geese and to estimate the number of geese at each site. Aerial and ground counts conducted simultaneously were regularly compared and found to be consistent.

Every morning, radio-tracking of geese began simultaneously at several roosts. Among the radio-tagged geese detected we randomly picked one and tracked it from its departure from the roost until it landed in a foraging patch. The presence of the goose was then monitored continuously for up to 3 hours (mean = 1.5 h). During this period we recorded all disturbance events, the exact times of their occurrence, the nature of the event (e.g. aeroplane, hikers and hunters) and the new location where the goose landed. The same sampling scheme was repeated in the afternoon, as geese usually came back to roosts in mid-day before initiating a new foraging trip. At the end of monitoring sessions, the neighbouring area was haphazardly covered by car. If a radio-tagged goose was detected in another flock, we

initiated a new monitoring session. Hereafter, we define a foraging bout as the period of time a radio-tagged goose was monitored on the ground at a foraging site from its first detection until it took off or the monitoring ended.

STATISTICAL ANALYSES

We estimated movements of radio-tagged females among the three regions of the staging area using multi-state capture–recapture models (Brownie *et al.* 1993) implemented in program MARK (version 1.9; White & Burnham 1999). In multi-state models, capture histories reflect both encounters and location (or state) at capture. In our case a ‘capture’ consisted of a radio detection, and the first detection within a year was considered the initial capture. Thus, detection history A0BB describes an individual detected in region A in period 1, not detected in period 2 and detected in region B in periods 3 and 4. We obtained maximum-likelihood estimates of the following parameters. P_t^r = the probability that the signal of a goose is detected at time t in region r , given that the bird is alive and in the study area at time t . S_t^r = the probability that a goose in region r at time t survives until time $t + 1$. This is an apparent survival probability as its complement confounds the probability of dying and the probability of permanently emigrating outside the study area. Ψ_t^{rs} = the probability that a goose in region r at time t is in region s at time $t + 1$ given that the individual survived from time t to $t + 1$.

We assumed that movement probabilities from t to $t + 1$ followed a first-order Markovian process, i.e. they only depended on the region at time t .

Sample size did not allow estimation of movement probabilities on a daily basis. To obtain a sufficient number of locations for each time period, we pooled daily detections of radio-tagged geese over 6-day periods. A goose detected repeatedly in the same region within a 6-day period was assigned to that region. A goose detected in more than one region within a 6-day period was assigned to the region with most encounters. When ties occurred, the goose was assigned to the region that minimized information loss on regional movements. For instance, a goose detected in A at $t - 1$ and $t + 1$ and in both regions A and B at period t was assigned to region B for period t because the goose was known to have made that movement. Such ties occurred in < 5% of the cases. We limited our data set to nine periods each year (28 March to 21 May) with, respectively, three and six time periods before and during the hunting season.

Goodness-of-fit tests entirely suitable for multi-state capture–recapture models do not exist. A first alternative approach is to perform separate goodness-of-fit tests of the Cormack–Jolly Seber (CJS) model for each state using program RELEASE (version 3.0; Burnham *et al.* 1987). TEST2 of RELEASE assesses the assumption of equal detectability of individuals known to be alive in period t and $t + 1$, whereas TEST3 examines whether

all individuals alive at period t have the same probability of being alive at period $t + 1$. However, this approach does not deal appropriately with geese that changed region between period t and period $t + 1$. Therefore, we also performed a goodness-of-fit test of the CJS model with all states pooled. This overall test gives information on the assumption of equal detection and the presence of transients across staging regions.

Model selection was based on the Akaike information criterion (AIC) with the small-sample bias adjustment, AIC_c . We presented AIC_c differences between fitted models (ΔAIC_c) and normalized Akaike weights, $AIC_c\omega$ (Lebreton *et al.* 1992; Burnham & Anderson 1998). The primary use of AIC_c was to select appropriate models for estimating movement probabilities. We then used these estimates to test a priori predictions, most of which were directional hypothesis (i.e. the alternative hypothesis specified the direction of the difference between movement probabilities). We had to use this testing approach rather than model selection because of our inability to incorporate these directional hypotheses into capture–recapture models.

We formalized our predictions within the framework of multi-state models. If region s is located east of r , we can write movement probabilities from region r to region s between t and $t + 1$ as Ψ_t^{rE} , and from region s to region r as Ψ_t^{rW} . Hence, the first prediction becomes:

$$\bar{\Psi}^{rE} > \bar{\Psi}^{rW}$$

where $\bar{\Psi}$ denotes mean movement probabilities over the eight time intervals.

The second prediction states that movement probabilities from eastern to western regions (i.e. reverse migration) were higher for years with hunting than for years without. Therefore, we can write:

$$\bar{\Psi}_{\text{no hunt}}^{EW} > \bar{\Psi}_{\text{hunt}}^{EW}$$

where $\bar{\Psi}$ denotes mean movement probabilities during the last five time intervals (i.e. after the opening of hunting). To test differences between mean estimates of detection and movement probabilities derived from independent data sets, we used the chi-square statistic developed by Sauer & Williams (1989) and implemented in program CONTRAST.

Our last three predictions deal with the increase in disturbance level in years with hunting and its effect on regional movements. To evaluate disturbance levels, we estimated the probability of completing a foraging bout of length $t(D_t)$ at a site under the risk of a disturbance event using the Kaplan–Meier product-limit estimator (Kaplan & Meier 1958). Each foraging bout was considered as an independent trial in which the geese were under disturbance risk. As field observations were randomly allocated to different radio-tagged geese, we are confident that geese that would be prone to repeated disturbances did not bias this estimate. The Kaplan–Meier approach accounts for

censored observations and uses a non-parametric hazard function with no assumption about the distribution of the disturbance events. All sources of disturbance leading to departure of the geese were akin to mortality in a standard Kaplan–Meier survival analysis while bouts terminated by the observers were censored. We also estimated H_t , the probability of completing a foraging bout without being disturbed by a hunting related event. In that case, a foraging bout could either end by a hunting disturbance or be censored if the goose left due to other disturbances, or if the observers quit. We restricted the data set to foraging bouts recorded after the opening of hunting on 15 April and excluded observations in refuges. We used the Cox regression method (Cox & Oakes 1984) with PROC PHREG (Allison 1995; SAS Institute Inc. 1999) to test for differences in the probability of completing a foraging bout in relation to time spent at risk (D_t and H_t) between years and among regions with and without hunting. This ‘proportional hazard model’ allows testing without having to specify an underlying hazard function.

We tested the prediction that the probability of staying in a region between time periods t and $t + 1$ (i.e. $\Psi_t^{rs} = 1 - (\Sigma \Psi_t^{rs})$) was positively correlated with the probability of completing a foraging bout of a standard 60-min length (H_{60}) under the risk of a hunting disturbance during time period t for the five time intervals after the opening of the hunt.

Results

GOOSE COUNTS

In 1997 and 1998, the average number of greater snow geese showed a clear peak in each region suggesting a progressive wave of geese first arriving in the south-

west (LSP) and progressively moving to the north-east (UEST and LEST; Fig. 2). In 1999 and 2000 the pattern was somewhat different. After the opening of the hunt, the seasonal decline in the number of geese at LSP was slower than in previous years while the number of geese staging in the UEST and LEST quickly reached a plateau.

MODEL SELECTION FOR REGIONAL MOVEMENTS

We tracked 37, 70, 60 and 59 geese in 1997, 1998, 1999 and 2000, respectively. No geese died during the 1997 and 1998 staging periods. Hunters shot two radio-tagged geese in 1999 and 2000, respectively, and a third goose was found dead in 1999. We obtained 5215 daily locations of radio-tagged geese during the 4 years. Individuals were located between 32% and 56% of the days each year. By pooling the data, we obtained 2034 6-day periods with 90.2% involving only one region, 9.2% with two regions and 0.6% with three. Hence, we felt confident that the pooling required for the multi-state capture–recapture analyses was biologically meaningful.

Goodness-of-fit tests separated by year and region provided no evidence of lack of fit, with 11 of the 12 tests being not significant. The only exception was TEST2 for region UEST in 2000 ($\chi^2_{13} = 49.52$, $P < 0.0001$) and it was probably due to frequent movements of geese in and out this region, a phenomenon taken into account in the multi-state models. Goodness-of-fit tests with all regions pooled provided no evidence of lack of fit (all years, $P > 0.37$).

Biology should play an important role in model selection strategy and one should consider an a priori set of realistic candidate models rather than all possible models (Lebreton *et al.* 1992; Burnham & Anderson

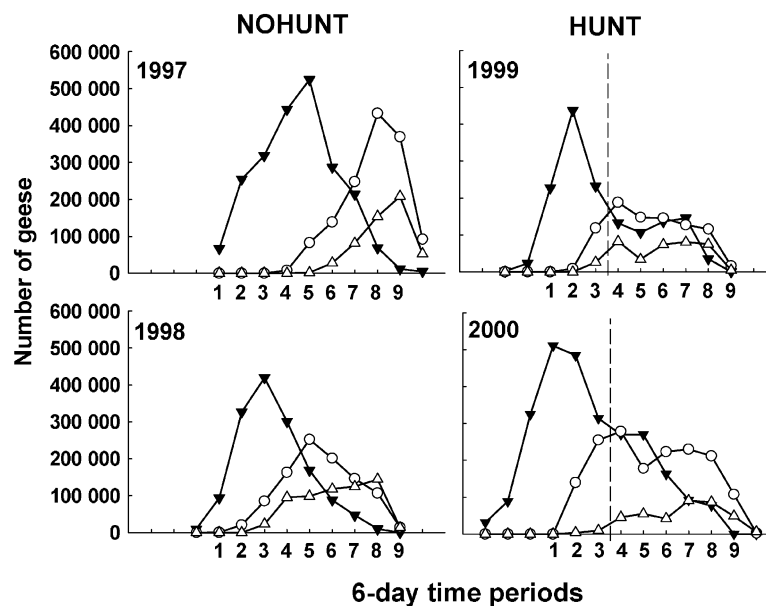


Fig. 2. Counts of spring staging greater snow geese averaged over 6-day periods in the LSP (inverted triangles), UEST (circles) and LEST (triangles) regions of Quebec from 1997 to 2000. Vertical dashed lines indicate the beginning of the hunt.

Table 1. Model selection of regional movements of greater snow geese in Quebec in the combined data sets spring 1997–98 (NOHUNT) and spring 1999–2000 (HUNT). ΔAIC_c , $AIC_c\omega$, number of parameters (k) and rank of the multi-state models are presented

Model rank	Model	k	ΔAIC_c	$AIC_c\omega$
NOHUNT				
1	$S_{(6-t)(4-t)} P_t \Psi_{yqt}^{LSP-UEST} \Psi_t^{others}$	61	0.000	0.98
2	$S_{(6-t)(4-t)} P_t \Psi_{yqt}^{rs}$	76	8.05	0.01
HUNT				
1	$S_{2-t} P_y^r \Psi_{yqt}^{LSP-UEST} \Psi_t^{others}$	63	0.00	0.99
2	$S_{2-t} P_y^r \Psi_{yqt}^{rs}$	84	11.05	0.00

Model notation: S = apparent survival; p = detection probability; Ψ = movement probability; y = year-dependence; t = time-dependence; rs = region-dependent movement probability. $S_{(n1-t)(n2-t)}$ refers to a model where apparent survival is fixed to 1 for the first n time intervals (n different each year) and year- and time-dependent afterward. $S_{(n-t)}$ has the same constraints except that apparent survival is equal between years. $\Psi_{yqt}^{LSP-UEST} \Psi_t^{others}$ indicates that movement probabilities between LSP and UEST are year- and time-dependent whereas all other movements are only time-dependent.

1998). Because we predicted that movement probabilities should differ between years with and without hunting, we aimed at obtaining the most accurate parameter estimates for each of these two situations. Because the general model (time- and region-specific parameters for apparent survival, movement and detection probabilities) had too many parameters for our data set, we used a two-step approach. We first reduced variation in the apparent survival and detection parameters within each of the annual data sets. Secondly, we combined detection histories for the 2 years without hunting (the NOHUNT data set) and the 2 years with hunting (the HUNT data set) to model movement probabilities.

Transitions from LEST to LSP and from LEST to UEST never occurred in 1997, so we fixed these movement probabilities to 0. Initially, geese were absent from UEST and LEST because they first arrived in LSP, the most southerly region, so we fixed movement probabilities to 0 until the first geese appeared in these regions. Because of the short period duration we assumed that true mortality was negligible except during hunting. Therefore, we fixed apparent survival to 1 for the first six time intervals in 1997, the first four time intervals in 1998 and the first two time intervals in 1999 and 2000.

In all 4 years the best model had time-dependent apparent survival for time intervals when it was not fixed to 1 but equal among the three regions. Detection probabilities were time- and region-dependent in 1998 and only region-dependent in the other years. In 3 years our best model with respect to apparent survival and detection probability received good support among the set of candidate models ($AIC_c\omega = 0.68$) and moderate support in the fourth year ($AIC_c\omega = 0.54$; see the Appendix).

We used these reduced models to start the analysis of the combined data set (HUNT and NOHUNT). In the NOHUNT data set, the best model had detection probabilities equal for the 2 years but year-dependent apparent survival (Table 1). For the HUNT data set, the best model had apparent survival equal for the 2 years but detection probabilities year-dependent (Table 1).

All movement probabilities were time-dependent. Within each data set, the best model had movement probabilities between LSP and LEST and between UEST and LEST equal between years but year-dependent between LSP and UEST. Support for the best models was very strong in each case ($AIC_c\omega = 0.98$ and 0.99; Table 1).

APPARENT SURVIVAL AND DETECTION PROBABILITIES

Apparent survival probabilities decreased only at the end of the season in years without hunting but this decline started earlier (i.e. after the opening of the hunt) in years with hunting (Fig. 3).

Variations in detection probabilities did not follow a consistent pattern except that detection probabilities were lower in years with hunting than without [$\bar{p}_{no\ hunt} = 0.94 \pm 0.005$ (SE) and $\bar{p}_{hunt} = 0.82 \pm 0.018$, two-tailed test $\chi^2_1 = 94.1$, $P < 0.0001$].

REGIONAL MOVEMENTS

In years without hunting, the probabilities of moving from LSP to UEST were much higher (yearly average $\bar{\Psi}_{1997} = 0.25 \pm 0.08$ and $\bar{\Psi}_{1998} = 0.32 \pm 0.08$) than from UEST to LSP ($\bar{\Psi}_{1997} = 0.014 \pm 0.01$ and $\bar{\Psi}_{1998} = 0.057 \pm 0.017$; Fig. 4). This indicates that when geese moved eastwards from LSP they had a low probability of returning. The movement from LSP to UEST was later and more abrupt in 1997 than in 1998, when it started earlier and was more evenly spread out. This may be related to the delayed spring in 1997.

Similarly, in years without hunting the probabilities of moving from UEST to LEST were much higher ($\bar{\Psi}_{1997-98} = 0.112 \pm 0.028$) than from LEST to UEST ($\bar{\Psi}_{1997-98} = 0.018 \pm 0.009$; Fig. 5). We noted that the probability of moving from UEST to LEST was lower than from LSP to UEST (Figs 4 and 5). This indicates that many geese that had moved from LSP to UEST did not continue afterwards to LEST but remained in the UEST area until departure to the Arctic. Finally,

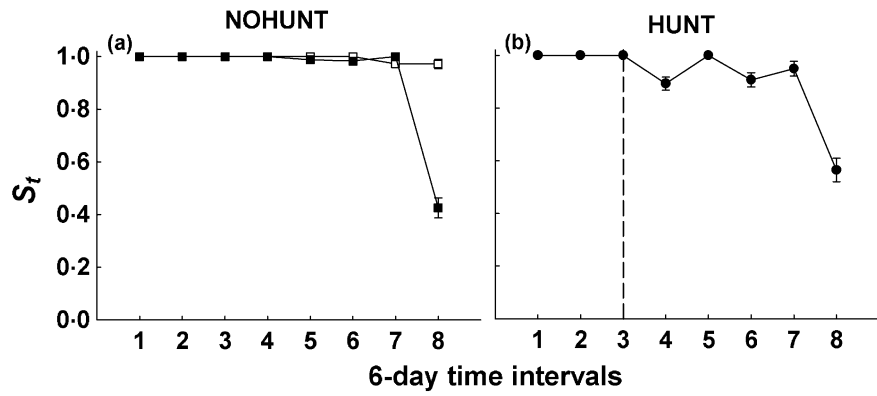


Fig. 3. Six-day apparent survival estimates (± 1 SE) of greater snow geese in southern Quebec. (a) Estimates for the NOHUNT data set derived from model 1 of Table 1 for 1997 (open squares) and 1998 (closed squares); (b) estimates for the HUNT data set derived from model 1 of Table 1 for 1999–2000 (see text for details). Vertical dashed lines indicate the beginning of the hunt.

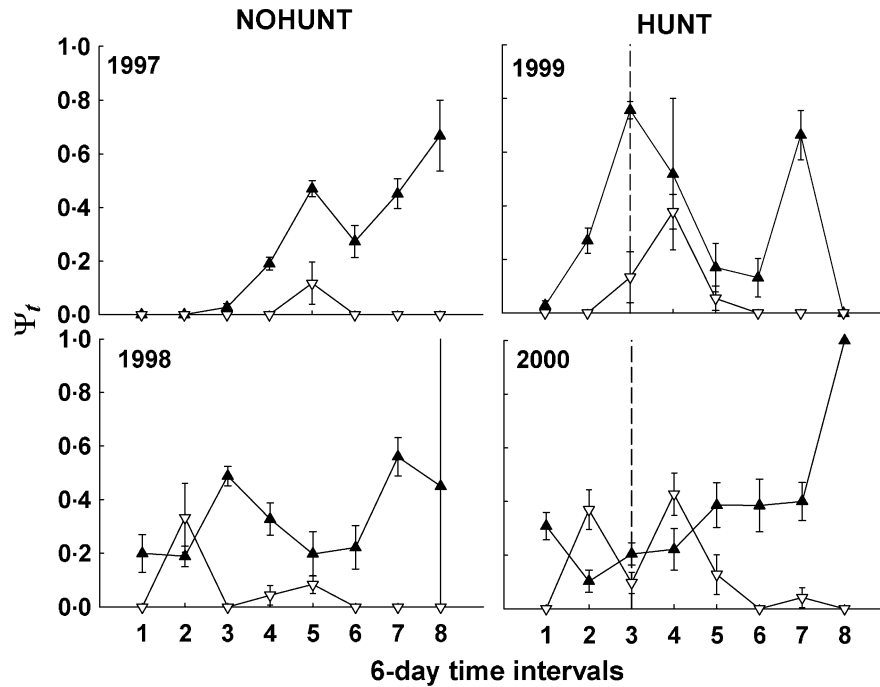


Fig. 4. Estimates (± 1 SE) of movement probabilities of geese from LSP to UEST (triangles) and UEST to LSP (inverted triangles) between 6-day periods. Estimates are derived from model 1 of Table 1 for each of the NOHUNT and HUNT data sets. Vertical dashed lines indicate the beginning of the hunt.

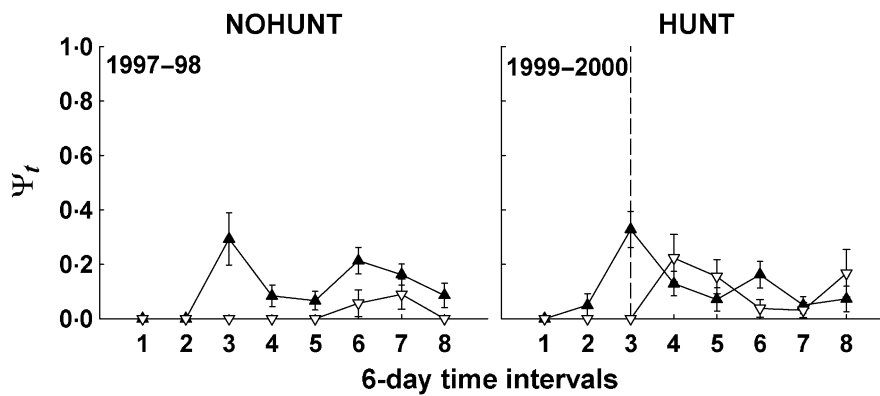


Fig. 5. Estimates (± 1 SE) of movement probabilities of geese from UEST to LEST (triangles) and LEST to UEST (inverted triangles) between 6-day periods. Estimates are derived from model 1 of Table 1 for each of the NOHUNT and HUNT data sets (see text for details). Vertical dashed lines indicate the beginning of the hunt.

the probability of moving directly from LSP to LEST was very low ($\bar{\Psi}_{1997-98} = 0.037 \pm 0.008$) and most geese that eventually moved to LEST previously stopped in UEST.

In summary, our results clearly indicate that in the 2 years without hunting migration was a unidirectional, eastward process with few backward movements, thus supporting our first prediction.

The eastward movements of geese (i.e. from LSP to UEST to LEST) during the 2 years with hunting did not differ markedly from previous years. Departure from LSP to UEST occurred in two different waves in 1999 (time intervals 3 and 7) but increased more progressively in 2000 (Fig. 4). Movement probabilities from UEST to LEST peaked again in the third and sixth time intervals (Fig. 5) and direct movements from LSP to LEST remained low ($\bar{\Psi}_{1999-2000} = 0.052 \pm 0.014$). In contrast, westward movements (from LEST to UEST to LSP) were much more common in years with hunting than in those without (Figs 4 and 5). A peak in backward movements from UEST to LSP and LEST to UEST occurred in the week following the beginning of hunting (interval 4). Overall, mean backwards movement probabilities after the beginning of hunting were more than four times higher than in years without hunting (LSP to UEST, $\bar{\Psi}_{no\ hunt}^{EW} = 0.022 \pm 0.008$, $\bar{\Psi}_{hunt}^{EW} = 0.105 \pm 0.014$, one-tailed test $\chi^2_1 = 24.30$, $P < 0.001$; LEST and UEST, $\bar{\Psi}_{no\ hunt}^{EW} = 0.024 \pm 0.012$, $\bar{\Psi}_{hunt}^{EW} = 0.102 \pm 0.023$, $\chi^2_1 = 8.34$, $P = 0.004$). Therefore, our second prediction was upheld.

EFFECT OF DISTURBANCE

Overall, the disturbance level (all sources) was much higher in years with hunting than in years without ($\chi^2_1 = 95.20$, $P < 0.001$; Fig. 6), and this supported our third prediction.

We retrieved parameter estimates from the second best model for the HUNT data set (i.e. model 2 of Table 1; $S_{2y}, p_y^r, \Psi_{ytr}^r$) to get separate estimates of movement probabilities for each year with hunting, and calculated an annual Ψ_{tr}^r . This more general model fitted the data at least as well as the best model. The probability of staying in a region between two time periods (Ψ_{tr}^r) was not correlated with the probability of completing a 60-min foraging bout without being disturbed by hunting (H_{60}) (there were five data sets, two regions in 1999 and three in 2000; $r = -0.77-0.89$, $n = 5$ each time, $P > 0.04$; significance level $\alpha = 0.01$, Bonferroni correction). Therefore, our fourth prediction was not supported by the data.

In 1999, the probability of completing a foraging bout without being disturbed by hunting was similar in UEST and LEST ($\chi^2_1 = 0.24$, $P = 0.62$) but could not be calculated at LSP because no hunting event was recorded. In 2000, this probability differed among the three regions ($\chi^2_2 = 7.11$, $P < 0.029$), with LSP and LEST regions presenting the greater risk of being disturbed (Fig. 7). The overall disturbance level was similar among the three regions in all years (all tests, $P > 0.12$, except 1997, $P = 0.067$; Fig. 6). In summary, regional movements were not related to regional variations in disturbance level as predicted (fifth prediction). On the contrary, in 2000, geese moving westwards from UEST to LSP experienced more hunting disturbance than if they had stayed in the UEST.

Discussion

GOOSE MOVEMENTS AND THE IMPACT OF HUNTING

The tracking of individual geese confirmed that the greater snow goose spring migration through southern

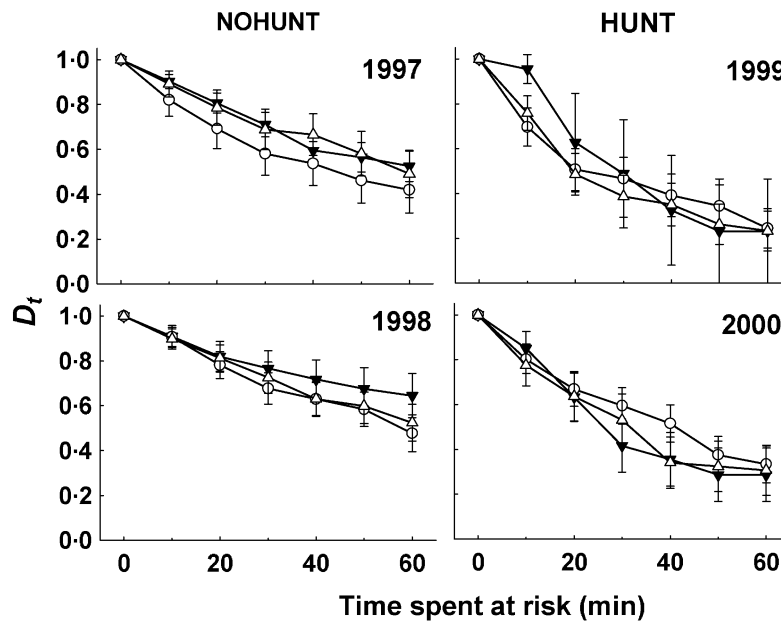


Fig. 6. Estimates ($\pm 95\%$ confidence interval) of the probability of completing a foraging bout without being interrupted by an event (D_t) in relation to time spent at risk of disturbance by geese at LSP (inverted triangles), UEST (circles) and LEST (triangles) after 15 April in 1997–2000.

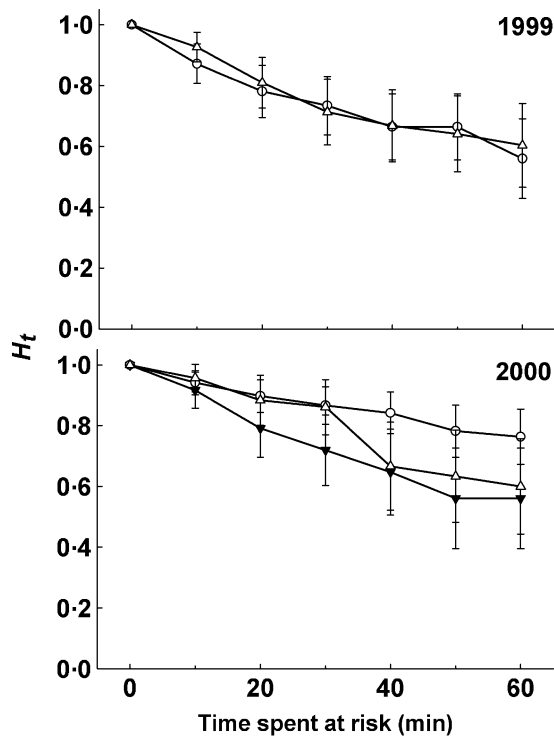


Fig. 7. Estimates ($\pm 95\%$ confidence interval) of the probability of completing a foraging bout without being disturbed by hunting (H_t) in relation to time spent at risk of disturbance by geese at LSP (inverted triangles), UEST (circles) and LEST (triangles) after 15 April in 1999 and 2000.

Quebec is unidirectional, with geese first arriving from their wintering areas to LSP and later moving eastwards to UEST and LEST. In LSP, geese mainly feed on waste corn, which is readily available in stubble fields, but the latter represent only 3–7% of agricultural habitats available in spring (Béchet 2002). Depletion of waste corn may thus force geese to leave the LSP region for the estuary. The estuary becomes increasingly attractive over time with the onset of new growth of grasses and legumes in hayfields, especially in LEST where *Spartina* marshes are a poor quality habitat (Bédard & Gauthier 1989). The area of stubble cornfields available at the beginning of spring at LSP and the timing of snowmelt in the estuary probably influence the timing of movement to eastern regions. This could explain why the number of geese in the LSP region peaked later in 1997, a year of late snowmelt at UEST and LEST, than in 1998, a year of early snowmelt.

The spring hunt, which resulted in over 40 000 harvested geese each year (H. Lévesque, Canadian Wildlife Service, personal communication), caused an increase in the overall disturbance level in all regions. In addition, hunting regulations allowed hunters to sneak up on geese, which can more easily deter them from foraging in the fields and force them to search for alternative foraging places. Some hunters often tracked disturbed geese to their new foraging sites and approached them again and again to make a successful kill. In 1999, too few radio-tagged geese were still

present at LSP after the opening of the hunt to record any hunting disturbance events. Moreover, harvest surveys indicated that only 18% of the total harvest came from LSP that year compared with 34% in 2000 (H. Lévesque, Canadian Wildlife Service, personal communication). Hunting disturbance in 2000 at LSP was thus as high or higher than in other regions. Hence, westward movements of geese did not prevent them from being exposed to hunting disturbances, at least in 2000. Rather, these movements might represent failed attempts to avoid hunting disturbance. Moreover, backward movements peaked shortly after the opening of the hunt. Considering the directional pattern of migration outlined above, geese that had already reached UEST and LEST before 15 April had not experienced hunting in LSP or UEST before. Returning to the previously used region could have been an attempt to escape hunting disturbances by looking for places where, in their recent experience, there was no hunting. This could explain why movements did not occur from regions with high disturbance level to those with lower level.

The level of disturbance that prevailed on a given day influences the use of refuges by geese the following day (Bélangier & Bédard 1989). In our study, the probability of staying in a region was not related to disturbance levels. This may result from the low power of our tests, as only five data points were available for each correlation. In Scotland, Percival, Halpin & Houston (1997) observed that although hunting disturbance slightly increased the emigration rate of barnacle geese *Branta leucopsis*, many individuals persisted in using heavily disturbed sites. Other confounding factors such as food depletion also influence the probability of staying (Sutherland & Anderson 1993). However, this variable would be very difficult to estimate over the whole staging area considered due to patchily distributed food resources.

In an adaptive management framework (i.e. the systematic process of using information from management actions to improve understanding and inform future decision-making; Nichols, Johnson & Williams 1995), this 4-year study represents a quasi-experimental design with two control and two treatment years. This type of experimental design lacks both randomization and replication, and we should thus be cautious in drawing inferences (Nichols, Johnson & Williams 1995). None the less, our results suggest that hunting disturbance caused large changes in movements of staging geese, especially by increasing the rate of backward movements. The directions of movements were not directly related to variation in disturbance levels, probably because of the confounding effect of food resource availability and depletion.

Overall disturbance level was similar among regions during the 4 years despite differences in hunting disturbance. Included in the overall disturbance was scaring; this remained low at LSP and UEST throughout the years ($\leq 15\%$ of all disturbances) but was higher at

LEST (30–40% of all disturbances; Béchet 2002). Furthermore, the regional distribution of scaring did not change among years. Hence, although scaring could have enhanced the effect of hunting, it is unlikely to be the main factor responsible for the changes in regional movements.

Human-induced disturbance becomes a critical issue when it influences population dynamics (Gill, Norris & Sutherland 2001). In years with hunting the increase in backward movements represented an augmentation in the frequency of long-distance flights and thus in energetic costs. Another consequence of the backward movements was that migration no longer tracked the seasonal changes in resource availability previously observed. Hence, these movements may have forced some geese to move back to regions where resources were already depleted. All these effects would contribute to reduce nutrient accumulation during staging. Indeed, there is evidence that fat and protein reserves of greater snow geese before departure for the Arctic declined considerably during the 2 years with hunting (Féret *et al.* 2003). Endogenous reserves stored in spring are essential to complete the 3000-km migratory flight to breeding grounds and contribute to egg formation and the energy budget of incubating females (Gauthier, Giroux & Bédard 1992; Choinière & Gauthier 1995; Reed, Hughes & Gauthier 1995). The reduction in stored reserves in years with hunting led to lower body condition of laying geese, reduced breeding effort, delayed laying and lower clutch size than in years without hunting (Mainguy *et al.* 2002; Bêty, Gauthier & Giroux 2003).

METHODOLOGICAL CONSIDERATIONS

Multi-state capture–recapture models are particularly useful for estimating movement probabilities and for testing a priori predictions on survival, capture and movement probabilities (reviewed by Nichols & Kaiser 1999). To our knowledge, our study is the first to use this approach to evaluate short-term movements in a dynamic process like migration. Because of the limited number of geese tracked and the long staging period, we pooled data across 6-day periods. The effect of pooling data on parameter estimates has not yet been fully explored. A related question concerns the fact that observation periods were continuous rather than discrete. In standard survival analysis continuous observations only induce a small positive bias in survival estimates (Hargrove & Borland 1994). As movement probabilities are estimated conditional on survival, we suspect that a slight bias in survival should have little or no influence on movement probability estimates.

The decrease in apparent survival at the end of the season is due to permanent emigration from the study area caused by the departure of geese for the Arctic. In 1999 and 2000, the apparent survival decreased earlier, starting shortly after the onset of the hunt, and this probably reflects additional, true mortality of geese.

Even though apparent survival estimates are not reliable estimates of true survival, these parameters are needed to estimate movement probabilities properly. The lower detection probability observed during years with hunting may result from either higher dispersal of geese, making them more difficult to track (A. Béchet *et al.*, personal observations), or weaker signals in 1999–2000 due to a different radio manufacturing. These variations in detection probabilities, however, were taken into account in the estimation of movement probabilities and did not influence our conclusions.

Radio-transmitters can sometimes negatively affect birds (Schmutz & Morse 2000). In greater snow geese Menu *et al.* (2000) found no impact of neck-collars on survival, although Demers *et al.* (2003) found a higher divorce rate for radio-tagged females. Geese had been marked at least 7 months before the observations began, giving them enough time to habituate to the radio. Moreover, Demers *et al.* (2003) found no difference in activity budgets among radio-tagged, neck-collared and unmarked females in spring. Radio-tagged individuals were well mixed into flocks of geese throughout the staging area and were distributed among all main roosts. We are thus confident that movements of radio-tagged geese were representative of the entire population.

MANAGEMENT IMPLICATIONS

The opening of a spring hunt was a management action unprecedented since 1916 in North America. It is now gradually being implemented for the mid-continent lesser snow geese, where a more ambitious programme calls for a 50% reduction in the population (Johnson 1997). We show that a side-effect of such actions is the modification of the migratory pattern of geese. This may also negatively impact their reproduction (Mainguy *et al.* 2002; Féret *et al.* 2003), which will further contribute to population control. Such changes may occur in other waterfowl populations exposed to similar management actions. It could also affect unprotected populations that are still submitted to a spring hunt (e.g. in Russia; E. Syroechkovski Jr, Russian Academy of Sciences, personal communication).

A secondary aim of the spring hunt in Quebec was to minimize crop damage by geese, which has been growing with the increase in the population (Filion, Luszcz & Allard 1998). Whereas geese have used perennial hayfields since the 1960s, depredation on highly sensitive seedlings of corn and cereal in the LSP region was first reported in 1998. The proportion of this type of damage in the total annual compensations paid to farmers (*c.* 0.5–1.3 million Canadian dollars) increased more than 10 times from 1998 to 2000 (Béchet 2002). Typically, seedlings appear in LSP around the second week of May, when most geese have left the area (Filion, Luszcz & Allard 1998). By causing westward movements from UEST hunting can therefore increase the risk of damage to seedlings later in the season.

Synchrony in the hunt opening date across regions may be in part responsible for these backward movements. We therefore propose that staggered opening dates in the three regions (e.g. 15 April in LSP, 20 April in UEST and 25 April in LEST) could help to restore the normal migration pattern. Such a scheme could also permit further testing of hypotheses about the effect of disturbance on stopover scheduling.

Acknowledgements

This research was supported financially by the Canadian Wildlife Service (Quebec region), Ducks Unlimited via the Institute for Wetland and Waterfowl Research and the Fonds pour la Formation des Chercheurs et l'Aide à la Recherche (FCAR, Ministère de l'Éducation du Québec) through research grants to G. Gauthier and J.-F. Giroux. Polar Shelf Continental Project provided support for radio-tagging of geese. A. Béchét was supported by scholarships from the Université du Québec à Montréal and the Province of Quebec Society for the Protection of Birds. We are grateful to F. St-Pierre, J. Lefebvre, F. Demers and N. Nadeau for field assistance. We thank E. Reed for useful discussion, encouragement and comments on the first draft of this paper. K. Abraham, L.-A. Giraldeau, J.-D. Lebreton and P. Drapeau also provided constructive comments to improve the manuscript. A. Béchét is grateful to the Patuxent Wildlife Research Center (USGS, USA) for providing working space and assistance during the writing of this paper.

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Received 27 May 2002; final copy received 17 February 2003

Appendix

Model selection of regional movements of greater snow geese in Quebec in spring 1997–2000. ΔAIC_c , $AIC_c\omega$, number of parameters (k) and ranks of the multi-state models are presented. Only apparent survival and detection probabilities were modelled

Year	Model rank	Model	k	ΔAIC_c	$AIC_c\omega$	Year	Model rank	Model	k	ΔAIC_c	$AIC_c\omega$
1997	1	$S_{6y} p^r \Psi_t^{rs}$	31	0.000	0.54	1999	1	$S_{2y} p^r \Psi_t^{rs}$	45	0.00	0.70
	2	$S_{6y} p \Psi_t^{rs}$	29	0.98	0.33		2	$S_{2y} p \Psi_t^{rs}$	41	1.93	0.26
	3	$S_{6y} p_t \Psi_t^{rs}$	35	3.00	0.12		3	$S_{2y} p_t \Psi_t^{rs}$	49	6.99	0.02
	4	$S_{6y} p_t^r \Psi_t^{rs}$	49	40.25	0.00		4	$S_{2y}^r p_t^r \Psi_t^{rs}$	57	16.62	0.00
	5	$S_{6y}^r p_t^r \Psi_t^{rs}$	53	45.74	0.00		5	$S_{2y}^r p_t^r \Psi_t^{rs}$	75	40.85	0.00
1998	1	$S_{4y} p_t \Psi_t^{rs}$	45	0.00	0.68	2000	1	$S_{2y} p^r \Psi_t^{rs}$	45	0.00	1.000
	2	$S_{4y} p^r \Psi_t^{rs}$	42	2.22	0.22		2	$S_{2y} p_t \Psi_t^{rs}$	49	16.08	0.000
	3	$S_{4y} p \Psi_t^{rs}$	39	3.89	0.09		5	$S_{2y} p_t^r \Psi_t^{rs}$	63	19.05	0.000
	4	$S_{4y} p_t^r \Psi_t^{rs}$	59	14.96	0.00		4	$S_{2y} p \Psi_t^{rs}$	43	19.63	0.000
	5	$S_{4y}^r p_t^r \Psi_t^{rs}$	63	18.00	0.00						

Model notation: S = apparent survival; p = detection probability; Ψ = movement probability; y = year dependence; t = time-dependence; r = region-dependence; rs = region-dependent movement probability. $S_{n,t}$ refers to a model where apparent survival is fixed to 1 for the first n time periods and time-dependent afterwards.