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The effects of disturbance on behaviour, habitat use and energy of spring staging snow geese

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Summary

1. For many species, human-induced disturbances can severely influence an individual's pay-off; however, energy-cost variations from different disturbance types have rarely been reported.

2. We evaluated the dynamic behavioural responses of staging greater snow geese *Anser caerulescens atlanticus* to different types of disturbance in southern Quebec, Canada, between 1997 and 2000. We specifically considered the impact of a unique measure, a spring conservation hunt implemented in agricultural habitats in 1999.

3. We tracked 237 radio-tagged females for 2764 h and recorded 697 take-offs following fortuitous disturbance, scaring and hunting in three regions characterized by different habitats. Geese used cornfields in south-western Quebec, *Scirpus* marshes and hayfields in the upper St Lawrence estuary, and *Spartina* marshes and hayfields in the lower estuary.

4. Overall, disturbance levels increased in the upper and lower estuary during years with hunting, mostly through an increase in hunting and scaring activities.

5. The probability of geese returning to a refuge after disturbance in agricultural habitats increased in years with hunting except in the corn-growing region. The short-term energy gain of geese resuming feeding after disturbance was less than before disturbance, and this difference was greater in years with hunting. Distances flown after disturbance decreased with flock size and were longer after scaring and hunting than after fortuitous disturbances in the *Scirpus* region.

6. Overall, habitat use varied among years and associated estimated energy gain decreased markedly in both years with hunting in the *Spartina* and corn-growing region, but did not change in the *Scirpus* region. Changes in behaviour due to disturbance, and especially those associated with hunting, probably contributed to the reduced body condition of staging greater snow geese during years with hunting.

7. *Synthesis and applications*. From a methodological viewpoint, we highlight the importance of tracking the behaviour of individual animals after disturbance to properly evaluate its impact. From a conservation perspective, we provide empirical arguments to limit the hunting of breeding waterfowl during their prenuptial migration in order to facilitate their fattening and forthcoming reproduction. From a management standpoint, we suggest that a side-effect of disturbance induced by spring hunting to control overabundant populations may be reduced fattening and breeding output among birds that survive. Together, these data emphasize further the importance of measuring the direct and indirect effects of disturbance rather than assuming effects from the incidence of the disturbance alone.

Key-words: *Anser caerulescens atlanticus*, energy cost, hunting, radio-tracking, spring stopover

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Introduction

Because of potential conflicts between wildlife conservation and other uses of rural environments, there is considerable interest in quantifying the impact of disturbance on animal populations (Hill *et al*. 1997; Gill, Norris & Sutherland 2001; Alonzo, Switzer & Mangel 2003). However, virtually no study has dealt with the dynamic behavioural response of animals to disturbance. In particular, few studies illustrate how disturbance events affect the foraging movements and subsequent habitat use of animals. The behavioural response of animals to disturbance will depend on species-specific tolerance levels, disturbance type and frequency, group size for socially foraging animals, and local conditions such as the availability of alternative foraging sites (Madsen 1998a).

In addition to being a source of mortality, hunting can also be a major source of disturbance for birds, and this is why the activity is regulated in many countries (Nichols & Johnson 1989; Harradine 1991; Fox & Madsen 1997). More specifically, hunting has been prohibited during prenuptial migration because of potential effects on forthcoming reproduction. However, this practice has been revised recently to allow spring conservation hunts of over-abundant white goose species in North America. Hunting regulations were amended to stop population growth in the greater snow goose *Anser caerulescens atlanticus* K. (Canadian Wildlife Service 2001). As other goose populations are also increasing in North America and Europe (Ankney 1996; Madsen, Cracknell & Fox 1999), such controversial management actions could be implemented elsewhere in the future. In other parts of the world (e.g. Russia), spring hunts on declining populations of waterfowl are still allowed in the absence of solid scientific evidence of negative effects (E. Syroechkovski Jr, personal communication). Whereas the effect of hunting disturbance on waterfowl has been largely explored in autumn and winter (Madsen 1995, 1998b; Evans & Day 2001), there have been few assessments of its effect during spring migration (but see Madsen 1995; Béchet *et al*. 2003), a critical fattening period for the forthcoming period of reproduction (Gauthier, Giroux & Bédard 1992; Prop *et al*. 1998).

Our objective was to estimate the effects of disturbance on the foraging behaviour of greater snow geese during their spring stopover in years with and without hunting, and in three regions differing in habitat availability. First, we evaluated variation of different disturbance risks in years with and without hunting. Secondly, we tested the hypotheses that (i) the probability that geese return to a refuge after disturbance, (ii) the loss in short-term energy gain resulting from habitat changes after disturbance, and (iii) the distances flown following disturbance would vary with disturbance type. Because habitats generally differ between refuge and non-refuge areas and because flight is energetically costly, these three behavioural variables were considered critical components of the effect of disturbance. Thirdly, we compared the overall habitat use by foraging geese between years with and without hunting. Finally, we discussed how the effects of disturbance could explain variations in habitat use at a large scale and the potential energetic impacts of disturbance at the population level.

Study area and methods

STUDY SPECIES AND STUDY AREA

Greater snow geese are long-distance migrants that breed in the eastern high Arctic of Canada and western Greenland, and winter along the Atlantic coast of the USA (Gauthier, Giroux & Bédard 1992). During their spring and autumn migration, they stage in southern Quebec (Reed, Giroux & Gauthier 1998). In spring, the first birds arrive in southern Quebec by mid-March and the last ones leave for the Arctic around the third week of May.

The spring staging area extends from Lake Champlain at the USA–Canada border along the St Lawrence River to Matane (Fig. 1). We divided this area into three contiguous regions, the Lake St Pierre (LSP), the upper estuary (UEST) and the lower estuary (LEST). In the LSP region, waste corn in stubble and ploughed fields is the main food source for geese and these fields are scattered within a 2500-km^2 area extending up to 60 km inland from the St Lawrence River (Giroux & Bergeron 1996). The birds roost on managed flooded fields, rivers (Richelieu and St Lawrence) and reservoirs. In UEST, *Scirpus* marshes are used both as roosting and feeding sites (Giroux & Bédard 1988). Geese also feed in adjacent hayfields (< 10 km inland) on Timothy grass *Phleum pratense* L., clover *Trifolium pratense* L., alfalfa *Medicago sativa* L. and waste oat grains *Avena sativa* L. (Bédard & Gauthier 1989). Some cornfields are also used in the south-western portion of this region. Finally, *Spartina* marshes are used for roosting and feeding in LEST; feeding also occurs in hayfields similar to those found in UEST but located < 5 km inland (Gauthier, Bédard & Bédard 1988).

In 1999 and 2000, hunting was allowed on all agricultural lands from 15 April to 31 May. Hunting-free areas (hereafter called refuges) were limited to roosting sites (rivers, flooded lowlands), all marshes along the St Lawrence estuary and a few coastal fields (total of 550 ha) managed as alternative feeding areas in UEST. The hunt involved more than 9000 hunters (H. Lévesque, Canadian Wildlife Service, personal communication) distributed throughout southern Quebec.

RADIO-TAGGING AND TRACKING

A total of 310 adult female greater snow geese was captured in August at the Bylot Island colony, Nunavut (73°00′N, 80°00′W), between 1996 and 1999, and were fitted with radio-collars (Demers *et al*. 2003). Captures

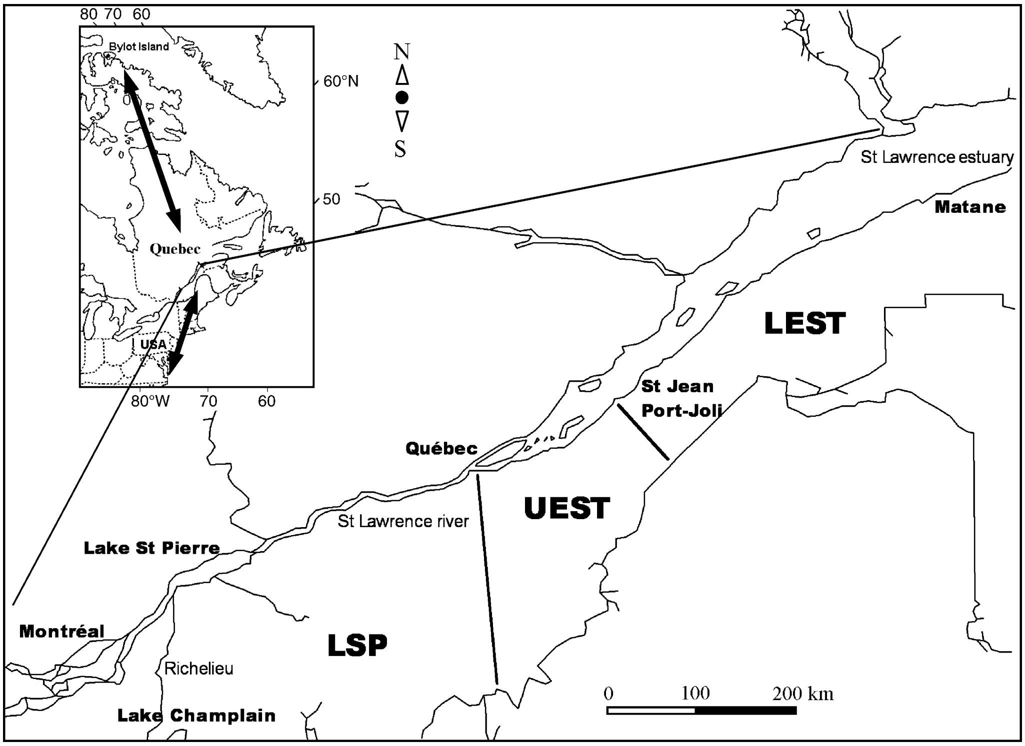

Fig. 1. The St Lawrence River valley in southern Quebec, Canada, with the three regions used by greater snow geese during their spring stopover: the Lake St Pierre region (LSP, corn-growing area), the upper estuary (UEST, *Scirpus* marsh area) and the lower estuary (LEST, *Spartina* marsh area). Arrows in the inset map represent the general migration routes.

consisted of small (< 15 geese) family groups of flightless successful breeders with their young because non-breeders leave the area to moult (Reed *et al.* 2003). Radios with collars weighed 59 ± 9 g (i.e. 2·5 ± 0·02% of female body mass) and lasted 16–24 months with a signal range of 1–2 km on the ground.

From 1997 to 2000, radio-tagged geese were tracked from their arrival on the staging area (range 11–30 March) until their departure for the Arctic (range 20–26 May). Hence, we benefited from a quasi-experimental situation with 2 years of monitoring without (1997–98) and with (1999–2000) hunting. Six crews with vehicles covered the entire staging area from Lake Champlain to Matane. Every morning, radio-tracking of geese began simultaneously at dawn at the main roosting sites in each region. Among the radio-tagged birds detected, we randomly picked one and tracked it continuously for up to 3 h (average 1·5 h). In most cases, geese flew to agricultural habitats and we tracked them until they landed in a field, which corresponded to the beginning of a foraging bout. At UEST and LEST, geese could stay in the marsh to feed. We began the observation as soon as light conditions permitted. We recorded the location of the geese to the nearest 100 m on 1 : 50 000 maps, the habitat type, the time at the beginning of the foraging bout and, ultimately, the time and cause of take-off. A new foraging bout was initiated when geese landed either at the same or at a new location (> 100 m). Flock size was determined at the beginning of each foraging bout and the number of geese arriving or departing was monitored throughout the bout. Each monitoring session thus constituted successive foraging bouts. Starting in 1998, we measured the feeding rate of the flock containing the radio-tagged bird by scanning 200 randomly chosen individuals at the beginning of the bout and every 30 min afterward, and counting the number of geese with the head below horizontal (Altmann 1974). At the end of a monitoring session, the neighbouring area was randomly searched by vehicle and each goose flock encountered was scanned for the presence of radio-tagged birds. If one was detected, we initiated a new monitoring session. The same sampling scheme was repeated in the afternoon as birds usually came back to roosting sites at mid-day before initiating a new foraging trip. We distinguished between (i) a disturbance causing take-off and (ii) geese choosing to take-off themselves, by the number of geese taking-off: all or most of the geese taking-off simultaneously was caused by a disturbance; geese taking-off gradually in small groups was caused by themselves. Three sources of disturbance were identified.

Fortuitous. Fortuitous take-offs were caused by predators or predator-like animals (raptors and other large birds, foxes *Vulpes vulpes* and coyotes *Canis latrans*) or by human activities other than scaring or hunting (e.g. motorcycles, vehicles and aircraft). Disturbances of unknown sources (21% of all disturbances) were also included in this category because we knew that they were neither due to scaring nor hunting.

Table 1. Estimates of hourly metabolizable energy (HME) of spring staging greater snow geese in southern Quebec

Habitat	HME (kJ h^{-1})	Sources
Stubble cornfields	286 (429)*	This study
Ploughed cornfields (0·1)	29 (43)*†	_
(0·25)	72 (107)*†	_
(0·5)	143 (214)*†	_
First-year hayfields	228‡	Bédard & Gauthier (1989)‡
Hayfields	97‡	Bédard & Gauthier (1989)‡
Scirpus marshes	146	Bédard & Gauthier (1989)
Spartina marshes	65	Bédard & Gauthier (1989)

*HME is unknown for greater snow geese feeding on corn grains. As a substitute, we used the intake rate value of Bédard & Gauthier (1989) for geese feeding on small-grain cereals to estimate HME of corn. However, because this value may be underestimated, we also used a value 1·5 × higher (indicated in parentheses; see Methods for details).

†The reduction of corn intake rate in ploughed fields compared with stubble fields is unknown. We therefore used different values representing the intake rate in ploughed fields as a proportion (indicated in parentheses) of the value in stubble fields.

‡Bédard & Gauthier (1989) established the metabolizable energy of three different diets (A, B, C) composed of an increasing proportion of wasted small cereal grains and a decreasing proportion of grass and legume foliage in hayfields. As first-year hayfields contain a high proportion of grains, we reported the mean value of diet C for this agricultural habitat. We reported the combined mean value of diet A and B for HME in other hayfields.

Scaring. Scaring take-offs resulted from passive scaring devices such as propane-cannons or from humans driving or walking towards geese to chase them.

Hunting. Hunting take-offs were caused by shooting by hunters who were either hiding in a blind surrounded by decoys or sneaking towards the flocks.

ENERGY GAIN CALCULATIONS

To assess the consequences of habitat changes on energy gains, we used estimates of hourly metabolizable energy gain (HME) as reported in the literature for greater snow geese (Table 1). HME depends on the functional response of foraging geese (intake rate as a function of food density) and the energy density and digestibility of the plants consumed. The functional response of greater snow geese feeding on corn is unknown and we were unable to estimate it by faecal output assessment (Bédard & Gauthier 1986) because of the long defaecation intervals resulting from the high digestibility of corn. As a surrogate, we used the goose intake rate of small grains (*Avena*) in stubble fields (19 g dry weight h^{-1}; Bédard & Gauthier 1989) as a minimal value for stubble cornfields. This yielded a HME value of 286 kJ h^{-1} based on a gross energy of 17·3 kJ g^{-1} and digestibility of 0·87 for corn (G. Gauthier, unpublished data). Because Bédard & Gauthier (1989) believed that their intake rate estimate for *Avena* was low and because of the larger size of corn grains, we also performed the analyses with a value 1·5 times higher (429 kJ h^{-1}) to verify the sensitivity of our results to this value. In LSP, waste corn grains are up to 30 times less available in ploughed than in stubble cornfields (J.-F. Giroux, unpublished data). As the functional response of intake rate relative to corn density is probably not linear but type II (Holling 1959), we performed the analyses using three different values of HME in ploughed cornfields, i.e. 0·1, 0·25 and 0·5 times the HME in stubble cornfields.

STATISTICAL ANALYSES

All statistical analyses were performed separately for each region because of differences in habitat and food availability for geese.

Disturbance risk

We first tested the effects of year (1997–2000) and hunt (i.e. we reduced annual effects to years with vs. without hunting) on disturbance risk. We estimated the probability of completing a foraging bout of length *t* at a site under the risk of fortuitous, scaring or hunting disturbance using the Kaplan–Meier estimator (Kaplan & Meier 1958). Each foraging bout was considered an independent trial in which the birds were under the risk of disturbance. As field observations were randomly allocated to different radio-tagged birds, we were confident that birds that would be prone to repeated disturbances would not bias the estimate. The Kaplan–Meier approach does not require assumptions about the distribution underlying the occurrence of disturbance events, and can account for censored observations. A foraging bout could either end by a disturbance (akin to mortality in a standard Kaplan–Meier survival analysis) or be censored if the birds left by themselves or if the observer quitted at the end of a monitoring session. This approach avoided the potential biases associated with the traditional estimation of disturbance rates based on the number of events and hours of observation. We used the Cox regression method (Cox & Oakes 1984) with PROC PHREG (Allison 1995; SAS Institute Inc. 1999) to test differences of disturbance risk among years (year effect) and between years with and without hunting (hunt effect).

Effects of hunting and disturbance type on goose behaviour

We tested the effects of hunt and disturbance type (dtype; fortuitous, scaring or hunting) on (i) the probability of returning to a refuge, (ii) the short-term loss in energy gain due to habitat change and (iii) distance flown (i.e. the straight line distance between ground locations before and after disturbance). In all models, we controlled for flock size (FS) by calculating the mean number of birds counted at the beginning and at the end of an observation bout. We tested all possible models with fixed effects and the interactions year × dtype and hunt × dtype. No other interactions were considered because of a lack of biological rationale. To avoid pseudoreplication (Otis & White 1999), an individual tracked more than once was attributed a weight inversely proportional to the number of times it was tracked, such that the sum of weights equalled 1 for each individual within an analysis. Because foraging flocks are highly labile, individuals often responded differently to the same disturbance. We thus considered different radio-tagged birds within the same flock as independent (less than 10% of the disturbances recorded concerned > 1 radio-tagged geese).

We analysed the probability of returning to a refuge after disturbance by fitting logistic models with a binomial error distribution. As this probability may increase in the middle and at the end of the day (De Koster 1993), we controlled for that by adding an hourly index (hour), linearly decreasing from dawn to 15:00 and from 15:00 to dusk.

To analyse short-term loss in energy gain, we calculated an index of the instantaneous difference in energy gain experienced by disturbed geese as:

$$\Delta\mathrm{HME} = (\mathrm{HME}_{ha} \times \mathrm{FR}_{ha}) - (\mathrm{HME}_{hb} \times \mathrm{FR}_{hb})$$

where HME_{ha} and FR_{ha} are the HME and feeding rate (FR) in the habitat used immediately after disturbance, and HME_{hb} and FR_{hb} are the same values in the habitat used before disturbance. Habitat-specific mean feeding rates observed in 1998 were used for 1997. Because none of the usual transformations allowed modelling this difference assuming a normal distribution of the error terms, the ΔHME was categorized into 100-kJ h^{-1} classes.

Because geese often landed in the same field after disturbance, distances flown were skewed towards 0 and could not be modelled assuming a normal error distribution. Hence, we similarly categorized them into 5-km classes in LSP and UEST, and 2-km classes in LEST. We modelled the cumulative probabilities of the ordered categories of ΔHME and distance flown using proportional odd models (Peterson & Harrell 1990) with a multinomial distribution and a cumulative logit link. This allowed testing the effect of dtype and hunt on the probability of occurrence of different ΔHME (i.e. short-term loss in energy gain) and distances flown following disturbance.

Feeding rates, habitat use and overall energy gain

We first tested whether feeding rates varied among years for a given region and habitat. We then estimated the overall habitat use and energy gains realized by geese in the three regions during years with and without hunting, using a combined hourly metabolized energy index (CHMEI). For each foraging bout i of a radio-tagged goose in habitat h, the time spent foraging was calculated as:

$$\mathrm{TF}_{hi} = T_{hi} \times \mathrm{FR}_{hi}$$

where T_{hi} is the duration of the observation bout and FR_{hi} the averaged feeding rate in h. The overall proportion of time spent foraging in habitat h was calculated as:

$$F_h = \left(\sum_i \mathrm{TF}_{hi}\right) / \mathrm{TF}$$

where TF was the total amount of time that a goose was observed foraging in a region. Individuals cumulatively tracked for less than 1 h were discarded. The CHMEI of the geese was calculated as:

$$\mathrm{CHMEI} = \sum_h (F_h \times \mathrm{HME}_h)$$

where HME_h was the habitat-specific HME (Table 1). Hence, this index represents the mean energy intake per hour spent foraging in each region, controlling for the proportion of time devoted to foraging in each habitat. We fitted linear models with a normal error distribution to test if overall energy gains of geese (variable CHMEI) changed in years with hunting (variable hunt),

Significance of effects

The significance of effects was assessed by model selection (Burnham & Anderson 1998). All models were fitted using the maximum likelihood optimization procedure GENMOD (SAS Institute Inc. 1999) and model selection relied on the Akaike information criterion with the small sample adjustment, AIC_c (Burnham & Anderson 1998). The model with the lowest AIC_c was accepted as the best approximating model for the data. Because AIC_c is on a relative scale, we only present the $\Delta\mathrm{AIC}_c$ with respect to the lowest value. The normalized Akaike weights, $\mathrm{AIC}_c\ \omega$ (Burnham & Anderson 1998), were used as an index of relative plausibility when comparing models. The reliability of logistic models was measured by goodness-of-fit tests based on a Pearson χ^2. When the test was significant, we corrected for this extra-binomial variation by a variance inflation factor, which modifies AIC_c into a quasi-likelihood AIC_c (QAIC_c; McCullagh & Nelder 1983). We present means ± 1 SE.

Table 2. Probabilities (±95% confidence intervals) of completing a 60-min foraging bout without being disturbed for spring staging greater snow geese in southern Quebec. Thus, a higher probability value indicates a lower disturbance level

		Disturbance types			
Year	Region	Fortuitous	Scaring	Hunting	All sources
1997	LSP	0·51 ± 0·06	0·99 ± 0·01	_	0·50 ± 0·05
1998	LSP	0·59 ± 0·06	0·99 ± 0·01	_	0·58 ± 0·06
1999	LSP	0·60 ± 0·08	0·98 ± 0·02	_*	0·59 ± 0·08
2000	LSP	0·53 ± 0·06	0·86 ± 0·04	0·69 ± 0·09	0·45 ± 0·06
1997	UEST	0·54 ± 0·10	0·80 ± 0·08	_	0·42 ± 0·10
1998	UEST	0·60 ± 0·08	0·84 ± 0·06	_	0·49 ± 0·08
1999	UEST	0·56 ± 0·09	0·57 ± 0·09	0·69 ± 0·10	0·29 ± 0·08
2000	UEST	0·53 ± 0·06	0·61 ± 0·08	0·81 ± 0·07	0·38 ± 0·07
1997	LEST	0·64 ± 0·10	0·80 ± 0·08	_	0·50 ± 0·10
1998	LEST	0·68 ± 0·07	0·82 ± 0·06	_	0·55 ± 0·08
1999	LEST	0·73 ± 0·10	0·41 ± 0·09	0·69 ± 0·09	0·27 ± 0·08
2000	LEST	0·67 ± 0·12	0·53 ± 0·12	0·70 ± 0·12	0·33 ± 0·11

*No hunting disturbance was recorded on radio-tagged greater snow geese in 1999 in LSP because of a low hunting pressure and a few radio-tagged geese remaining in that region after the beginning of the hunting season.

Results

RADIO-TRACKING AND DISTURBANCE RISK

We radio-tracked 42, 72, 56 and 67 female snow geese for 642, 681, 476 and 965 h from 1997 to 2000, respectively (11·9 ± 1·7 h bird^{-1} year^{-1}). We recorded 527 take-offs following fortuitous disturbance, 106 after scaring and 64 after hunting during 2456 foraging bouts. Fortuitous disturbances remained at similar levels throughout the study in all regions (best models had no effect, AIC ω > 0·40; Table 2). Although scaring was negligible at LSP, it nonetheless increased slightly in years with hunting (model with a hunt effect, AIC ω = 0·72; Table 2). At UEST, scaring tended to increase in years with hunting (model with no effect, AIC ω = 0·49; model with a hunt effect, AIC ω = 0·37, ΔAIC_c = 0·56) while hunting disturbance decreased from 1999 to 2000 (AIC ω = 0·72). At LEST, scaring disturbance varied among years (model with a year effect, AIC ω = 0·74), with higher values in 1999 and 2000 than in previous years (1·2–2·6 times higher). At LSP and UEST, the overall disturbance level varied among years (model with a year effect, AIC ω > 0·62) and was generally higher in years with hunting at UEST (1·2–1·9 times higher). At LEST, disturbance increased 2·2 times in years with hunting (model with a hunt effect, AIC ω = 0·71; Table 2).

PROBABILITY OF RETURNING TO A REFUGE FOLLOWING DISTURBANCE

In all regions, the probability of returning to a refuge after disturbance increased until mid-afternoon and from then to dusk (sum of AIC_c ω for hour effect = 0·92, 0·68, and 0·80 in LSP, UEST and LEST, respectively; Fig. 2). Moreover, larger flocks were less likely to return to a refuge than smaller ones (FS effect was retained in the first or second model in all regions; ΔAIC_c < 1·78). In UEST, the probability of returning to a refuge was 2·7 times higher during hunting than in previous years (best model with a hunt effect, AIC_c ω = 0·28), whereas in LEST this probability differed among years (model with a year effect, AIC_c ω = 0·36) but was also highest in the two hunting years (Fig. 2). However, the overall evidence for a direct effect of hunt was weak to moderate (sum of AIC_c ω across models = 0·24, 0·45 and 0·17 in LSP, UEST and LEST, respectively). Finally, there was little evidence for an effect of dtype in any region (sum of AIC_c ω < 0·28).

LOSS IN SHORT-TERM ENERGY GAIN OF DISTURBED GEESE

In LSP, the ΔHME following a disturbance varied with disturbance type but differently in years with and without hunting. Depending on the cornfield HME values used, the interaction hunt × dtype was retained in the best model (AIC_c ω > 0·40) or was almost as good as the best model in the remaining three cases (ΔAIC_c < 1·71). Overall, the hunt effect was less supported (sum of AIC_c ω > 0·44) than dtype (sum of AIC_c ω > 0·88). In years with hunting, only scaring led to an increased reduction in short-term energy gain of geese after disturbance, the reduction being comparable for the other disturbance types in years with and without hunting (Fig. 3a,b).

In UEST, energy gain of geese after a disturbance decreased much more in years with hunting (2·5 times, odd ratios) than in years without (the best model had the hunt effect for all cornfield HME values used, AIC_c ω > 0·36; Fig. 3c). Overall, the hunt effect was well supported (sum of AIC_c ω > 0·69) but not the dtype (sum of AIC_c ω < 0·19). The same pattern was found at LEST (the best model had the hunt effect, AIC_c ω = 0·27, while the second best model retained no effect, AIC_c ω = 0·22; ΔAIC_c = 0·35; Fig. 3d), with more evidence overall for a hunt effect (sum of AIC_c ω = 0·47) than for a dtype effect (sum of AIC_c ω = 0·23).

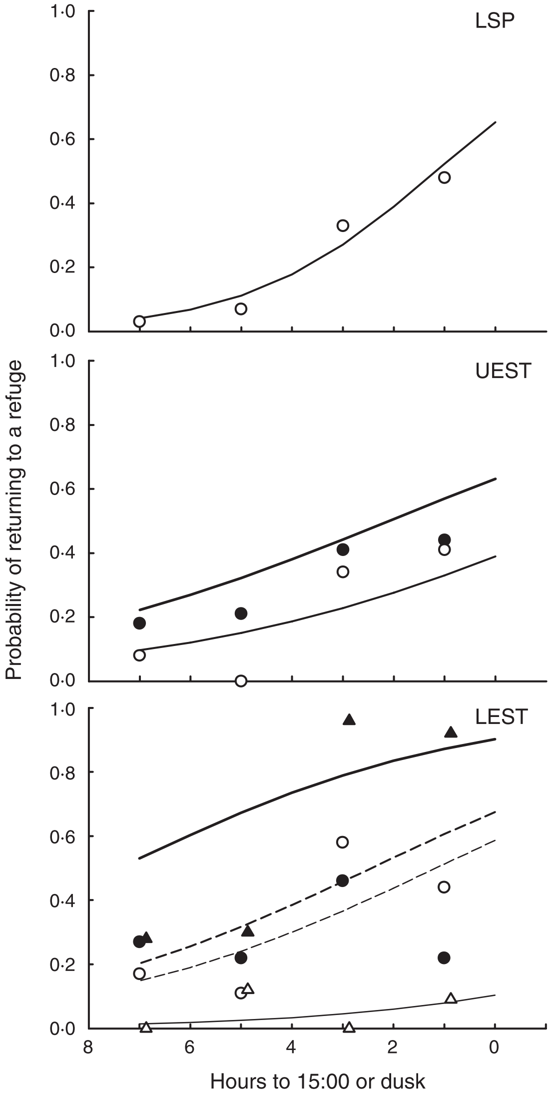

Fig. 2. Probability of returning to a refuge after disturbance for greater snow geese staging in southern Quebec in relation to the number of hours remaining before 15:00 or dusk. In LSP, observed (open circles) and predicted (line) probability for all years. In UEST, observed and predicted probability in years with hunting (filled circles; bold line) and without hunting (open circles; light line). In LEST, observed and predicted probabilities in 1997 (open circles; dashed light line), 1998 (open triangles; solid light line), 1999 (filled circles; dashed bold line) and 2000 (filled triangles; solid bold line).

DISTANCES FLOWN AFTER DISTURBANCE

In all regions, distances flown after disturbance decreased with flock size (FS, sum of AIC$_c$ ω > 0·65). In UEST, the distances flown varied with disturbance type (best model AIC$_c$ ω = 0·46; sum of AIC$_c$ ω for dtype = 0·75). Distances flown after scaring and hunting were, respectively, 3·9 and 7·1 longer than after fortuitous disturbance (odd ratios) and median distances flown after disturbance increased from 0 (fortuitous), to 0·6 (scaring) and 2·3 km (hunting; Fig. 4). There was little evidence for an effect of disturbance type in LSP and LEST (sum of AIC$_c$ ω < 0·38) and the hunt effect was weak in all regions (sum of AIC$_c$ ω < 0·41).

FEEDING RATE, HABITAT USE AND OVERALL ENERGY GAIN

Feeding rates increased in years with hunting in most habitats, except in ploughed cornfields and *Scirpus* marshes in UEST and hayfields in LEST (Table 3). In all regions, CHMEI varied among years (best model, AIC ω > 0·56) but could not be explained by a simple hunt effect (AIC ω < 0·21; Fig. 5). In LSP, CHMEI tracked the use of corn by geese, especially stubble fields, and was thus sensitive to the choice of HME values. The CHMEI peaked in 1998, when stubble fields were most heavily used (Figs 5 and 6). In contrast, use of stubble cornfields was lower in 2000, leading to a 20–60% drop in CHMEI depending on the *HME* values used for cornfield (Figs 5 and 6; the decrease was accentuated for low HME values in ploughed cornfields).

In UEST, CHMEI of geese decreased slightly (20% lower) after 1997 and remained stable afterwards. It was only slightly affected by the choice of cornfield HME values (< 20 kJ h^{-1}) because of the low use of this habitat there (Fig. 5). Finally, the striking increases in use of *Spartina* marshes by geese in years with hunting at LEST (from 20% to 50% higher; Fig. 6) caused a large drop in CHMEI in those years (Fig. 5). This result was not affected by the choice of HME values in cornfields.

Discussion

Spring hunting increased the overall disturbance level for geese, especially in both estuary regions. Disturbed geese returned more often to a refuge in years with hunting than in those without, they flew longer distances after a scaring or a hunting disturbance than after a fortuitous one, and disturbed geese used habitats that yielded less metabolizable energy, especially in hunting years. These behavioural changes reduced the overall energy gains of geese during their staging period in years with hunting.

The increase in the probability of returning to a refuge after disturbance in hunting years for two of the three regions indicates that both scaring and hunting activities generate disturbance of high severity that can induce direct costs, such as increased movements towards refuges or to alternative feeding sites. In addition to the cost of decreased time available for foraging due to increased time spent flying (Bélanger & Bédard 1990; Riddington *et al.* 1996), these movements increase energy expenditure due to the high cost of flying and may lead birds to habitats of lower quality, decreasing further energy gains. Indeed, we found that immediate reduction of energy gains after disturbance was more frequent during hunting years in all regions.

Disturbance type affected subsequent energy gains in the corn-growing region, and distance flown increased from fortuitous disturbance to hunting in the *Scirpus* region. Geese often tended to land at the same site after fortuitous disturbances, whereas they moved further

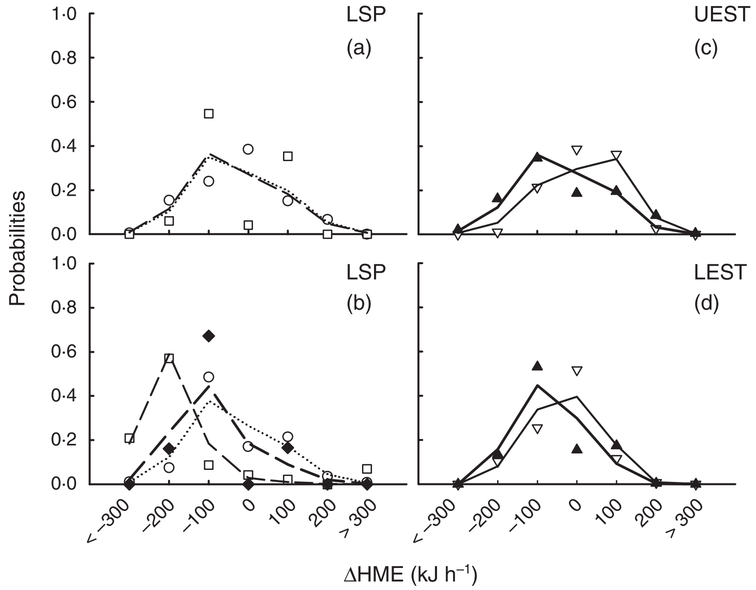

Fig. 3. Probabilities of experiencing a reduction (negative values) or an increase (positive values) in hourly metabolizable energy gain (ΔHME) due to habitat change following a disturbance in spring staging greater snow geese in southern Quebec (1997–2000). The HME of stubble cornfield is set to 286 kJ h^{-1} and 0·25× lower in ploughed cornfields. In LSP, observed and predicted probabilities after fortuitous disturbance (open circles; dotted light line), scaring (open squares; dashed light line) and hunting (diamonds; dashed bold line) in years without (a) and with (b) hunting. In UEST and LEST, observed and predicted probabilities in years without hunting (open triangles; light line) and with hunting (filled triangles; bold line).

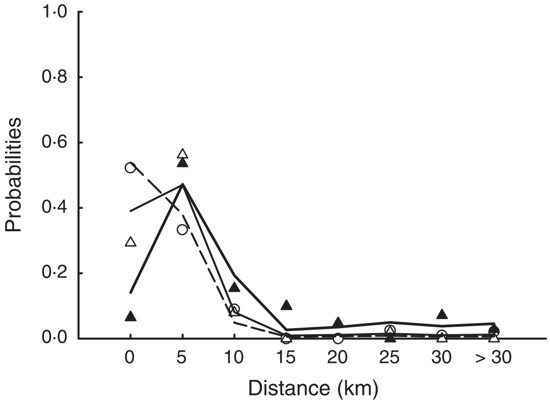

Fig. 4. Probabilities that greater snow geese fly different distances after disturbance in the UEST region of southern Quebec (1997–2000). Observed and predicted probabilities of distances flown after fortuitous (open circles; dashed light line), scaring (open triangle; solid light line) and hunting (filled triangle; solid bold line) disturbance. Flock size was set to 10 000.

away after scaring activities and even more so after hunting-related disturbances. It has been shown that pink-footed geese *Anser brachyrhynchus* increased foraging flight distances from roost to feeding sites located at > 25 km after the onset of hunting (Madsen 1988). However, to our knowledge, our results are among the first to document an increase in distances flown with a gradient of disturbance levels (but see Beale & Monaghan 2004). Habituation is believed to occur when disturbance consists of predictable and directional stimuli (Bélanger & Bédard 1989; Fox & Madsen 1997) but it may depend strongly on species-specific susceptibility to disturbance (Burger 1981). Geese may habituate to fortuitous disturbances that are not purposely orientated towards chasing them from their foraging sites, but do not appear to habituate readily to scaring or hunting. We also found that distances flown after disturbance decreased as flock size increased. In larger flocks, relatively fewer geese may be aware of the

Table 3. Mean (± SE) feeding rate (percentage of time with head below horizontal) of greater snow geese in flocks with radio-marked birds in various habitats used during their spring staging in southern Quebec (1998–2000). Means followed by the same letters are not significantly different among years for a given habitat and region (Wald χ^2 test)

Year	Region	Stubble corn	Ploughed corn	Hayfields	First-year hayfields	*Scirpus* marshes	*Spartina* marshes
1998	LSP	45·9 ± 1·8 a (124)	32·2 ± 3·3 a (101)	25·0 ± 6·4 a (36)	_	_	_
1999	LSP	64·6 ± 2·7 b (61)	50·5 ± 3·0 b (90)	58·4 ± 4·9 b (48)	_	_	_
2000	LSP	54·3 ± 2·5 c (63)	38·4 ± 2·0 a (203)	47·0 ± 3·4 b (95)	_	_	_
1998	UEST	47·7 ± 4·5 a (31)	56·8 ± 2·0 a (16)	64·4 ± 2·6 a (13)	69·9 ± 3·3 a (39)	67·1 ± 2·1 a (136)	_
1999	UEST	54·5 ± 5·5 ab (18)	37·6 ± 6·7 b (13)	72·4 ± 2·2 b (65)	75·1 ± 2·0 a (65)	53·9 ± 3·1 b (136)	_
2000	UEST	59·6 ± 2·3 b (42)	27·5 ± 5·2 b (26)	72·8 ± 1·9 b (197)	82·4 ± 7·3* (5)	53·2 ± 2·4 b(298)	_
1998	LEST	_	_	70·3 ± 2·3 a (86)	74·2 ± 1·4 a (82)	_	46·3 ± 18·6 ab (21)
1999	LEST	_	_	69·1 ± 5·7 a (45)	72·1 ± 3·9 a (36)	_	51·4 ± 5·0 a (61)
2000	LEST	_	_	72·2 ± 2·2 a (63)	73·3 ± 4·3* (7)	_	67·8 ± 2·2 b (173)

*Sample size too small for statistical test.

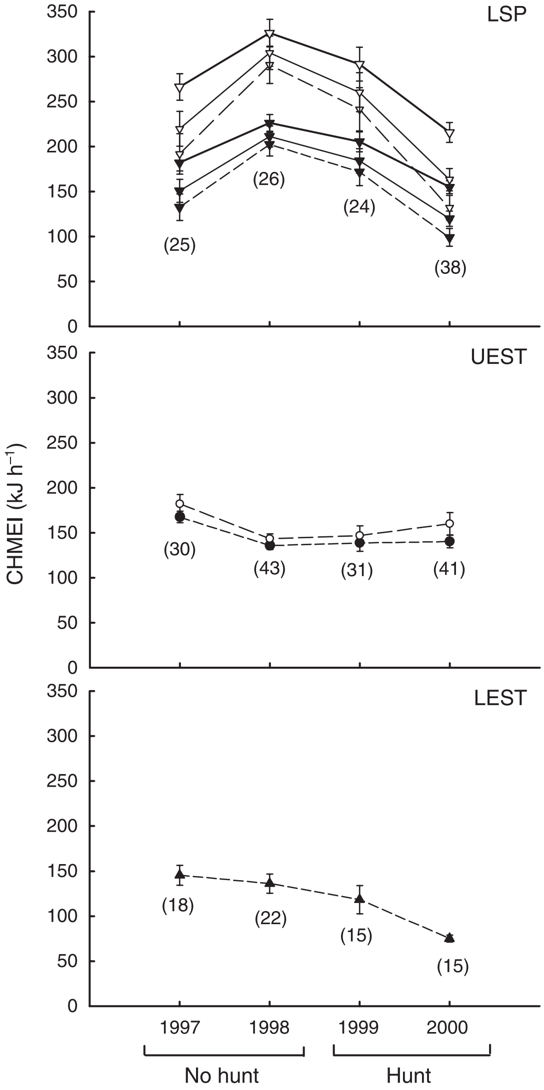

Fig. 5. Combined hourly metabolized energy index (CHMEI ± SE) calculated for spring staging greater snow geese in three regions of southern Quebec in years without (1997–98) and with (1999–2000) a spring hunt. In LSP, the indexes are based on HME values in stubble cornfields of 286 kJ h^{-1} (filled inverse triangles) and 429 kJ h^{-1} (1·5× higher, open inverse triangles), and in ploughed fields of 0·1 (dashed line), 0·25 (solid line) and 0·5 (solid bold line) times the value in stubble cornfields. In UEST, the indexes are based on HME values in stubble cornfields of 286 kJ h^{-1} (filled circles) and 429 kJ h^{-1} (1·5× higher, open circles) and in ploughed fields of 0·1 times the value in stubble cornfields. Presence of cornfields is negligible in LEST. Sample sizes (number of radio-tagged birds tracked > 1 h in total) are in parentheses.

cause of the take-off launched by vigilant individuals and this may favour the return of most geese to the food patch used prior to disturbance.

The effect of hunting disturbance also depends on the location and quality of alternative foraging sites, including those on refuges (Madsen 1998b; Conner, White & Freddy 2001). In the corn-growing region, refuges are rivers and flooded agricultural lowlands, where food is quickly depleted, making these sites unattractive for foraging. The remaining foraging area is vast and, when they are disturbed, geese can find alternative fields but at the expense of long-distance flights. In contrast, the narrow coastal strips of hayfields in the *Spartina* region do not offer the potential for large variation in travel distances, as geese can either choose a nearby field of equivalent quality or return to the marshes, which offer safe but low quality feeding opportunities.

Overall energy gain (CHMEI) markedly decreased during the 2 years with hunting in the *Spartina* region and in 2000 in the corn-growing region. These trends were associated with decreased use of high-quality habitats. The magnitude of the hunting effect on the overall energy gain was thus related to the variability in habitat quality in each region. In the lower estuary, where the effect was strongest, *Spartina* marshes were of much poorer quality than hayfields for foraging (Bédard & Gauthier 1989). The dramatic increase in use of *Spartina* marshes in 2000 was also confirmed by the isotopic signature of *Spartina* in goose tissues from this region (Féret *et al.* 2003). Similarly, stubble cornfields were also of higher quality than the most abundant alternative habitats, ploughed cornfields, at Lake St Pierre. In the upper estuary, however, *Scirpus* marshes offer similar quality food to hayfields (Bédard & Gauthier 1989) and we did not find a marked decrease in overall energy gain in this region in hunting years. Additionally, scaring was purposely directed towards geese using hayfields, to prevent crop damage, while hunters preferentially settled in high-quality habitats preferred by geese. Hence, these two disturbance types decreased the availability of high-quality habitats for geese, especially at LEST. Therefore, our results support the hypothesis that scaring and hunting increase the use of low-quality habitats.

The use of the hourly metabolizable energy of geese as an index of habitat quality to evaluate the effect of disturbance is innovative (reviewed by Hill *et al.* 1997). This estimate depends on the functional response of geese, which may increase to compensate for greater disturbance levels. However, our energy values for marshes and hayfields are likely to be maximal as they were established for spring staging geese fattening up (Bédard & Gauthier 1989; Gauthier, Giroux & Bédard 1992). Cornfield values are more uncertain but nonetheless cover most of the magnitude reported in the literature for other goose species based on the assumption that geese fulfil their daily requirement by feeding solely on cornfields (Frederick & Klaas 1982; Krapu, Reinecke & Jorde 1995). The profitability of ploughed vs. stubble cornfields remains uncertain and the lower it is, the greater the effect of disturbance would be. Thus, our conservative values for ploughed cornfields (probably higher than in reality) may have masked even stronger effects.

Féret *et al.* (2003) showed that abdominal fat and breast muscle protein of greater snow geese at the end of staging was 29–48% and 5–11% lower, respectively, in years with hunting relative to years without, for all regions. Our overall energy gain results are consistent with this reduction in body condition in the *Spartina*

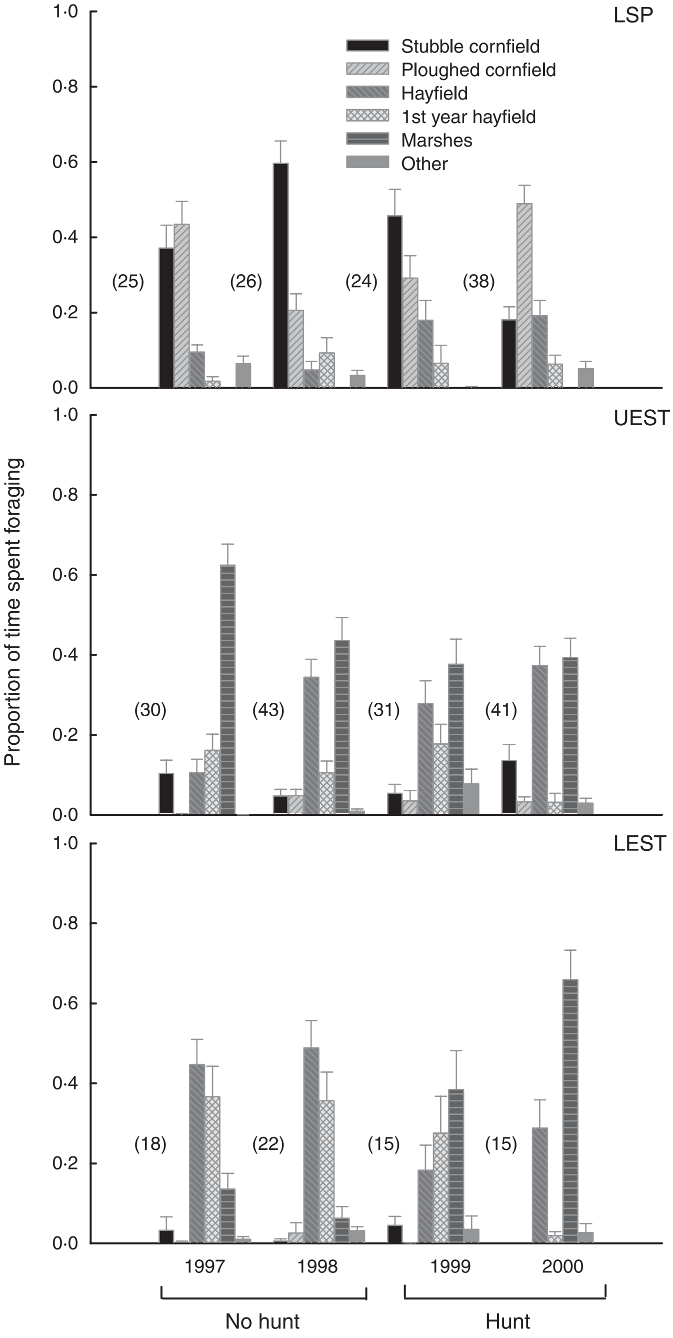

Fig. 6. Proportion (± SE) of time spent by foraging greater snow geese in different habitats in the LSP, UEST and LEST regions during spring staging in southern Quebec in years without (1997–98) and with (1999–2000) hunting. Sample sizes (number of radio-tagged birds tracked > 1 h in total) are in parentheses.

region (1999–2000) and the corn-growing region (2000) but not in the *Scirpus* region, where the CHMEI did not change. Therefore, energy gain variations, as measured by the CHMEI, probably cannot explain entirely the poor body condition of geese in years with hunting. First, we did not consider the decrease in absolute time spent foraging associated with the increased disturbance rate, but only the relative time spent in various habitats. Secondly, even though overall habitat use was not modified in the upper estuary, distances flown increased with hunting disturbance, thus increasing energy expenditure in years with hunting. Thirdly, the CHMEI is an indicator of energy gains within a region but does not account for the time spent by geese in each region and hence does not reflect the overall habitat use of individuals during their total stopover.

Gill, Norris & Sutherland (2001) have recently questioned the use of simple behavioural responses to evaluate the effects of disturbance. They argued that species leaving disturbed sites might be less impacted than those remaining because the former have access to alternative habitats elsewhere while the others do not. Here, we emphasize the importance of determining the quality of the habitats used after disturbance and highlight energy costs involved in moving from one habitat to another. Our results, in combination with those of Féret *et al*. (2003) and Mainguy *et al*. (2002), indicate that hunting disturbance can have negative effects on behaviour of spring staging geese, and ultimately adversely affects their prenuptial fattening and ensuing reproduction. Therefore, our study gives strong support to the hypothesis that disturbance is an important side-effect of hunting that may also impact on the population dynamic of animals through changes in fecundity when it occurs during the prenuptial period. Although this may be viewed as a positive effect for populations like greater snow geese where the management goal is to reduce population growth (Batt 1998), this is clearly not the case for others where the management goal is to increase populations.

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