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ENERGETIC COST OF MAN-INDUCED DISTURBANCE TO STAGING SNOW GEESE

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Abstract: We estimated energetic cost of man-induced disturbance to fall-staging greater snow geese (*Chen caerulescens atlantica*) in Québec. Two responses of birds to disturbance were considered (1) birds fly away but promptly resume feeding following a disturbance (Response A) and (2) birds interrupt feeding altogether (Response B). Daylight foraging time decreased by 4 to 51% depending on disturbance levels. Average rate of disturbance (1.46/hr) in Response A resulted in a 5.3% increase in hourly energy expenditure (HEE) combined with a 1.6% reduction of hourly metabolizable energy intake (HMEI). In Response B, HEE increased by 3.4%; HMEI decreased by 2.9 to 19.4%. Increases in nighttime feeding time and daily feeding rate were evaluated as compensatory mechanisms. A 4% increase in night feeding could compensate for energy losses caused solely by disturbance flights (Response A), but a 32% increase in nighttime feeding was required to restore energy losses incurred in Response B. No increase in daily feeding rate was observed between days with different disturbance levels ($P > 0.05$). We conclude that man-induced disturbance can have significant energetic consequences for fall-staging greater snow geese.

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Despite the importance of staging periods in the life cycle of arctic-nesting geese (Thomas 1983), ecological consequences of human disturbance to staging birds has only recently received attention (Korschgen et al. 1985, Madsen 1985, Bélanger and Bédard 1989). Human activities reduce foraging time of nonbreeding geese and modify their distribution within various habitats (Owens 1977, White-Robinson 1982, Madsen 1985). However, disturbance will be detrimental to staging geese only if it reduces energy intake so much that it cannot be compensated by either increasing rate of food intake during undisturbed periods or by avoiding disturbance by nighttime feeding.

During fall migration, greater snow geese stop for 5–7 weeks in Québec, where they use tidal *Scirpus* spp. marshes of the upper St. Lawrence estuary (Gauthier et al. 1984), particularly areas closed to hunting (Giroux and Bédard 1988). We have previously reported (Bélanger and Bédard 1989) behavioral responses of geese to disturbance and concluded that high levels of disturbance in fall were particularly harmful to geese by decreasing not only time devoted to foraging but also use of sanctuaries.

In this paper, we examine energetic consequences of the birds' responses to disturbance.

In particular, we compare the energetic cost of 2 major responses displayed by birds: Response A—fly away but promptly return to the foraging site and resume feeding, and Response B—fly away, leave the foraging site for a roost site, and interrupt feeding. We also model and compare 2 extreme consequences of Response B: (1) a net loss of foraging time as disturbed birds simply increase resting, preening time, or both (passive reaction); and (2) birds compensate for lost foraging time by reducing time normally allocated to resting (e.g., increase night feeding, increasing daytime ingestion rate [compensatory reaction]), or a combination of both.

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STUDY AREA AND METHODS

Our study was conducted in the 147-ha Montmagny bird sanctuary, 70 km east of Québec City along the St. Lawrence River (47°00'N,

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Table 1. Estimated cost of the basal metabolic rate and amount of time spent in various activities by staging greater snow geese, Québec, 1985–86.

Activity type	Cost ^b	Day		Night ^a	
		%	min/hr	%	min/hr
Foraging	3.0	52.7	31.6	53.2	31.9
Flying	15.0	0.6	0.4		
Resting	1.3	36.8	21.9	46.8	28.1
Alert	2.1	6.4	3.8		
Preening	2.3	1.1	0.9		
Swimming	2.2	2.4	1.4		

^a Only foraging and resting behaviors were identified at night.
^b Multiple of basal metabolic rate from Gauthier et al. (1984).

70°35'W). Details on the study area, terminology, sampling procedures, and behavioral responses of geese to disturbance are presented in Bélanger and Bédard (1989). Observations were conducted in the fall of 1985 and 1986. Data were recorded from dawn to dusk and at all tidal stages during the entire goose migratory stopover period. We made 287 hours of observation, representing means of 5.4 hours/day in 1985 and 4.8 hours/day in 1986. We recorded 452 disturbances for an average daily rate of 1.46 disturbances/daylight hour of observation. The mean rate did not differ significantly ($P > 0.05$) between years, so data were pooled (Bélanger and Bédard 1989). Daily mean rate of disturbance varied from 0 to 3.4/daylight hours of observation. Human activities accounted for $\geq 80\%$ of all disturbances recorded; hunting and transport-related activities (mainly aircraft overflights) ranked first (Bélanger and Bédard 1989). Disturbed geese spent an average of 55.9 seconds in flight/disturbance (Response A). When feeding was interrupted (40.4% of all disturbances, Response B), they eventually resumed feeding after a mean interruption of 726 seconds/disturbance (Bélanger and Bédard 1989).

Data on general time-activity budgets of greater snow geese staging in *Scirpus* spp. marshes are derived from previous reports (Gauthier et al. 1984, 1988). The mean percentage of time devoted to and the costs of various behavioral activities were estimated (Table 1). To detect changes in feeding rate, we used the focal sampling technique (Lehner 1979) to observe randomly selected foraging birds during 10-minute blocks. The following behaviors were recorded in real time on a portable TRS-

Table 2. Projection of total time spent in flight and time to resume feeding (Response A) by fall-staging greater snow geese at different hourly disturbance rates, Québec, 1985–86.

Disturbance rate (no./hr)	Time spent in flight (sec) ^a	Time to resume feeding (sec) ^b
0.0	24 ^c	
0.5	52	363
1.0	80	726
1.5	108	1,089
2.0	136	1,453
2.5	164	1,816

^a Calculated from a mean time of 56 sec/disturbance.
^b Calculated from a mean time of 726 sec/disturbance.
^c Derived from the percentage of time allocated to flight by geese during a day (Gauthier et al. 1988).

80 microcomputer (Tandy Corp., Fort Worth, Tex.): walking (head down or up), feeding (grazing and grubbing), alert (head up), and others (social interactions, occasional preening, etc.).

Basal metabolic rate (BMR) of spring-staging greater snow geese was established by Gauthier et al. (1984) at 686 kJ/day or 28.6 kJ/hour. Measures of HEE were obtained by multiplying BMR by the estimated energetic cost factor of each activity and the calculated percentage of time devoted to it. Hourly metabolizable energy intake of snow geese in *Scirpus* spp. marshes has been reported to be 77.5 kJ/hour or 1,860 kJ/day (Bédard and Gauthier 1989). Energy balance was expressed as HMEI minus HEE.

We used the Shapiro-Wilk statistical test to verify the normal distribution of variables. The percentage of time devoted to the different behaviors by disturbed geese was compared using 1-way ANOVA or the Kruskal-Wallis test depending on the normality of the data. The acceptable level of statistical significance was established at 5%, and means (\pm SE) are presented.

RESULTS

Time spent in flight and time to resume feeding following a disturbance did not differ among days with different disturbance levels ($F = 1.02$, 2,4 df, $P = 0.412$); therefore, daily means were used in subsequent analyses. A disturbance rate of 0.5/hour approximately doubled the flight time, while a maximum rate of 2.5/hour was estimated to cause a 5-fold increase in flight movements compared to undisturbed geese (Table 2). Computed time needed to resume feeding was 5 times greater at a daily disturbance rate of 2.5/hour than at 0.5/hour (Table 2).

Table 3. Activity budget (% of time devoted to a given behavior) of individual foraging greater snow geese in Québec, 1985–86, under different disturbance levels (*N* = 155 observations).

Behavior	No. of disturbances/hr									
	<0.049		0.05–0.99		1.00–1.49		1.5–1.99		>2.0	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Walking	19.3	2.1	20.1	9.8	14.8	2.3	18.1	2.9	16.0	2.5
Grubbing	70.4	2.2	72.1	9.6	76.3	2.7	73.0	3.1	74.3	2.7
Feeding ^a	3.4	0.8	4.6	1.8	2.7	0.4	3.7	0.6	3.1	0.3
Alert	4.9	0.8	2.2	0.7	4.7	1.9	3.7	0.8	6.1	1.3
Others ^b	1.9	0.3	1.0	0.4	1.3	0.4	1.6	0.8	0.6	0.3

^a Ingestion of a plant part when grubbing.
^b Social interactions, preening, etc.

Neither the total time spent “alert” nor the number of times/minute that geese put their head up (alert posture) differed among days with different disturbance rates ($H = 5.13$, 4 df, $P = 0.228$ and $H = 1.56$, 4 df, $P = 0.816$, respectively) (Table 3). The percentage of time allocated to the categories “alert” and “others” therefore was constant among disturbance rates. We found no difference in time allocated to different foraging activities of snow geese, particularly in time spent feeding among days with various disturbance levels ($H = 1.50$, 4 df, $P = 0.827$) (Table 3). Furthermore, feeding rate or feeding success (no. ingestions/min) did not increase significantly with disturbance rates ($H = 3.33$, 4 df, $P = 0.504$).

We compared the energetic consequences of adopting Response A or B in the event of a disturbance (Table 4). There would be a maximum reduction of 4% of feeding time in Response A but a reduction of 7.7% for compensatory reaction and 51.0% in Response B for passive reaction (Table 4). Activity budgets of geese under different disturbance levels were

then transformed into energetic values in terms of HMEI and HEE (Table 5). In Response A, each 0.5/hour increment in the disturbance rate reduced HMEI by about 1.2 kJ, or a 1.6% decrease. Hourly energy expenditure increased with disturbance rates at an average rate of 2.7 kJ/hour per 0.5 disturbance/hour. At the average disturbance rate recorded (1.46/hr), HEE rose by 5.3% as a result of additional time in flight alone.

In Response B, variations in HMEI and HEE were more important. During passive reaction, a mean decrease of 15.0 kJ/hour (19.4%) was observed in HMEI for each 0.5 unit increase in disturbance rate, and there was little variation in HEE (73.9–76.7 kJ/hr). However, if the loss of feeding time was partly integrated in normal goose activity (compensatory reaction), a 2.9% decrease in HMEI (2.3 kJ/hr) was observed, and HEE increased by 2.5 kJ/hour (3.4%) (Table 5). We calculated the energy balance (HMEI minus HEE) for each bird response and for different disturbance levels (Fig. 1). In both Response A and B, an energy deficit of ≥ 7.5 kJ/hour ($\frac{1}{4}$

Table 4. Effects of different disturbance rates on the daytime activity budget (% of time devoted to a given behavior) of fall-staging greater snow geese in Québec, 1985–86.

Rate (no./hr)	Response A			Response B				
	Flying	Feeding	Others ^a	Flying	Feeding		Others	
					Passive reaction	Compensatory reaction	Passive reaction	Compensatory reaction
0.0	0.6	52.7	46.7	0.6	52.7		46.7	
0.5	1.5	51.8	46.7	1.5	41.7	51.8	56.8	46.7
1.0	2.2	51.1	46.7	2.2	30.9	51.1	66.9	46.7
1.5	3.0	50.3	46.7	3.0	20.0	50.3	77.0	46.7
2.0	3.8	49.5	46.7	3.8	9.1	49.5	87.1	46.7
2.5	4.6	48.7	46.7	4.6	1.7	45.0	97.1	50.4

^a Resting, preening, alert.

Table 5. Estimated daytime hourly metabolizable energy intake (HMEI) and hourly energy expenditure (HEE) (kJ/hr) of fall-staging greater snow geese under different disturbance rates, Québec, 1985–86.

Disturbance rate (no./hr)	Response A		Response B			
	HMEI	HEE	HMEI		HEE	
			Passive	Compensatory	Passive	Compensatory
0.0	77.5	74.5	77.5		74.5	
0.5	76.2	77.5	61.3	76.2	74.7	77.5
1.0	75.1	80.0	45.4	75.1	74.2	80.0
1.5	74.0	82.8	29.4	74.0	74.1	82.8
2.0	72.3	85.5	13.4	72.3	73.9	85.5
2.5	71.6	88.2	2.5	66.2	76.7	87.2

BMR) was observed for rates ≥ 1.0 /hour. At the average rate of disturbance observed, neither Response A nor Response B allowed geese to balance their daytime energy budget (Fig. 1).

At the mean disturbance rate that prevailed during our study, we calculated that geese incurred hourly losses of 8–42 kJ depending upon whether they immediately resumed feeding (Response A) or stopped feeding (Response B) (Fig. 1). Assuming a nighttime food intake equivalent to that observed in daytime, geese must increase the time spent feeding 4–32% to make up for these losses in case of Response A and B, respectively (Fig. 2).

DISCUSSION

Drent et al. (1979) stressed the importance of integrating energetic costs of man-induced disturbance in energy budgets of Anserini. To our knowledge, however, only Davis and Wiseley (1974), who studied effects of aircraft-induced disturbance, and Frederick et al. (1987), who simulated effects of different hunting management schemes on behavior and energetics of lesser snow geese (*C. c. caerulescens*), have attempted such analyses. We estimated that daylight foraging time of greater snow geese in fall would decrease 4–51% depending on disturbance levels and bird responses. Owens (1977) noted that brent geese (*Branta bernicla bernicla*) increased their flight time 7-fold due to disturbance and that they lost $\geq 11.7\%$ of their feeding time during the day. Disturbance of staging lesser snow geese in Yukon and Alaska at an average rate of 0.25/hour caused a 2.6% decrease in feeding time (Davis and Wiseley 1974). When disturbance rate was increased to

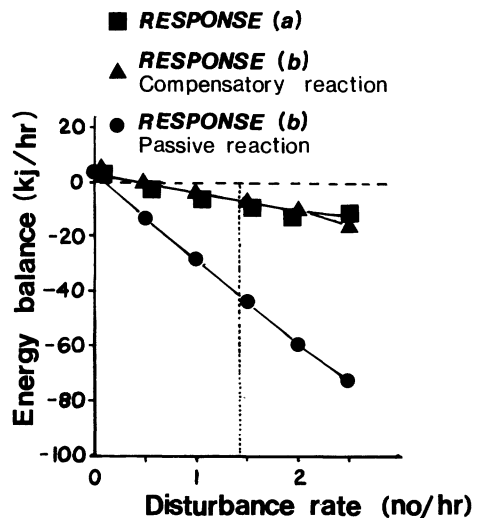


Fig. 1. Relation between the estimated energy balance of fall-staging snow geese and various levels of disturbance. The dashed line indicates an energy balance (input = output); the dotted line shows the average rate of disturbance observed.

0.5/hour, feeding time decreased by 8.5% (Davis and Wiseley 1974). We estimated that the average rate of disturbance resulted in a 5.3% increase of HEE and a 1.6% reduction of HMEI. In Response B, HMEI decreased by 2.9 to 19.4%; HEE increased by 3.4%. Therefore, neither Response A nor Response B allowed geese to balance their daytime energy budget. In brent geese, disturbed flocks increased their daytime energy expenditure by approximately 15% due to disturbance flights (White-Robinson 1982). Davis and Wiseley (1974) claimed that an average seasonal disturbance rate of 0.5/hour would cause a reduction of 20.4% in the energy reserves of staging lesser snow geese.

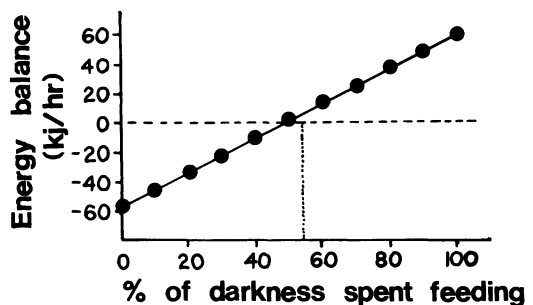


Fig. 2. Relation between estimated energy balance and percentage of time spent feeding at night by fall-staging greater snow geese. The dashed line indicates an energy balance (input = output); the dotted line shows the average rate of disturbance observed.

An increase in night feeding as a compensatory mechanism for loss of daytime feeding opportunities due to man-induced disturbance has been suggested in many wildfowl studies (Thornburg 1973, Pedroli 1982, Tuite et al. 1983), but quantitative assessment has not been reported. Nocturnal feeding in Anserini is a common phenomenon often associated with heavy hunting pressure during the day (Owen 1972, Owens 1977, Burton and Hudson 1978). We found that a 4% increase in night feeding could compensate for energy losses caused solely by disturbance flights (Response A), compared to a 32% increase in nighttime feeding required to restore energy losses incurred in Response B. No increase in daily feeding rate was observed between days with different disturbance levels. Thus, geese did not compensate for loss of feeding time by increasing their daily foraging behavior to maximize food intake during undisturbed periods.

Our estimates of energetic costs of human disturbance to staging geese represent average situations. Responses of individual birds to disturbance likely depend on environmental and physiological conditions of individuals birds. For instance, a given bird may interrupt feeding following a disturbance in the morning but not in the afternoon. Moreover, the nature of disturbance and several biotic (flock size) and abiotic factors (date, time, tidal level) affect responses of goose flocks to disturbance (Bélanger and Bédard 1989). Weather conditions also are expected to influence sensitivity of geese to disturbance, but we did not incorporate this factor in our analysis. Finally, it is possible that repetitive disturbance may have a cumulative impact on geese. Indeed, for various reasons, geese could become more tolerant to particular disturbance types or certain disturbance rates. For instance, we observed that fall disturbance rate of greater snow geese was negatively related to date, probably because they became accustomed to gunfire (Bélanger and Bédard 1989).

Most studies evaluating energetics of waterfowl have been conducted on captive or semi-captive birds and have concerned their basal activities (Owen 1970, Burton et al. 1979). Responses of gregarious birds to disturbances such as aircraft overflights cannot be totally simulated (Davis and Wiseley 1974), and bioenergetic measurements are thus difficult to obtain. Our

energetic model using free-living birds has many assumptions. First, the time geese spent in the alert stage was set as constant among days with different disturbance rates. White-Robinson (1982) reported no difference in alertness by brent geese among habitats (salt marsh and farmland) with different levels of disturbance; however, Owen (1972) observed that time spent in alertness by white-fronted geese (*Anser albifrons*) increased in response to disturbance rate. Second, we used activity budgets and estimated energetic values (BMR, HMEI, and HEE) established in spring as a measure of goose activity during an undisturbed period. Fall-staging greater snow geese at Montmagny spent 36% of the daily budget feeding (J. F. Giroux and J. Bédard, Université Laval, pers. commun.), which is less than that observed in spring (Table 1). However, we reported that geese were heavily disturbed in the no-hunting area in fall (Bélanger and Bédard 1989). The seasonal difference in time devoted to feeding by geese might have been caused by differences in disturbance rate. Although staging geese also are disturbed to some extent in spring, we considered activity budgets at that time to be a more realistic measure of activity of undisturbed geese in the *Scirpus* spp. marshes.

Energetic values used in our study were originally established for spring staging geese. Even though accumulation of lipid reserves occurs to some extent during fall in many goose species (Wypkema and Ankney 1979, Sedinger and Bollinger 1987), fattening is probably less important at that time in greater snow geese (G. Gauthier, Université Laval, pers. commun.); therefore, energetic values that we used may be slightly overestimated. Nevertheless, we consider our conclusions valid because constant values were used to compare undisturbed and disturbed situations and because we were mainly interested in comparing energy balance of geese under various disturbance levels, rather than determining the exact values of goose energetics in fall.

MANAGEMENT IMPLICATIONS

High levels of disturbance may have harmful energetic consequences on fall staging snow geese in Québec. More than 2.0 disturbances/hour may cause an energy deficit that no behavioral compensatory mechanism (night feeding, for in-

stance) can counterbalance. The St. Lawrence River is the only known staging area of importance for the greater snow goose; the entire population (350,000 birds in spring 1988; J. Bédard, Université Laval, unpubl. data) stops there in spring and most of it (>80%) stops there in fall (C. Maisonneuve and J. Bédard, Université Laval, unpubl. data). A comprehensive understanding of energetic requirements of greater snow geese on their staging grounds in relation to human disturbance is essential for optimum management. A primary goal for managers should be to reduce human disturbance, particularly aircraft overflights as suggested by Bélanger and Bédard (1989). Sanctuary should also be large enough (e.g., >200 ha) so that geese could fly away but promptly return to the foraging site and resume feeding (Response A rather than B).

More information is needed on distribution, activities, and energetics of geese at night to determine if night feeding compensates for loss of daytime feeding opportunities. Studies on activity and energy budgets of geese in fall also should be conducted to validate our energetic models. Finally, our study provides a framework to test specific hypotheses in the field and to guide future research on the impact of man-induced disturbance on energetics of waterfowl.

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