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Has habitat degradation affected foraging behaviour and reproductive success of lesser snow geese (*Chen caerulescens caerulescens*)?[1]

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Abstract: Some individuals respond to habitat degradation by dispersing to less degraded areas while others remain but display altered behaviours, potentially compensating for the habitat change. We examined the latter possibility by evaluating foraging behaviour and size of lesser snow geese over a period during which their habitat became severely degraded. We show that in this now-degraded habitat, adults spend more of their total time in motor activities and less time in vigilance and comfort behaviours. Goslings spend less of their total time foraging and more in comfort and other behaviours. The pecking rate of both adults and goslings while foraging increases, as do motor and searching behaviours of adults. These changes have not enabled the birds to keep pace with the loss of vegetation, and the size of goslings has continued to decline, likely leading to a reduction in reproductive success. The persistent use of degraded salt marsh is probably related to philopatry and will further damage the marsh.
Keywords: body size, foraging behaviour, geese, habitat degradation, herbivory, philopatry, salt marsh, time budget.

Résumé : Lorsqu'ils sont confrontés à la dégradation de leur habitat, certains individus se déplacent vers d'autres secteurs moins détériorés alors que d'autres demeurent au même endroit mais modifient leur comportement, probablement pour s'adapter aux nouvelles conditions de leur habitat. Nous avons étudié cette dernière alternative en évaluant le comportement d'alimentation et la taille de petites oies des neiges durant une période où leur habitat s'est sévèrement dégradé. Nous avons découvert que dans les sites dégradés, le temps total consacré par les oies adultes aux activités motrices est supérieur à celui consacré aux comportement de vigilance et ceux associés au confort. Les oisons passent moins de temps à se nourrir et consacrent plus de temps aux autres comportements, dont ceux associés au confort. Durant l'alimentation, le taux de becquetage des adultes et des oisons est plus élevé, tout comme les comportements de motricité et de recherche des adultes. Ces changements ne permettent toutefois pas aux oies de s'adapter aux pertes de végétation. Par conséquent, la taille des oisons continue de diminuer, ce qui risque d'entraîner une baisse du succès reproducteur. La persistance des oies à utiliser les marais salés dégradés est probablement due à leur philopatrie, mais cette habitude contribuera à endommager davantage les marais.
Mots-clés : budget d'activité, comportement d'alimentation, dégradation de l'habitat, herbivorisme, marais salés, oies, philopatrie, taille corporelle.

Nomenclature: Porsild & Cody, 1980; American Ornithologists' Union, 1998.

Introduction

Habitats can become degraded through catastrophic weather events (MacMahon *et al.,* 1989; Perez-Rivera, 1991; Coughenour & Singer, 1996; Kinnaird & O'Brien, 1998), anthropogenic activities (Eybert, Constant & Lefeuvre, 1995; Galetti & Aleixo, 1998; Bruun & Smith, 2003; Johnson & Collinge, 2004), or even through the action of species present in a habitat (Hanley, 1982; Hester *et al.,* 1999; Jefferies, Rockwell & Abraham, 2003). Some individuals respond to such change by dispersing to less or non-degraded habitat if it is available (MacMahon *et al.,* 1989; Bruun & Smith, 2003), while others remain but display altered behaviours that may allow them to exploit the degraded habitat (Hanley, 1982; McCorquodale, 1993; Kohlmann & Risenhoover, 1994; Hester *et al.,* 1999; Rockwell *et al.,* 2003). As the rate of anthropogenically induced habitat change increases at the global scale (Galetti & Aleixo, 1998; Brickle *et al.,* 2000; Bruun & Smith, 2003), it becomes increasingly important to examine the reaction of individuals and species to such change, as this may aid in the design of conservation or mitigation programs. A valuable source of information on the response to habitat degradation comes from long-term studies that span the actual period of degradation. One such study is that of the lesser snow geese (*Chen caerulescens caerulescens*, hence-

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forth snow geese) nesting at La Pérouse Bay in northern Manitoba, Canada.

The intertidal salt marsh at La Pérouse Bay has been used for at least the past 50 y by lesser snow geese, both as a nesting and brood-rearing area by local snow geese and as a spring staging area for those nesting further north (Cooke, Rockwell & Lank, 1995). Since 1968, the number of snow geese in the Mid-continent population has increased by approximately 6% annually (Abraham & Jefferies, 1997). Destructive foraging by this ever-increasing number of snow geese initiated processes that have led to increasing degradation of the salt marsh and adjacent habitat at La Pérouse Bay (Jefferies, Rockwell & Abraham, 2003).

This habitat degradation has had a negative impact on the reproductive success of snow geese continuing to rear their broods on the long-used central salt marsh at La Pérouse Bay. Gosling size and mass, gosling survival from hatch to fledging, and juvenile survival have declined, resulting in an overall decrease in reproductive success (Cooch *et al.,* 1991a,b; Francis *et al.,* 1992; Cooch, Rockwell & Brault, 2001). The impacts are doubtless related to difficulties faced by the birds in obtaining adequate food resources during the post-hatch, brood-rearing period (Cooke, Rockwell & Lank, 1995).

Many snow goose families that nest near the traditionally used salt marsh at La Pérouse Bay appear to be meeting the challenge of insufficient forage availability by dispersing to less degraded sites up to 30 km east and southeast of La Pérouse Bay during brood rearing (Cooch *et al.,* 1993; Cooch, Rockwell & Brault, 2001). Body size and survival of goslings in such families are significantly higher than for those that do not disperse. The expectation has been that families would stop using the now-degraded central salt marsh at La Pérouse Bay for brood rearing (Cooch *et al.,* 1993).

Surveys through 2003, however, have shown that although the availability of forage in this salt marsh has continued to decline (Jefferies & Rockwell, 2002), several hundred snow goose families still forage there during the brood-rearing period and the parents of more than 40% of those families have foraged there in 2 or more years (Pezzanite, 2003; R. F. Rockwell, unpubl. data). Two questions are raised by these observations: 1) do the foraging behaviours of families currently using the marsh differ from those of families that foraged there when the marsh was less degraded, perhaps reflecting a compensatory behavioural shift as food resources declined, and 2) are those families that persistently use the degraded marsh obtaining adequate supplies of forage to support gosling growth? We addressed these issues with data on foraging and body size collected from 1980 through 2001.

Methods

SITE DESCRIPTION AND GENERAL BEHAVIOURAL METHODOLOGY

The primary salt marsh traditionally used for brood-rearing at La Pérouse Bay is located along the shore of La Pérouse Bay at 58° 43' 17" N, 93° 25' 43" W in the northwest corner of Wapusk National Park, approximately 30 km east of Churchill, Manitoba, Canada. The marsh was originally vegetated by nearly continuous dense swards of grasses (primarily *Puccinellia phryganodes)* and sedges (primarily *Carex subspathacea).* The swards have been replaced by mudflats that are hypersaline in summer and that support remnant, low-density patches of grasses and sedges along with salt-tolerant annual species such as *Salicornia borealis* and *Atriplex glabiscula* (Srivastava & Jefferies, 1996; Jefferies & Rockwell, 2002).

Behavioural data on lesser snow geese using the area during the brood-rearing period were collected over a 20-y period. Observations were made from a 5-m-high observation tower located in the centre of a salt marsh on the western edge of La Pérouse Bay using a standardized behavioural sampling protocol applied to randomly selected individual pairs of geese and their broods (Altmann, 1974; Gregoire & Ankney, 1990; Williams, Loonen & Cooke, 1994; Mulder, Williams & Cooke, 1995). Only data from families with 1-5 goslings were included in the analyses since families of 6 goslings or more usually indicate intra-specific nest parasitism and/or adoption (Lank *et al.,* 1989a,b; Williams, 1994). Identification of gender in adult geese was based on banding records (for banded birds), body size (males are typically larger than females), brooding behaviour (goslings typically only sit with, or under the wing of, the female), or the presence of a brood patch on females (visible for up to approximately 4 weeks post-hatch).

Observations began 1 week after hatch and ended at fledging. Observations were conducted during daylight hours beginning between 0500 and 0700, and ending between 2200 and 2400 Central Daylight Saving Time. Families may have been sampled more than once in behavioural observations, but owing to flock size and observation periods this represents little more than sampling with replacement. Thus, we assume that any departures from strict independence are minor.

TIME BUDGETS

Data on time budgets for goslings and adults were available for 1980 (considered "past") and 1999 ("recent"). Behavioural data in 1980 were collected in real time, while in 1999 geese were videotaped with a SONY Hi-8 Handycam and behavioural data were extracted while viewing the film after the field season. In both cases, the behavioural state of each adult and gosling being monitored was instantaneously recorded every 10 s for up to 10 min. Behavioural states (*sensu* Altman, 1974) recorded included feeding, head-up and extreme head-up, swimming, walking, preening, stretching, bathing, drinking, sleeping, attacking or threatening other geese, and engaging in social interactions (usually intra-brood). Behaviours were then categorized as feeding (while walking, standing, or sitting), comfort (bathing, preening, stretching, resting, social), motor (swimming, running or walking, each while not feeding), and vigilant (head-up or extreme head-up, each while not walking) (Williams, Loonen & Cooke, 1994). Owing to the rarity of some behavioural states in goslings, vigilance and motor categories were combined, although the bulk of the samples involved motor activities.

The proportion of instantaneous samples spent in each of the categories was calculated for each individual, providing an estimate of the relative amount of time spent in each behavioural state (Altman, 1974). Owing to well-documented differences in brood-rearing behaviours of adult females and males (Lazarus & Inglis, 1978; Lessells, 1987; Sedinger & Raveling, 1990), data for adult females and males were evaluated separately.

Evaluations of annual changes in behaviour must take into account differences in hatch dates from year to year, since differences in the ages of goslings at the time of observations and differences in the number of days (or weeks) from hatch for adults may affect behavioural responses. "Gosling age class" designations were assigned to the behavioural observations of both goslings and adults throughout the brood-rearing period. Given the hatching synchrony of snow geese at La Pérouse Bay (Cooke, Rockwell & Lank, 1995), the designations were based on 1-week intervals from mean hatch for a given year. Observations made within 1 week of mean hatch were considered to be in age class 1, those made during the next week were in age class 2, and so on. Since each year's mean hatch date was used as a point of reference, this relative age designation controls the time budget data for any annual differences in mean hatch date. Gosling age class is a surrogate for age of goslings and a measure of how far into brood rearing observations were made for adults.

FORAGING BEHAVIOUR

Additional observations were made to determine if finer details of foraging behaviour (*i.e.,* pecking and movement while feeding) may have changed in consort with habitat loss. Observations prior to 1999 were collected in real time, but in 1999 and 2000 geese were videotaped and data was extracted from the films after the field season. Observations of an individual began when it assumed a head-down posture and took its first peck and ended either at the end of 10 min, when the bird stopped foraging, when the bird went out of visual range, or when a disturbance occurred [*e.g.,* a polar bear (*Ursus maritimus*) walked into the area]. Total observation time, number of steps taken while feeding (standardized to steps per minute), and the number of pecks taken in 10 s were recorded. Ancillary studies indicated that number of steps taken while feeding and pecking rates estimated from real-time observations did not differ from those estimated using normal-speed playback of filmed behaviours. As in the time budget evaluation, gosling age classes were assigned to observations of the geese to adjust for differences in annual mean hatch dates.

Data for adults were available from 1985, 1999, and 2000 and gosling age classes 2 to 4. Preliminary analyses showed no difference in pecking or step rates between females or males in 1999 and 2000, and those data were pooled into a "recent" year class with data from 1985 representing a "past" year class. For the same reasons noted above, the behaviours of females and males were evaluated separately. Data for goslings were available from 1984, 1985, 1988, 1989, 1999, and 2000 and gosling age classes 3 and 4. Preliminary analyses showed no significant difference in pecking or step rates among the four early years or the two late years and data were pooled within each to form "past" and "recent" year classes.

GOSLING SIZE AND MASS

Goslings using the intertidal marsh at La Pérouse Bay were measured during banding operations using procedures given in Dzubin and Cooch (1992). Measurements of size (tarsus and culmen) and mass were available from 1980, 1984 and 1985, 1988 to 1990, and 1998 to 2000. Size and mass are related to age in growing animals like snow geese goslings. Since hatching date varies annually more than the date of banding and measurement (which is logistically constrained), annual differences in gosling size could reflect annual differences in age. Because we did not know the ages of the goslings measured in this study, we used the length of the 9th primary as a covariate to adjust for annual variation in gosling age when evaluating whether size and mass changed as a function of year, as suggested by Lesage and Gauthier (1998). Adjusting gosling size or mass for annual variation in gosling age in this way, however, assumes that the relationship between size and age (or a surrogate such as 9th primary length) does not change across years (Cooch, Dzubin & Rockwell, 1999). We tested this assumption explicitly in our analyses.

DATA ANALYSES

We followed a pluralistic approach to analyses, as recommended by Scheiner (2004), in which both Neyman-Pearson (NP) methods (*e.g.,* ANOVA) and Information Theoretic (IT) methods (*e.g.,* AIC) were used to provide evidence in support of answers to biological questions specified prior to the analyses. We were interested in assessing the extent of differences in the behaviours exhibited by adults and goslings and in gosling size over the 15- to 20-y period during which their foraging habitat became degraded (hereafter the "time effect"). As explained above, we reduced the likelihood that any such effect would simply reflect differences in annual phenology by referencing the data to yearly hatching date using the variable gosling age class. However, since general behavioural patterns could change as the season proceeds past hatch and thereby influence the extent of any difference over years, we also assessed the dependency of the time effect on the reference variable.

We based our NP analyses of these issues on the saturated model involving time (T), gosling age class (G), and their interaction (T×G). We tested for the presence of any effects of these three model sources with MANOVA (time budgets), ANOVA (pecking rates and feeding bout steps), and ANCOVA (body size and mass) and present the relevant test statistics and their associated probabilities rather than arbitrary designations of significance (Mayo, 2004). PROC GLM from SAS® 8.02 (SAS Institute, 2001) was used for these analyses.

In our IT analyses of whether behaviours or gosling size changed over the period associated with habitat degradation, we assessed four *a priori* competing models involving time and gosling age class (T + G + T×G, T + G, T and G) following Williams, Nichols, and Conroy (2002). AICc values (AIC modified for sample size and parameter number), differences in AICc between all models and the one with minimum AICc (Δ_i), and model weights (w_i) were computed according to Burnham and Anderson (2002) from residual sums of squares or log-likelihoods generated with PROC GLM and PROC MIXED using SAS® 8.02 (SAS Institute, 2001). Time-specific means and standard errors were generated for each of the four models using the LSMEANS option in PROC GLM. Time effects with respect to each model were found as $\text{mean}_{\text{recent}}$ - $\text{mean}_{\text{past}}$, and associated standard errors were computed as the standard errors of the difference (Sokal & Rohlf, 1995). We used the multi-model inference (IT) approach (*i.e.,* model averaging; Anderson, Burnham & Thompson, 2000; Burnham & Anderson, 2002) to combine estimates of time effects across the competing models using model weights, with a measure of model uncertainty incorporated into the standard errors.

Time budget proportions (p) were angularly transformed (arcsine[$p^{1/2}$]) prior to analyses to stabilize variances and eliminate estimation convergence problems associated with the proportions summing to 1 (Sokal & Rohlf, 1995; Fowler & Ely, 1997; R. F. Rockwell, unpubl. data).

Results

TIME BUDGETS

We found that time budgets of adults and of goslings differed over the time period associated with habitat degradation (MANOVA for T [time period] source for adult females, males, and goslings, respectively: Wilks' lambda = 0.29, 0.52, 0.82; associated F = 95.03, 35.73, 19.47; df (numerator, denominator) = 4, 152; 4, 152; 3, 266; $P \leq 0.01$, 0.01, 0.01). We detected weaker support for the dependency of this time effect on gosling age class as seen in the substantially smaller F-statistics (MANOVA for T×G source: Wilks' lambda = 0.79, 0.90, 0.88; associated F = 4.80, 2.02, 5.76; df = 8, 304; 8, 304; 6, 532; $P \leq 0.01$, 0.04, 0.01). The pattern of model fit from the IT approach (Table I) is consistent with the inferences from MANOVA except that evidence for dependency of the time effect on gosling age class for males is even more equivocal.

We estimated the overall extent of behavioural differences between the two time periods (recent and past) from the four models as explained above. Although there was some evidence that these time effects might depend on gosling age class, the specific estimates for each age class fell within the standard errors for these overall multi-model means (Figure 1a). It is clear that for both female and male adults there has been a substantial increase in motor behaviour over the period associated with habitat degradation. There has also been a decrease in vigilance for both sexes and a decrease in comfort behaviour for females. Interestingly, there has been no change in feeding behaviour for either sex. In sharp contrast to the adult situation, there has been a substantial decrease in the proportion of time spent feeding by goslings (Figure 1b). Coincident with that decrease, there has been an increase in the time spent in the other behavioural activities.

FORAGING BEHAVIOUR

The pecking rates of adult and gosling lesser snow geese differed between the two time periods (ANOVA for T source: F = 65.12, 4.21, 32.82; df = 1, 223; 1, 62; 1, 91; $P \leq 0.01$, 0.04, 0.01; females, males, and goslings, respectively), although the support for a difference in males is not strong. There is weak evidence for dependency of the time effect on gosling age class for adult females and no

TABLE I. A comparison of time budget models involving time period (T), gosling age class (G), and their interaction (T×G) for adult and gosling lesser snow geese from La Pérouse Bay.

Model	$AICc_i$	Δ_i	w_i
ADULT FEMALES			
T G T×G	-1,306.20	0.00	0.99
T G	-1,285.50	20.70	0.00
T	-1,292.60	13.60	0.01
G	-1,104.50	201.70	0.00
ADULT MALES			
T G T×G	-1,242.80	0.90	0.37
T G	-1,243.70	0.00	0.58
T	-1,239.10	4.60	0.06
G	-1,143.70	100.00	0.00
GOSLINGS			
T G T×G	-1,619.20	0.00	0.99
T G	-1,597.40	21.80	0.00
T	-1,605.50	13.70	0.01
G	-1,543.60	75.60	0.00

Computations of $AICc_i$, Δ_i, and w_i follow Burnham and Anderson (2002).

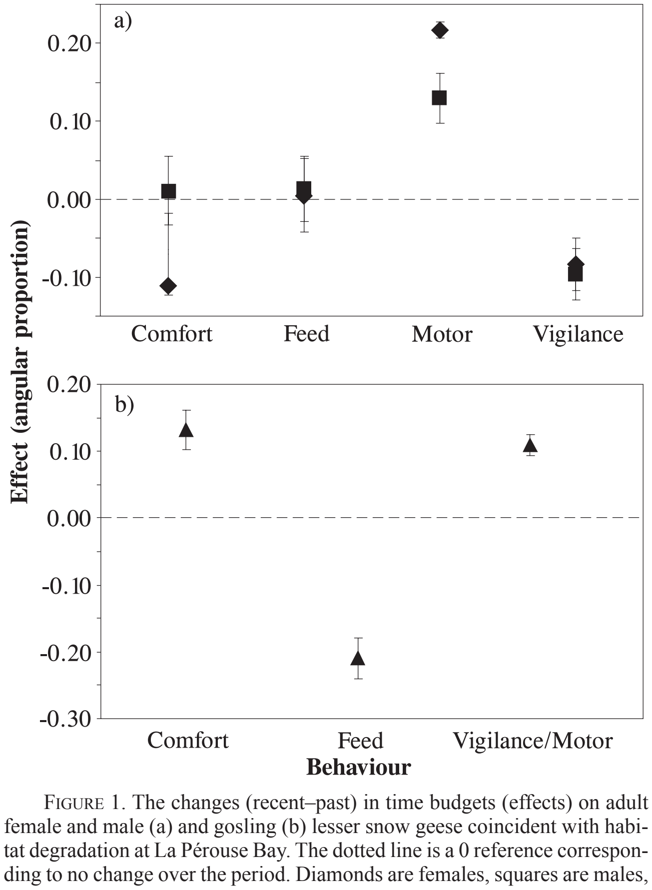

FIGURE 1. The changes (recent–past) in time budgets (effects) on adult female and male (a) and gosling (b) lesser snow geese coincident with habitat degradation at La Pérouse Bay. The dotted line is a 0 reference corresponding to no change over the period. Diamonds are females, squares are males, and triangles are goslings. Bars are ± SE. Sample sizes (past, recent) are for adult females (144,17), adult males (143,18), goslings (217,57). Proportions (p) were angularly transformed to arcsine ($p^{1/2}$).

evidence of such a dependency in adult males (ANOVA for T×G source: F = 3.90, 0.85; df = 2, 223; 2, 62; $P \leq 0.02$, 0.44). The evidence for gosling age class dependency of the time effect in goslings is stronger (F = 27.02; df = 1, 91; $P \leq 0.01$). The pattern of model fit from the IT analyses (Table II) supports the presence of a time effect in adults and goslings but only strongly supports dependency of that year effect on gosling age class for goslings.

We estimated the mean size of the time effect for pecking rate of adults and goslings over the four models (Figure 2a). Gosling age class specific estimates of pecking rate fell within the standard errors of these overall multi-model means. Pecking rates of both adults and goslings have increased substantially over the period coincident with degradation of the salt marsh.

The step rate during feeding of both adult females and males differed between the two time periods, but that of goslings did not (ANOVA T source: F = 77.27, 15.72, 1.19; df = 1, 232; 1, 63; 1, 280; $P \leq 0.01$, 0.01, 0.28). There is some support for dependency of the time effect on gosling age class for adult females, but not for males or goslings (F = 11.17, 0.83, 0.90; df = 2, 232; 2, 63; 1, 280; $P \leq 0.01$, 0.39, 0.47). Results from the IT analyses (Table II) are consistent with the inferences from ANOVA. We estimated the mean size of the time effect in step rate over the four models for adults and goslings (Figure 2b). Gosling age class specific estimates of step rate fell within the standard errors for these overall means. The step rates of adults have substantially increased during the period associated with habitat degradation. Considering the size of the standard error along with the ANOVA and IT results, the step rate of goslings has not likely changed to any appreciable extent.

GOSLING SIZE AND MASS

As explained above, when using 9th primary length to control for age differences in regressions of size and mass on year, one must assume that the relation of size or mass and 9th primary length does not itself change over time. To test this, we included a year × 9th primary (Y×P) term in our ANCOVA and considered two models (Y + P + Y×P and Y + P) in our IT evaluation. Note that we are using year as a continuous variable in these analyses rather than the dichotomous (recent *versus* past) classification variable of the behavioural analyses.

For both tarsus and culmen, respectively, the assumption is well supported in females (ANCOVA Y×P source: F = 0.02, 0.34; df = 1, 766; 1, 766; $P \leq 0.88$, 0.56) and males (ANCOVA Y×P source: F = 0.15, 2.46; df = 1, 643; 1, 645; $P \leq 0.69$, 0.21). Results from the IT approach were consistent. We used model weights to form composite estimates of the regression slopes of size on year and standard errors, including model uncertainty (Burnham & Anderson,

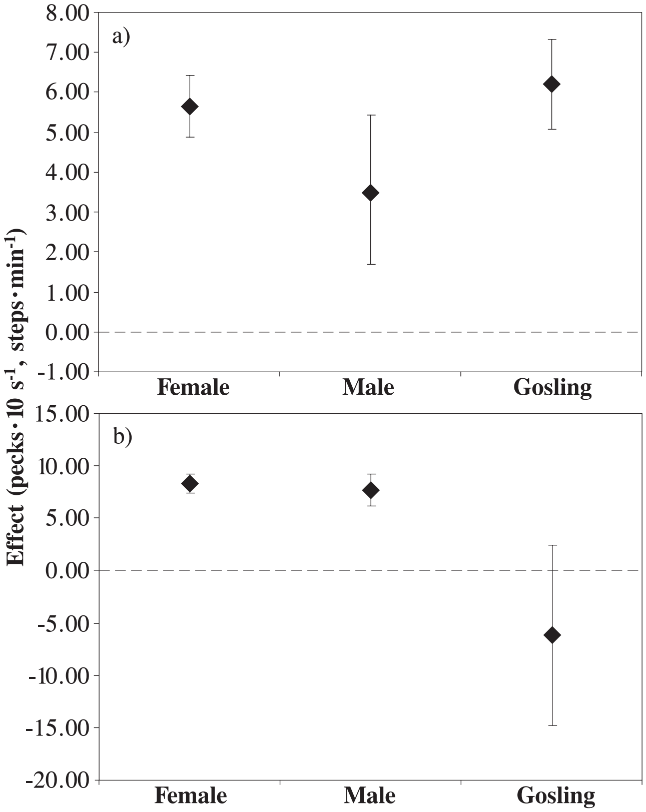

FIGURE 2. The changes (recent–past) in pecking (a) and step (b) rates (effects) (pecks·10 s^{-1}, steps·min^{-1}) on adult female and male and gosling lesser snow geese at La Pérouse Bay. The dotted line is the 0 reference corresponding to no change over the period. Bars are ± SE. Sample sizes (past, recent) are as follows: peck rates: adult females (185,44), adult males (25,44), goslings (34,61); step rates: adult females (194,44), adult males (25,44), goslings (221,63).

TABLE II. A comparison of pecking and step-rate models involving time period (T), gosling age class (G), and their interaction (T×G) for adult and gosling lesser snow geese from La Pérouse Bay.

Model	$AICc_i$	Δ_i	w_i
PECKING RATE			
ADULT FEMALES			
T G T×G	284.82	0.00	0.55
T G	286.15	1.33	0.28
T	287.27	2.45	0.16
G	309.22	24.41	0.00
ADULT MALES			
T G T×G	115.10	3.72	0.09
T G	113.57	2.19	0.19
T	111.38	0.00	0.58
G	114.22	2.84	0.14
GOSLINGS			
T G T×G	141.41	0.00	0.97
T G	149.91	8.50	0.01
T	149.42	8.00	0.02
G	155.61	14.20	0.00
STEP RATE			
ADULT FEMALES			
T G T×G	346.84	0.00	0.92
T G	354.26	7.42	0.02
T	352.31	5.47	0.06
G	387.94	41.10	0.00
ADULT MALES			
T G T×G	109.96	2.34	0.16
T G	108.54	0.91	0.33
T	107.63	0.00	0.51
G	118.74	11.11	0.00
GOSLINGS			
T G T×G	984.68	3.10	0.08
T G	982.83	1.26	0.21
T	981.88	0.31	0.33
G	981.58	0.00	0.38

Computations of $AICc_i$, Δ_i, and w_i follow Burnham and Anderson (2002).

2002). The year (slope) estimates for female and male tarsus are -0.24 ± 0.04 and -0.27 ± 0.07 and for culmen are -0.11 ± 0.03 and -0.13 ± 0.06 (all $\text{mm}\cdot\text{y}^{-1}$). These correspond to a 1-2% annual geometric decline in these two measures of size over the period associated with habitat degradation.

The situation for mass is more complex as there is evidence for a Y×P interaction term in both females and males ($F = 20.33, 25.04$; df = 1, 765; 1, 644; $P \leq 0.01, 0.01$; and relative strength of IT weights of models with and without the Y×P term [$w_{Y\,P\,Y{*}P}/w_{Y\,P}$] of 29.8 and 77.7). This implies that the relation of size and 9th primary (our surrogate for age) changes from year to year, violating a basic assumption of the method (Cooch, Dzubin & Rockwell, 1999). It is perhaps not surprising that adjustments involving mass would be more labile than those of structural size since mass is more susceptible to annual variation in food conditions (Cooch *et al.,* 1991b; Cooch, 2002; R. F. Rockwell, unpubl. data). Although there is evidence for a substantial decline in mass for both females and males over the period examined ($F = 16.44, 14.82$; df = 1, 765; 1, 644; $P \leq 0.01, 0.01$; multi-model estimated slope ± SE = -10.80 ± 2.66, -10.48 ± 2.72 $\text{g}\cdot\text{y}^{-1}$ for females and males, respectively), we can not be certain that age effects have been completely controlled for by removing annual variation in 9th primary. Thus, the decline in mass could partially reflect a decline in gosling age over the period of study.

We addressed this problem in two ways. First, we examined the year-specific regression slopes of mass on 9th primary, and while they range from 0.68 to 11.50, all are positive and there is no consistent pattern across the years ($R^2 = 0.006$). Second, we regressed our best estimate of age at measurement ("annual mean banding date" – "annual mean hatch date") on year and found no evidence of a relationship (slope ± SE = -0.12 ± 0.25; $F = 0.22$; df = 1, 8; $P \leq 0.65$). We suggest that like the tarsus and culmen size measures, mass has declined over the period associated with habitat degradation and is unrelated to any systematic change in gosling age. The decrease corresponds to a 1-2% annual geometric decline.

Discussion

The proportion of time that adult snow geese spend in motor activities has increased substantially from 1980, when the salt marsh was a well-developed sward of grass and sedge, to 1999, when it had been reduced to little more than a saline mudflat (Jefferies & Rockwell, 2002). For both sexes, this time budget shift was made at the expense of vigilance, with females also displaying a reduction in comfort behaviours. Neither sex showed a reduction in the proportion of time spent foraging, likely reflecting the fact that this time allocation is already near the lower limit needed to replenish stores for fall migration (Williams, Loonen & Cooke, 1994). The increase in motor behaviours by both sexes is also seen in the increased number of steps taken while feeding by both adult females and males.

The increase in relative time spent in motor activities by both females and males can easily be related to the habitat changes that have occurred in the salt marsh at La Pérouse Bay. Over the time span of this study, the nearly continuous and dense sward of grass and sedge (> 90% vegetation cover and 30-50 $\text{g}\cdot\text{m}^{-2}$ aboveground biomass) has been fragmented and degraded to a vegetation mosaic (< 10% total vegetation cover) consisting of small, low-density patches of graminoids (with 5-15 $\text{g}\cdot\text{m}^{-2}$ above-ground biomass), interspersed within larger expanses of exposed sediment (Jefferies & Rockwell, 2002; Jefferies, Rockwell & Abraham, 2003). This coarse-grained distribution of potential foraging patches means that more time has to be spent searching for, and moving among, patches. The reduced density of forage plants within patches likely requires more movement for efficient feeding within patches, leading to the increase in steps taken during foraging bouts.

Coincident with declines in available resources, the pecking rates of adult snow geese have increased. This may reflect some form of compensation to offset, for example, smaller bite sizes related to the reduced size and/or abundance of available forage (Drent & Swierstra, 1977; McCorquodale, 1993; Kohlmann & Risenhoover, 1994). Lazarus and Inglis (1978) demonstrated that male Pink-footed geese (*Anser brachyrhynchus*) compensate for reductions in time spent feeding because of increased vigilance by increasing their pecking rate. Faster pecking rates may result in an increase in food taken per unit time (Owen, Wells, & Black, 1992; Boysen, Lima & Bakken, 2001), but the benefit would depend on bite size and food quality (Madsen, 1985), as well as handling time.

For goslings, the proportion of time spent feeding decreased over the period of habitat degradation. This shift in relative time budget was reflected in proportional increases in the comfort and vigilance/motor behavioural classes, the latter primarily reflecting motor activities. As with adults, this shift likely reflects, at least in part, a necessary response to the increased patchiness and reduced availability of forage plants. It is possible, however, that the time-budget shift may be related to the smaller size and poorer condition of goslings in more recent years. Such goslings may simply not be able to feed as much and may require more time resting (Sorensen & Taylor, 1995), leading, of course, to further reductions in growth. This positive feedback relationship may also explain the lack of increase in gosling step rate.

Consistent with some form of potential compensation, the pecking rate of goslings was higher in 1999 than in 1980. This is similar to the pattern seen in Barnacle Geese (*Branta leucopsis*), where pecking rate was observed to increase as available biomass decreased (Owen, Wells & Black, 1992). Despite this potential compensation, however, the body size and mass of goslings whose families use the central salt marsh at La Pérouse Bay has continued to decline. This indicates that despite some changes in behaviour, goslings are not able to obtain adequate food resources from this deteriorating habitat.

Since the body size of pre-fledging goslings is a good indicator of juvenile survival (Francis *et al.,* 1992; Cooch, 2002), it is reasonable to conclude further that the reproductive success of adults rearing their broods on this salt marsh has also declined over the period of habitat degradation (see also Cooch, Rockwell & Brault, 2001). Thus, the continued use of the marsh by several hundred families of lesser snow geese seems to be maladaptive. This is even more curious since approximately 40% of them have been observed there in two or more years (Pezzanite, 2003; R. F. Rockwell, unpubl. data). One might expect that after failed reproduction in one year, these adults would join the other thousands of pairs that nest in the La Pérouse Bay area but move to less degraded areas for brood-rearing where reproductive success is higher (Cooch *et al.,* 1993; Cooch, Rockwell & Brault, 2001). Persistent use of the degraded salt marsh at La Pérouse Bay may simply reflect traditional, learned use of the brood-rearing area, perhaps by a remnant cohort of aging females that are philopatric to the area (Cooke & Abraham, 1980; Healey, Cooke & Colgan, 1980; Rockwell *et al.,* 1993). Consistent with this, many of the females observed foraging on the degraded marsh are at least 10 y old, while those recaptured at more distant, less degraded sites are younger (Rockwell *et al.*, 1993; R. F. Rockwell, unpubl. data).

It could be argued that the maladaptive tendency of some individuals to use an increasingly degraded area for brood rearing each year might serve as phenotypic selection against philopatry. However, even if there were heritable variation for the trait, the effect of such selection would be minimal since the older females make an ever-decreasing contribution to the population's gene pool (Rockwell *et al.,* 1993). At the same time, however, the ecological consequences of even a maladaptive expression of philopatry are quite serious for the habitat. Persistent foraging by even a small number of families further retards any recovery of the plants and delays the potential re-establishment of the healthy ecosystem with graminoid swards that once existed at La Pérouse Bay.

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Literature cited

Abraham, K. F. & R. L. Jefferies, 1997. High goose populations: Causes, impacts and implications. Pages 7-72 *in* B. Batt (ed.). Arctic Ecosystems in Peril: Report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture, Canadian Wildlife Service, Ottawa, Ontario, and US Fish and Wildlife Service, Washington, DC.

Altmann, J., 1974. Observational study of behavior: Sampling methods. Behaviour, 49: 227-267.

American Ornithologists' Union, 1998. Check-list of North American Birds, 7th Edition. American Ornithologists' Union, Washington, DC.

Anderson, D. A., K. P. Burnham & W. L. Thompson, 2000. Null hypothesis testing: Problems, prevalence and an alternative. Journal of Wildlife Management, 64: 912-923.

Boysen, A. F., S. L. Lima & G. S. Bakken, 2001. Does the thermal environment influence vigilance behavior in dark-eyed juncos (*Junco hyemalis*)? An approach using standard operative temperature. Journal of Thermal Biology, 26: 605-612.

Brickle, N. W., D. G. C. Harper, N. J. Aebischer & S. H. Cockayne, 2000. Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. Journal of Applied Ecology, 37: 742-755.

Bruun, M. & H. G. Smith, 2003. Landscape composition affects habitat use and foraging flight distances in breeding European starlings. Biological Conservation, 114: 179-187.

Burnham, K. P. & D. R. Anderson, 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd Edition. Springer-Verlag, New York, New York.

Cooch, E. G., 2002. Fledging size and survival in snow geese: Timing is everything (or is it?). Journal of Applied Statistics, 29: 143-162.

Cooch, E. G., A. Dzubin & R. F. Rockwell, 1999. Using body size to estimate gosling age. Journal of Field Ornithology, 70: 214-229.

Cooch, E. G., R. F. Rockwell & S. Brault, 2001. Retrospective analysis of demographic responses to environmental change: A lesser snow goose example. Ecological Monographs, 71: 377-400.

Cooch, E. G., D. B. Lank, R. F. Rockwell & F. Cooke, 1991a. Long-term decline in body size in a snow goose population: Evidence of environmental degradation? Journal of Animal Ecology, 60: 483-496.

Cooch, E. G., D. B. Lank, R. F. Rockwell & F. Cooke, 1991b. Body size variation in lesser snow geese: Environmental plasticity in gosling growth rates. Ecology, 72: 503-512.

Cooch, E. G., R. L. Jefferies, R. F. Rockwell & F. Cooke, 1993. Environmental change and the cost of philopatry: An example in the lesser snow geese. Oecologia, 93: 128-138.

Cooke, F. & K. F. Abraham, 1980. Habitat and location selection in lesser snow geese: The role of previous experience. Proceedings of the International Ornithological Congress, 17: 998-1004.

Cooke, F., R. F. Rockwell & D. B. Lank, 1995. The Snow Geese of La Perouse Bay: Natural Selection in the Wild. Oxford University Press, Oxford.

Coughenour, M. B. & F. J. Singer, 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications, 6: 573-593.

Drent, R. & P. Swierstra, 1977. Goose flocks and food finding: Field experiments with Barnacle Geese in winter. Wildfowl, 28: 15-20.

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

Eybert, M. C., P. Constant & J. C. Lefeuvre, 1995. Effects of changes in agricultural landscape on a breeding population of Linnets *Acanthis cannabina* L. living in adjacent heathland. Biological Conservation, 74: 195-202.

Fowler, A. C. & C. R. Ely, 1997. Behavior of cackling Canada geese during brood rearing. Condor, 99: 406-416.

Francis, C. M., M. H. Richards, F. Cooke & R. F. Rockwell, 1992. Long term survival rates of lesser snow geese. Ecology, 73: 1346-1362.

Galetti, M. & A. Aleixo, 1998. Effects of palm heart harvesting on avian frugivores in the Atlantic rain forest of Brazil. Journal of Applied Ecology, 35: 286-293.

Gregoire, P. E. & C. D. Ankney, 1990. Agonistic behaviour and dominance relationships among lesser snow geese during winter and spring migration. Auk, 107: 550-560.

Hanley, T. A., 1982. Cervid activity patterns in relation to foraging constraints: Western Washington. Northwest Science, 56: 208-271.

Healey, R. F., F. Cooke & P. W. Colgan, 1980. Demographic consequences of snow goose brood-rearing traditions. Journal of Wildlife Management, 44: 900-905.

Hester, A. J., I. J. Gordon, G. J. Baillie & E. Tappin, 1999. Foraging behaviour of sheep and red deer within natural heather/grass mosaics. Journal of Applied Ecology, 36: 133-146.

Jefferies, R. L. & R. F. Rockwell, 2002. Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. Applied Vegetation Science, 5: 7-16.

Jefferies, R. L., R. F. Rockwell & K. F. Abraham, 2003. The embarrassment of riches: Agricultural subsidies, goose dynamics and their impact on arctic wetlands - Continuing saga. Environmental Reviews, 11: 193-232.

Johnson, W. C. & S. K. Collinge, 2004. Landscape effects on black-tailed prairie dog colonies. Biological Conservation, 115: 487-497.

Kinnaird, M. & T. G. O'Brien, 1998. Ecological effects of wildfire on lowland rainforest in Sumatra. Conservation Biology, 12: 954-956.

Kohlmann, S. G. & K. L. Risenhoover, 1994. Spatial and behavioural response of white tailed deer to forage depletion. Canadian Journal of Zoology, 72: 506-513.

Lank, D. B., E. G. Cooch, R. F. Rockwell & F. Cooke, 1989a. Environmental and demographic correlates of intraspecific nest parasitism in lesser snow geese *Chen caerulescens caerulescens*. Journal of Animal Ecology, 58: 29-45.

Lank, D. B., P. Minneau, R. F. Rockwell & F. Cooke, 1989b. Intraspecific nest parasitism and extra-pair copulation in lesser snow geese. Animal Behavior, 37: 74-89.

Lazarus, J. & I. R. Inglis, 1978. The breeding behaviour of the pink-footed goose: Parental care and vigilant behaviour during the fledging period. Behaviour, 65: 62-88.

Lesage, L. & G. Gauthier, 1998. Effect of hatching date on body and organ development in Greater Snow Goose goslings. Condor, 100: 316-325.

Lessells, C. M., 1987. Parental investment, brood size and time budgets: Behaviour of lesser snow goose families. Ardea, 75: 189-203.

MacMahon, J. A., R. R. Parmenter, K. A. Johnson & C. M. Crisafulli, 1989. Small mammal recolonization on the Mount St. Helens volcano: 1980-1987. American Midland Naturalist, 122: 365-387.

Madsen, J., 1985. Relations between change in spring habitat selection and daily energetics of Pink-footed geese *Anser brachyrhynchus*. Ornis Scandinavica, 16: 222-228.

Mayo, D., 2004. An error-statistical philosophy of evidence. Pages 79-96 *in* M. L. Taper & S. R. Lele (eds.). The Nature of Scientific Evidence: Statistical, Philosophical and Empirical Considerations. University of Chicago Press, Chicago, Illinois.

McCorquodale, S. M., 1993. Winter foraging behaviour of elk in the shrub-steppe of Washington. Journal of Wildlife Management, 57: 881-890.

Mulder, R. S., T. D. Williams & F. Cooke, 1995. Dominance, brood size and foraging behavior during brood-rearing in the lesser snow goose: An experimental study. Condor, 97: 99-106.

Owen, M., R. L. Wells & J. M. Black, 1992. Energy budgets of wintering Barnacle Geese: The effects of declining food resources. Ornis Scandinavica, 23: 451-458.

Pérez-Rivera, R., 1991. Change in diet and foraging behavior of the Antillean Euphonia in Puerto Rico after Hurricane Hugo. Journal of Field Ornithology, 62: 474-478.

Pezzanite, B. P., 2003. The foraging behavior of lesser snow and Ross's geese on La Pérouse Bay. Ph.D. thesis, City University of New York, New York.

Porsild, A. E. & W. J. Cody, 1980. Vascular Plants of Continental Northwest Territories, Canada. National Museum of Canada, Ottawa, Ontario.

Rockwell, R. F., E. G. Cooch, C. B. Thompson & F. Cooke, 1993. Age and reproductive success in lesser snow geese: Experience, senescence and the cost of philopatry. Journal of Animal Ecology, 62: 323-333.

Rockwell, R. F., C. R. Witte, R. L. Jefferies & P. J. Weatherhead, 2003. Response of nesting savannah sparrows to 25 years of habitat change in a snow goose colony. Écoscience 10: 33-37.

SAS Institute, 2001. SAS Version 8.02. SAS Institute, Cary, North Carolina.

Scheiner, S. M., 2004. Experiments, observations and other kinds of evidence. Pages 51-65 *in* M. L. Taper & S. R. Lele (eds.). The Nature of Scientific Evidence: Statistical, Philosophical and Empirical Considerations. University of Chicago Press, Chicago, Illinois.

Sedinger, J. S. & D. G. Raveling, 1990. Parental behavior of Cackling Canada geese during brood rearing: Division of labor within pairs. Condor, 92: 174-181.

Sokal, R. R. & J. Rohlf, 1995. Biometry, 3rd Edition. Freeman, San Francisco, California.

Sorensen, V. A. & D. H. Taylor, 1995. The effect of seasonal change on the group size, group composition, and activity budget of white-tailed deer, *Odocoileus virginianus*. Ohio Journal of Science, 95: 321-324.

Srivastava, D. S. & R. L. Jefferies, 1996. A positive feedback: Herbivory, plant growth, salinity and the desertification of an arctic salt marsh. Journal of Ecology, 84: 31-42.

Williams, B. K., J. D. Nichols & M. J. Conroy, 2002. Analysis and Management of Animal Populations. Academic Press, New York, New York.

Williams, T. D., 1994. Adoption in a precocial species, the lesser snow goose: Intergenerational conflict, altruism or a mutually beneficial strategy? Animal Behavior, 47: 101-107.

Williams, T. D., M. J. J. E. Loonen & F. Cooke, 1994. Fitness consequences of parental behavior in relation to offspring number in a precocial species: The lesser snow goose. Auk, 111: 563-572.