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ARE ABDOMINAL PROFILES USEFUL TO ASSESS BODY CONDITION OF SPRING STAGING GREATER SNOW GEESE?

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Abstract. Abdominal profile indices were developed to evaluate body condition in birds without capturing or handling them. We assessed the reliability of abdominal profile indices in predicting condition of spring staging Greater Snow Geese (*Chen caerulescens atlantica*). We first calibrated profile scores assigned to females against two direct measures of nutrient stores, abdominal fat and body mass corrected for body size. Abdominal profile indices were linearly and significantly related to both abdominal fat and body mass but the variance was high for individuals assigned to the same profile score ($R^2 = 0.08$ and $R^2 = 0.09$, respectively, $n = 230$). On average, an increase of one profile score corresponded to an increase of 100 g in body mass. Abdominal profiles were better predictors of average abdominal fat and body mass of birds assigned to the same profile category. To assess the usefulness of abdominal profiles in the field, we also examined if the technique could detect the negative effect of a spring hunt on nutrient storage by staging geese, an effect previously detected with internal measures of nutrient reserves. We monitored seasonal changes in abdominal profile indices of staging geese in years without (1997 and 1998) and with the spring hunt (1999 and 2000). In two out of three regions, abdominal profiles revealed that condition increased at a higher rate in nonhunting than in hunting years. The lack of a negative effect of hunting in the other region was likely due to variability among observers in abdominal profile scoring. We conclude that abdominal profile indices can be useful to assess body condition of spring staging Greater Snow Geese although the technique has serious limitations at the individual level, especially without proper training of observers.

Key words: *abdominal profiles, body condition, calibration, fat reserves, hunting disturbance, nutrient storage, Snow Geese.*

¿Son los Perfiles Abdominales Útiles para Determinar la Condición Corporal de *Chen caerulescens atlantica* durante Escalas Migratorias de Primavera?

Resumen. Los índices de perfil abdominal fueron desarrollados para evaluar la condición corporal de las aves sin tener que capturarlas o manipularlas. En este estudio examinamos la confiabilidad de dichos índices para predecir la condición corporal de gansos *Chen caerulescens atlantica* durante la época de escalas migratorias de primavera. Inicialmente, calibramos los puntajes de los perfiles asignados a un grupo de hembras con respecto a dos medidas directas de reservas nutritivas, la grasa abdominal y la masa corregida por el tamaño corporal. Los índices de perfil abdominal estuvieron lineal y significativamente relacionados con la grasa abdominal y la masa corporal ($R^2 = 0.08$ y $R^2 = 0.09$, respectivamente, $n = 230$), pero la varianza entre individuos asignados al mismo puntaje del perfil fue alta. En promedio, un incremento de un punto en el perfil correspondió a un incremento de 100 g en la masa corporal. Los perfiles abdominales predijeron de mejor manera los promedios de grasa abdominal y masa corporal de aves asignadas a la misma categoría del perfil. Para evaluar la utilidad de los perfiles abdominales en el campo, también examinamos si la técnica podía detectar el efecto negativo de la cacería de primavera sobre el almacenamiento de nutrientes en gansos que estaban haciendo escalas migratorias, un efecto previamente detectado por medio de medidas internas de las reservas nutritivas. Monitoreamos los cambios estacionales en los índices de perfil abdominal de gansos en años que estuvieron (1997 y 1998) y no estuvieron (1999 y 2000) expuestos a cacería en la primavera. En dos de las tres regiones, los perfiles abdominales indicaron que la condición corporal se incrementó a una tasa mayor en los años sin cacería. La ausencia de un efecto negativo de la cacería en

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la otra región probablemente fue debida a la variabilidad entre distintos observadores al establecer los valores del perfil abdominal. Concluimos que los índices de perfil abdominal pueden ser útiles para evaluar la condición corporal de estos gansos durante la época de escalas migratorias, pero la técnica tiene limitaciones serias a nivel individual, especialmente cuando los observadores no han sido entrenados adecuadamente.

INTRODUCTION

Accurate assessment of body condition in birds is important because endogenous reserves, especially fat, can affect reproduction and survival (Haramis et al. 1986, Bolton et al. 1993, Chastel et al. 1995). The most accurate methods to determine body condition are based on internal measures such as fat and protein extraction of carcasses (Johnson et al. 1985, Brown 1996), but these techniques are time consuming, costly, and require the death of the animals. External indices (e.g., body mass corrected for body size) are often used to estimate body condition as they are relatively inexpensive to obtain and animals are not sacrificed (Blem 1990, Jakob et al. 1996). However, these methods require the capture and handling of individuals, which can sometimes be difficult or stressful for them (Le Maho et al. 1992, Williams et al. 1993, Cox and Afton 1998).

Abdominal profile indices (API) were first developed by Owen (1981) to evaluate body condition of wild geese. This method consists of visually scoring the roundness of the birds' abdominal region, between the legs and the tail, from a distance. In many species like geese, ducks, and shorebirds, the abdominal cavity is a site of intense fat deposition and it bulges during periods of fattening (Blem 1976, Gauthier and Bédard 1985). This technique has been used to evaluate body condition in many waterfowl and wader species (Amat et al. 1991, Wiersma and Piersma 1995, Glahder et al. 1997, Boyd 2000, Madsen 2001, Drent et al. 2003, Prop et al. 2003). API are very convenient as they do not require capturing and handling birds, and large sample sizes can be obtained rapidly. However, the main disadvantages of the method are its subjectivity and the difficulty in standardizing the measurements (e.g., posture of the bird), which can reduce both the accuracy and precision. Before using API, it is important to calibrate profile scores against direct measures of energy stores. Surprisingly, such validation has been made in few species (Bewick's Swans [*Cygnus columbianus bewickii*], Bowler 1994; Pink-footed Geese [*Anser brachyrhynchus*], Drent et al. 2003; Hawaiian Geese [*Branta sandvicensis*], Zillich and Black 2002).

The main goal of this study was to assess the reliability of API in predicting body condition of spring staging Greater Snow Geese (*Chen caerulescens atlantica*). We first examined the relationship between API assigned to females and two direct measures of nutrient stores, abdominal fat and body mass corrected for body size. We then compared the seasonal changes in API of geese throughout the spring staging period in years with (1999 and 2000) and without (1997 and 1998) a spring hunt. These comparisons allowed us to assess the reliability of API in the field as hunting disturbance negatively affected nutrient storage by spring staging Snow Geese (Féret et al. 2003). In a previous study, we found that internal measures of nutrient reserves indicated that condition of geese arriving at the staging area did not differ between hunting and nonhunting years but that nutrient stores at departure were significantly lower in hunting years (Féret et al. 2003).

METHODS

STUDY SPECIES

Greater Snow Geese winter along the Atlantic coast of the U.S., stage along the St-Lawrence River in Quebec, Canada, during spring and fall migrations, and breed in the eastern high Arctic of Canada. In spring, birds arrive in Quebec by late-March and leave by the end of May (Béchet et al. 2003). During that period, individuals accumulate large amounts of fat and protein (Gauthier et al. 1992). Most geese reach their arctic breeding grounds in early June (Bêty et al. 2003).

STUDY AREA

This study took place from late March to mid May along the St. Lawrence River, southern Quebec (see Féret et al. 2003). Observations and captures of birds were performed in three distinct regions defined according to habitat types: Lake St. Pierre where geese feed extensively on waste corn in farmlands; the Upper Estuary, where geese predominately feed in freshwater

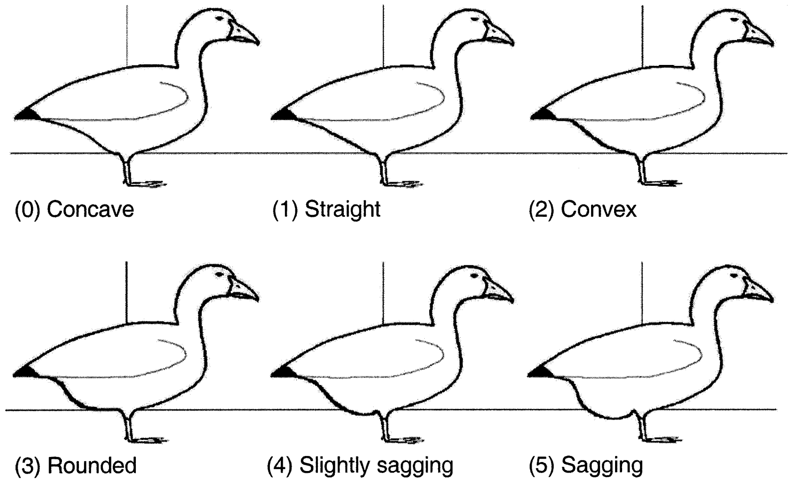

FIGURE 1. Categories used to score abdominal profiles of Greater Snow Geese.

Scirpus marshes; and the Lower Estuary characterized by saltwater *Spartina* marshes. In the two estuary sites, geese also use hayfields for feeding (Gauthier et al. 1988, 1992).

CALIBRATION OF ABDOMINAL PROFILES

We examined the relationship between abdominal profile indices (API) and body reserves of individuals by scoring profiles on a sample of captured adult (white-plumaged) female geese that were then weighed and sacrificed in order to determine their internal fat reserves. We used only females because breeding performance is related to body reserves in these birds (Bêty et al. 2003) and the sample of collected birds was also used to assess the general condition of birds in another study (Féret et al. 2003). Geese were captured using cannon nets shortly after their arrival (2000 only) or just before their departure (1999 and 2000) in the three study regions. We estimated arrival and departure dates based on seasonal variations in the number of geese counted daily in each region (Féret et al. 2003). We captured birds at three sites: Baie-du-Fèbvre at Lake St. Pierre, Île-aux-Oies in the Upper Estuary, and Isle-Verte in the Lower Estuary. In 2001, geese were collected only in the Upper Estuary a few days prior to their northward migration to the Arctic. The total number of capture events was three in 1999, eight in 2000 and two in 2001.

Cannon nets were set in farmlands used by geese for feeding or roosting and baited with oat or corn (Gauthier et al. 1992). Once the birds had approached the range of the nets (usually within a few hours), one observer (MF) assessed the API of 50 randomly selected adult birds just before firing the nets (2000 only). This sample, which provides a good estimate of the average API of birds in a flock (Bêty et al. 2003), was used to compare the average API attributed in the field with scores attributed to females held in enclosures (see below). The presence of males in the random samples of adults did not preclude such comparisons because both sexes store similar amount of fat during the spring staging period (Gauthier et al. 1992). The observer was positioned at 100 to 250 m from the flocks and used a spotting scope (20–60× magnification) to score API following recommendations of Owen (1981). Profiles were scored using a 6-category scale with an intermediate level between categories (Fig. 1).

After each capture, we randomly selected adult females (mean = 24, range = 11 to 44 individuals) and kept them in an enclosure. The enclosure was either in a large, open barn, or around farm buildings and ranged from 10–15 m^2. We then marked all birds with neck collars to allow individual recognition. We determined their API between 30 min and 9 hr after the capture. We introduced four to seven individuals at a time into a separate enclosure (about 12 m^2) and attributed API using binoculars at distances ranging from 3 to 10 m. Scoring was made by one observer (JB) in 1999 and two (MF and GP) in 2000 and 2001. In 2000, we assessed API of 10 to 15 birds per capture (total n = 74) a second time to examine repeatability in scores attributed by the same observer. To avoid recognition of previously observed individuals, a third person changed neck collars; however, as the observers knew the range and approximate distribution of API during the second assessment, we cannot exclude the possibility that our measure of within-observer repeatability was slightly overestimated.

For each capture, we sacrificed a random sample of females among those kept in enclosure. The remaining birds were released. Birds with high profile scores were relatively rare during the study (see Discussion). In order to better calibrate API, we thus occasionally selected and sacrificed birds with relatively high scores (API $\geq$ 2.5; 21 birds out of 230). We sacrificed 63 females in 1999, 130 in 2000, and 37 in 2001. Killed birds were put into sealed plastic bags and stored frozen. In the laboratory, birds were thawed, weighed (nearest 1 g), and measured (culmen, tarsus, and head lengths to the nearest 0.1 mm). Abdominal fat (surrounding the intestine and extending anterior and ventrally over the gizzard but excluding mesenteric fat within the intestinal loops) was removed and weighed (nearest 0.1 g). This fat deposit is a good indicator of overall body fat in geese (Thomas et al. 1983, Gauthier and Bédard 1985).

MONITORING OF ABDOMINAL PROFILES IN HUNTING AND NONHUNTING YEARS

We monitored the seasonal change in API in the three study regions throughout the spring staging period from 1997 to 2000. The spring hunt took place in southern Quebec between 15 April and 31 May in 1999 and 2000 on farmlands only (Féret et al. 2003). Each year, we assigned one observer to each of the three regions (except in the Upper Estuary where the region was divided in two with a different observer for the north and the south shore of the St. Lawrence River). Observers were given drawings of API scores and attended a field-training session with JB or MF at the start of each field season. We also used life-size silhouettes of each API score and intermediate levels for field training in 2000. Dummy geese were placed in habitats where geese were observed. Different observers monitored seasonal changes in API over the 4 years of the study except in the Lake St. Pierre region where the same observer made observations in all years. In each region, we scored the profile of about 50 randomly selected, unmarked adults generally every five days.

STATISTICAL ANALYSES

We used linear regression (proc GLM, SAS Institute 1999) to examine the relationship between mean API attributed before firing the nets and mean API estimated in enclosures. We also used linear regressions to relate API with abdominal fat and body mass. We controlled for variation in body size by using the residuals of the relationship between our condition measures and body size (Brown 1996, Jakob et al. 1996). We performed a principal component analysis (proc PRINCOMP, SAS Institute 1999) on morphometric measurements (culmen, tarsus, and head lengths). The three variables had loadings ranging from 0.50 to 0.62 on the first axis (PC1), which explained 71% of total variation in the data. We used individual PC1 scores as a measure of body size. Relative abdominal fat mass and relative body mass were defined as the residuals of the regression of abdominal fat or body mass on PC1 plus the mean mass of all individuals included in the model (Féret et al. 2003).

To examine if we could detect the effect of spring hunt on fat accumulation using API, we compared seasonal changes in profile scores of geese in nonhunting (1997 and 1998) and hunting years (1999 and 2000) using analysis of covariance. The general model included the following variables: region, year, date (as a covariate), and their interaction terms. In each region, we compared the seasonal change in API between pairs of years with and without a hunt (CONTRAST option in proc GLM, SAS Institute 1999). Because this approach involved several tests, we limited the overall experimentwise error rate by adjusting significance levels (α = 0.05) using Bonferroni corrections (Sokal and Rohlf 1995). All values reported in the text are means $\pm$ SE.

RESULTS

CALIBRATION OF ABDOMINAL PROFILES

Average abdominal profile indices attributed to free-ranging birds at each capture site was closely related to average API assigned to females in enclosures (linear model: $API_{field} = -0.05 + 1.01 \times API_{enclosure}$; $R^2 = 0.97$, $P < 0.001$, $n = 8$). The slope of the relationship did not differ significantly from 1 ($\beta = 1.01$, 95% CI: 0.85 to

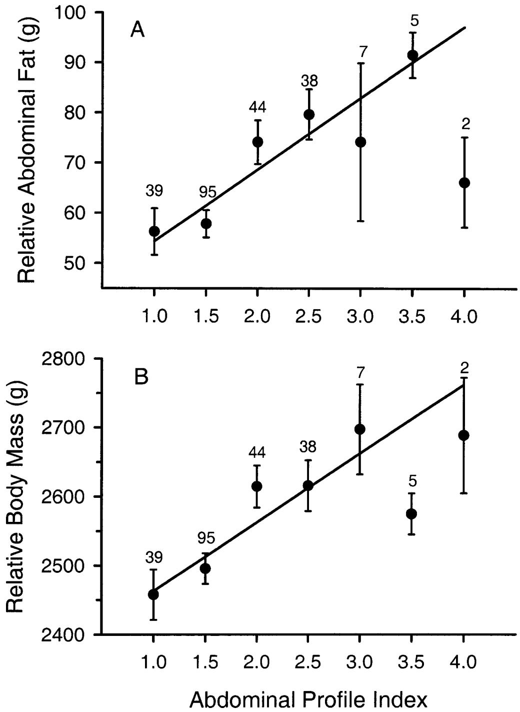

FIGURE 2. Relationship between abdominal profile indices (API) of adult female Greater Snow Geese and abdominal fat (A) or body mass (B), adjusted for body size. Values are means ± SE and numbers indicate sample size.

1.17), indicating that API assessed in enclosures accurately reflected API measured in the field.

API attributed to females in enclosures were positively related to relative abdominal fat (RAF = 40.1 + 14.3 × API, R^2 = 0.09) and relative body mass (RBM = 2363 + 100 × API, R^2 = 0.08; $P < 0.001$; n = 230 in each case, Fig. 2). An increase of one profile score corresponded to an increase of 100 g in body mass on average. However, the predictive power of nutrient stores (i.e., abdominal fat or body mass corrected for body size) by API was low at the individual level. Restricting the analyses to data collected by only one observer (MF) in 2000–2001 yielded very similar results ($R^2 < 0.06$, $P < 0.01$, n = 167). At the individual level, the predictive power of API was slightly better for birds captured just before their northward migration, which included the fattest birds (relative abdominal fat, R^2 = 0.10, and relative body mass, R^2 = 0.15; $P < 0.001$, n = 141 in each case). API were much better predictors of the average abdominal fat and body mass of females assigned to the

TABLE 1. Frequency distribution of the difference (in API score) between abdominal profile indices attributed to the same bird by the same observer (within-observer) or by different observers (between-observer).

Difference	Within-observer				Between-observer	
	Observer 1		Observer 2		Observer 1 vs. 2	
	n	%	*n*	%	*n*	%
0	43	58	54	73	77	42
±0.5	27	37	20	27	92	50
±1	4	5	0	0	16	9

same profile score (RAF = 54.0 + 7.0 × API, R^2 = 0.36, P = 0.15, n = 7; RBM = 2425 + 67 × API, R^2 = 0.64, P = 0.03, n = 7). For abdominal fat, the regression model using average masses was strongly affected by the value associated to the highest API category observed (API = 4). Excluding that value based only on two birds improved the strength of the relationship (RAF = 42.5 + 13.2 × API, R^2 = 0.85, $P < 0.01$, n = 6).

Repeatability of API assigned to birds in captivity was very high (Table 1). Differences in API attributed to the same birds by the same observer were ≤0.5 profile score for >94% of the second observations (n = 74). Differences between observers were also fairly low as 91% of the API assigned independently to the same bird differed by ≤0.5 profile score (n = 185, Table 1). The range of API observed for these analyses was 3 (from 1.0–4.0).

API OF STAGING GEESE AND EFFECT OF SPRING HUNTING

From 1997 to 2000, we observed significant annual variations in the seasonal changes in API of spring staging geese ($F_{3,6454}$ = 69.7, $P <$ 0.001) but these differences varied among regions ($F_{6,6454}$ = 40.8, $P < 0.001$). Thus, we compared seasonal changes in API between years with and without a spring hunt for each of the three regions separately. The rate of increase in API was significantly lower in hunting years (1999–2000) compared to nonhunting years (1997–1998) in both Lake St. Pierre and the Lower Estuary (Fig. 3, Table 2), except between 1998 and 2000 in the Lower Estuary due to the conservative significance level used (α = 0.004; Regression slopes: Lake St. Pierre, β_{1997} = 0.051 ± 0.003, β_{1998} = 0.047 ± 0.003, β_{1999} = 0.024

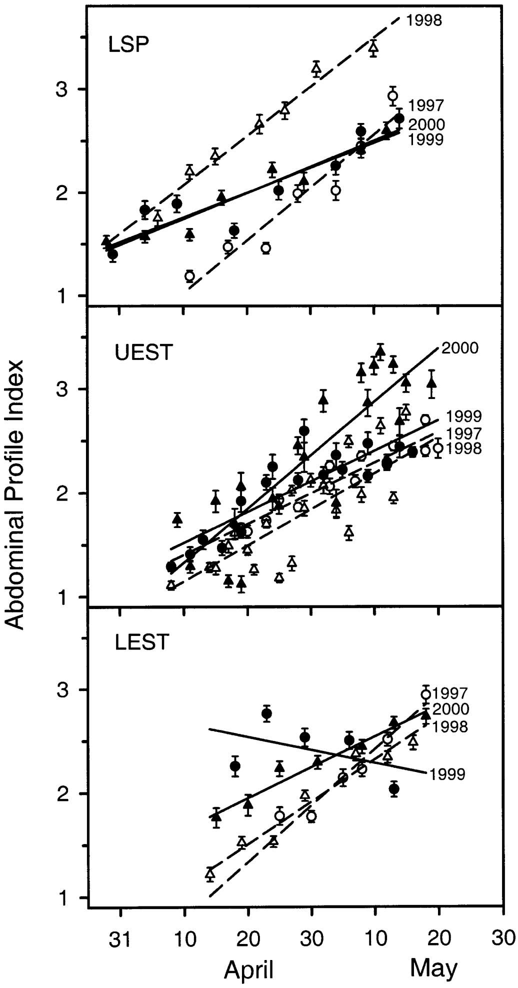

FIGURE 3. Seasonal changes in abdominal profile indices of adult Greater Snow Geese during the spring staging period in nonhunting years (1997, unfilled circles, and 1998 unfilled triangles; dashed lines) and hunting years (1999, filled circles, and 2000, filled triangles; solid lines) in three regions along the St. Lawrence River: Lake St. Pierre (LSP), Upper Estuary (UEST), and Lower Estuary (LEST). Values are means ± SE. Each symbol represents about 50 individuals.

± 0.002, β_{2000} = 0.025 ± 0.002. Lower Estuary, β_{1997} = 0.054 ± 0.004, β_{1998} = 0.041 ± 0.002, β_{1999} = −0.013 ± 0.004, β_{2000} = 0.030 ± 0.003). API even decreased during the first hunting year (1999) in the Lower Estuary. However, the situation differed somewhat in the Upper Estuary where the rate of increase in API in 1999 was similar to 1997 and 1998, whereas it was higher in 2000 than in the two nonhunting years (Fig. 3, Table 2; Regression slopes: Upper Estuary, β_{1997} = 0.029 ± 0.002, β_{1998} = 0.035 ± 0.001, β_{1999} = 0.029 ± 0.002, β_{2000} = 0.051 ± 0.002).

DISCUSSION

CALIBRATION OF ABDOMINAL PROFILE METHOD

Abdominal profile indices (API) were significantly and linearly related to direct measures of nutrient stores (i.e., abdominal fat and body mass, corrected for body size) in spring staging female Greater Snow Geese. However, the predictive power of nutrient reserves by API was low at the individual level. Using a similar approach, Bowler (1994) obtained a tighter relationship between body mass and API in female Bewick's Swans (Pearson *r* ranging from 0.46 to 0.52). Variation among species may be partly attributed to differences in distribution of fat in the abdominal cavity and rates of accumulation at this internal site relative to other sites of storage (e.g., subcutaneous or furcular regions; Rogers 1987). Accurate determination on a large bird like a swan may also be easier than in geese.

Owen (1981) suggested that API could be used to explain variation in reproductive success of geese at the individual or population level. Because the variance is high for individuals assigned to the same profile score in Greater Snow Geese, our study suggests that the likelihood of detecting significant association between life-history traits and individual body condition using API is low. The predictive power of body condition by API was higher for birds captured just before their northward migration. A possible explanation for that may be that API scores are determined more accurately in birds with bulging abdomens (i.e., the fattest birds), which were more abundant in the sample of departing birds. This may partially explain why API were nonetheless helpful in linking premigration body condition and timing of breeding in individual Greater Snow Geese (Bêty et al 2003). Similarly, API were successfully used to relate prebreeding condition and breeding success in Pink-footed Geese (Drent et al. 2003) and Barnacle Geese (*Branta leucopsis*, Prop et al. 2003). However, these associations are expected to be strong in birds like geese that rely heavily on nutrient storages for successful breeding. On the other hand, the closer linear relationships between average body condition indices and API indicates that profile scores may be useful and

TABLE 2. Pairwise comparisons of the rate of seasonal changes in abdominal profile indices between hunting years (1999–2000) and nonhunting years (1997–1998) in three regions along the St. Lawrence River (LSP, Lake St. Pierre; UEST, Upper Estuary; LEST, Lower Estuary; df = 1, 6454).

		Hunting years			
		1999		2000	
Region	Nonhunting years	F	P[a]	F	P[a]
LSP	1997	57.5	<0.001	53.6	<0.001
	1998	44.0	<0.001	40.4	<0.001
UEST	1997	0.0	0.99	62.3	<0.001
	1998	4.9	0.03	56.9	<0.001
LEST	1997	114.2	<0.001	20.3	<0.001
	1998	113.7	<0.001	7.8	0.005

[a] Significance level was adjusted with the Bonferroni method ($\alpha = 0.004$ for all tests).

reliable measures of nutrient stores for groups of Greater Snow Geese, as found in other species (Bowler 1994, Scott et al. 1995, Wiersma and Piersma 1995). Finally, the fairly good linearity between API and abdominal fat mass indicates that the difference in fat mass between adjacent API categories is relatively constant over the range of scores observed. Consequently, API can be considered as a continuous variable and could be analyzed using parametric tests (Drent et al. 2003).

One limitation of our study is that collection of geese for the calibration of API occurred in years with relatively low rate of seasonal increase in nutrient stores due to the spring hunt (1999 to 2001, Féret et al. 2003). Indeed, very few collected birds had high API (only 14 out of 230 with API > 2.5). This is in contrast with previous years (i.e., 1997 and 1998) when such high scores were more commonly encountered in the field (Bêty et al. 2003). Thus, the strength and the shape of the relationship between API and nutrient stores could potentially change for geese with high API scores (3 to 5); this would require further investigation.

EFFECT OF A SPRING HUNT ON NUTRIENT STORAGE BY GEESE

Seasonal changes in API of free-ranging birds indicate that spring hunting negatively affected the rate of increase in nutrient storage of geese in two out of three regions (Lake St. Pierre and Lower Estuary) of the staging area. These results are generally consistent with direct measures of body condition showing the negative impact of hunting on nutrient storage by geese (Féret et al. 2003). Hunting disturbance apparently reduces the ability of geese to store nutrients because of a decrease in feeding activity and an increase in flying time (Féret et al. 2003, Béchet et al. 2003, 2004). Drent et al. (2003) also detected negative impacts of human-induced disturbance on Pink-footed Geese using the API method.

The failure of the API technique to detect the negative effect of spring hunting on goose body condition in one region (Upper Estuary) likely reflects some limitations of the method, as such effect has been detected with direct measures (Féret et al. 2003). In the two regions where an effect of hunting was detected using API, only one (Lake St. Pierre) and three (Lower Estuary) different observers monitored the seasonal changes in API over the four years of the study compared to eight observers in the Upper Estuary. We observed marked dissimilarities in the seasonal changes of API between the north and the south shore of the Upper Estuary region in some years (differences between rates of condition increase, API per day, were 0.042 ± 0.004 in 2000, 0.024 ± 0.003 in 1998, 0.006 ± 0.003 in 1997 and 0.002 ± 0.004 in 1999). Because birds frequently move between the two shores in this region (Maisonneuve and Bédard 1993, Béchet 2002), there are no apparent biological reasons to explain such differences in condition gain. Moreover, analyzing the two shores separately for the effect of hunting generated inconsistent results. For instance, the rate of condition gain on the north shore was lower in one hunting year (in 1999 relative to 1998; $P < 0.001$) but an opposite trend was observed in the second hunting year (in 2000; $P < 0.001$). As observers differed between the north and south shores each year, it rather suggests that variability among observers in scoring API generated these spurious results in the Upper Estuary.

Although we showed that API scores of the same birds by two experienced observers were consistent in enclosures, observer effects in the field have been previously detected in fat scoring studies (Owen 1981, Krementz and Pendleton 1990, Brown 1996). Indeed, the technique requires subjective estimations, and observers often have difficulties to distinguish categories. Consequently, we suggest that the presence of observers not sufficiently trained may explain the different pattern observed in the Upper Estuary region. We recommend that all observers must be well trained on live birds and that regular comparisons of API scores among observers should also be done to ensure better results in future studies.

API may be more accurate in detecting differences in the rate of condition change than absolute differences in nutrient stores at a given time. Indeed, observers may use the API classification in a different way (i.e., consistently scoring higher or lower values) but nonetheless be constant over time (Krementz and Pendleton 1990). This could explain why rates of API increase at Lake St. Pierre, which were monitored by the same observer, were identical in 1997 and 1998 even though API values were consistently higher in 1998 than in 1997. The observer may have given higher API values in 1998 after he had seen the whole range of possible profiles in the first spring.

In conclusion, our results indicate that API can estimate body condition of spring staging Greater Snow Geese but the precision of the technique is limited at the individual level, especially if observers are not experienced and rigorously trained. However, the technique appears much more reliable at the group or population level.

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