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COVID19-induced reduction in human disturbance enhances fattening of an overabundant goose species

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A R T I C L E I N F O

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A B S T R A C T

Overabundant species can have major impacts on their habitat and induce trophic cascades within ecosystems. In North America, the overabundant greater snow goose (*Anser caerulescens atlanticus*) has been successfully controlled through special spring hunting regulations since 1999. Hunting is a source of mortality but also of disturbance, which affects the behavior and nutrient storage dynamics of staging snow geese. In 2020, the lockdown imposed by the COVID19 pandemic reduced hunting activity during their migratory stopover in Québec by at least 31%. This provided a unique opportunity to assess the effects of a sudden reduction in hunting disturbance on geese. We used long-term data on body mass combined with movement data from GPS-tracked birds in 2019 and 2020 to assess the effects of the 2020 lockdown on the spring body condition and behavior of greater snow geese. Body condition was higher in 2020 than in all years since the inception of spring hunting in 1999, except for 2019. However, in 2020 geese reached maximal body condition earlier during the staging period than in any other year and reduced by half time spent feeding in highly profitable but risky agricultural habitat in late spring compared to 2019. Although our study was not designed to evaluate the effects of the lockdown, the associated reduction in disturbance in 2020 supports the hypothesis that hunting-related disturbance negatively affects foraging efficiency and body condition in geese. Since spring body condition is related to subsequent breeding success, the lockdown could increase productivity in this overabundant population.

1. Introduction

Predictable anthropogenic food subsidies, such as agriculture, livestock, fishing or waste, can be responsible for major changes in natural communities and ecosystem functioning (Oro et al., 2013). Exploitation of subsidies by wildlife is thought to have largely contributed to the demographic explosion of many species (Castro et al., 2005; Fox and Abraham, 2017; Oro et al., 2013; Rotem et al., 2011). Overabundant species that depend on those subsidies can have major impacts on their habitat and induce trophic cascades within ecosystems (Allombert et al., 2005; Flemming et al., 2019; Jefferies et al., 2004; Lamarre et al., 2017). The onset of industrial agricultural practices in North America provides a prime example as it was a key component in the unprecedented increase of many goose populations, and led to severe overgrazing of some tundra ecosystems (Abraham et al., 2005; Gauthier et al., 2005; Jefferies et al., 2004).

Hunting can be an effective tool to manage overabundant populations because it impacts survival and its effect is easily controlled through regulations (Cromsigt et al., 2013). The greater snow goose (*Anser caerulescens atlanticus*), a migratory species breeding in the Canadian Arctic, was declared overabundant after it underwent radical population growth and increased from ∼25,000 to over 1,000,000

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individuals between 1965 and 1999 (Gauthier et al., 2005; Lefebvre et al., 2017). In 1998, wildlife management authorities liberalized hunting regulations for this species to stop population growth and prevent the potentially devastating impacts that such numbers of geese could have on tundra plant communities (Batt et al., 1998; Reed and Calvert, 2007). The most significant measure implemented was a special spring hunting season (legally referred to as the Conservation Harvest) introduced in 1999 in the Québec province, followed by a new extended winter hunting season with very liberal hunting regulations (the Conservation Order) introduced in winter 2009 in Eastern USA. These management actions were a success as the population stopped growing and has been oscillating between 750,000 and 1,000,000 individuals since 1999 (Lefebvre et al., 2017). From 1999 onwards, snow geese were hunted almost year-round: from their arrival on the Québec staging grounds in early fall until their departure from the same staging grounds to the Arctic in the following spring. This dramatic increase in hunting pressure induced a reduction in population growth primarily through decreased adult survival which declined from 83.0% in 1990–1998 to 72.5% in 1999–2002, the first years of the Conservation Harvest (Calvert and Gauthier, 2005).

Because overabundant geese also cause damage to farmlands (Filion et al., 1998), the Québec agricultural producers' union has been conducting organized scaring activities to limit depredation since 1999. People are hired to patrol agricultural areas and drive geese away from fields in a coordinated effort. Disturbance caused by hunting and scaring activities can have major impacts on waterfowl species (Bélanger and Bédard, 1990; Madsen, 1995; Madsen and Fox, 1995). In greater snow geese, such disturbances during staging increase energy expenditure and reduce nutrient storage and overall body condition prior to the spring migration to the Arctic (Béchet et al., 2004; Féret et al., 2003). A reduction in body condition during a critical part of the annual cycle when geese are fattening has been shown to negatively affect breeding (Bêty et al., 2003; Legagneux et al., 2012). Indeed, in the first two years following the implementation of the Conservation Harvest, body condition of nesting geese was reduced by 28%, breeding propensity was dramatically reduced, laying date was delayed by 2–7 days and clutch size was reduced by 1.5 eggs (Mainguy et al., 2002). The recruitment rate of females into the breeding population and the proportion of young in the fall flock also declined after the implementation of the Conservation Harvest (Juillet et al., 2012; Morrissette et al., 2010).

In spring 2020, the lockdown imposed in response to the COVID19 pandemic provided an unprecedented opportunity to document how wildlife responds to large-scale reductions in human activities (Bates et al., 2020; Corlett et al., 2020; Manenti et al., 2020; Rutz et al., 2020). In Québec, the government declared a generalized lockdown on March 16th, 2020, which was fully enforced by March 23rd, and lasted until May 4th. Restrictions were then lifted gradually over the 4 following weeks. During the lockdown, all economic activities except essential services such as agriculture were stopped, and people were largely confined in their homes with movements between regions forbidden. We anticipated that the lockdown reduced hunting pressure and scaring activities on greater snow geese staging in southern Québec. Reductions in hunting and scaring disturbance on the main stopover area has a strong potential to positively affect the foraging efficiency, energy budget and spring body condition of geese, which could lead to higher reproductive output in the subsequent breeding season (Morrissette et al., 2010).

The negative impacts of the spring Conservation Harvest on goose body condition were driven by changes in movements and behavior, as documented through a before-after-impact design by Béchet et al. (2003, 2004), and Féret et al. (2003). In this study, we first determine the magnitude of the reduction in hunting activity associated with the lockdown. Then, using data from previous studies (collected in 10 springs between 1979 and 2009) along with new data acquired in 2019 and 2020, we assess the impact of a reduction in hunting pressure on the behavior and body condition of spring staging geese.

Agricultural fields provide a high-quality foraging habitat for geese due to the presence of nutrient-rich crops (Bédard and Gauthier, 1989; Giroux and Bergeron, 1996); however, they are a riskier habitat than marshes because geese are exposed to hunters unlike in marshes where hunting is forbidden in spring. Geese usually commute daily between roosting sites in marshes, where some feeding can also occur, to farmlands which are predominantly used for foraging. Geese foraging in fields are exposed to disturbance and threats like scaring by farmers protecting their crops and, most importantly, hunting since 1999. The Conservation Harvest disrupted goose foraging behavior in agricultural fields by shortening foraging bouts and increasing flying time, which ultimately reduced their energy intake (Béchet et al., 2004). During spring 2020, we would expect a dampening of these conditions as a reduction in disturbance should lead to longer, uninterrupted foraging bouts, less time spent flying and an increased energy intake rate in agricultural fields, particularly in the first half of staging when the lockdown was strictest. Based on this hypothesis, we predicted that during the COVID19 lockdown, staging geese should accumulate more nutrient reserves and reach a better body condition more rapidly compared to previous years. We also predicted that geese should spend less time in risky agricultural fields at the end of the staging period, when we were able to track their movements. Indeed, if nutrient accumulation was more rapid in 2020 than in 2019 as expected, birds in good condition near the end of the staging period should be less prone to use a riskier habitat (cropfields) where hunting could occur, than the marsh habitat where hunting was always prohibited.

2. Methods

2.1. Data acquisition

2.1.1. Study model and site

Greater snow geese winter along the Atlantic coast of the United States and breed in the eastern high Arctic (Fig. 1). In spring, they migrate north through eastern Canada and stage in southern Québec between late March and late May (Reed et al., 1998). During this stopover, geese fatten up as they accumulate the large endogenous reserves needed to complete their migration and subsequent reproduction (Gauthier et al., 1992, 2003). Traditionally, snow geese fed on *Schoenoplectus americanus* in tidal marshes but since the 1980s, they have been increasingly relying on corn and hay in farmlands, a higher-quality food source (Bédard and Gauthier, 1989; Gauthier et al., 2005). Since 1999, hunting occurs from April 15th to May 31st in Québec (April 1st since 2000) and solely takes place on agricultural lands, inducing potential trade-offs between the risk of getting shot and the access to highly profitable food resources (Béchet et al., 2004).

2.1.2. Capture procedures

Geese were captured in spring during the migratory staging period at Île-aux-Oies (47°08N 70°29W, Fig. 2), a small agricultural island in the Saint-Lawrence estuary, 60 km northeast of Québec City (Canada). We used baited canon-nets placed in fields to capture geese between late April and mid-May every year between 2006 and 2009 as well as in 2019 and 2020 (see Morez et al., 2000 for details and Fig. A.1 for timing of captures). The firing of cannon-nets (6 to 15 cannon-netting events over a 3-week period) represents a negligible source of disturbance for the goose population considering that this activity occurred over $<0.01\%$ of the area used by staging geese in spring. Adults were sexed based on cloacal examination. Females were weighed to the nearest gram with an electronic scale and culmen and tarsus were measured to the nearest 0.1 mm using calipers ($n = 499$ in 2006, 715 in 2007, 650 in 2008, 686 in 2009, 370 in 2019 and 193 in 2020). Large adult females were equipped with GPS-GSM collars (OrniTrack-N44 - neck collar solar-powered GPS-GSM tracker; 45 g, approximately 1.5% body mass) in 2019 ($n = 10$) and 2020 ($n = 5$) and were tracked ever since. Collars were programmed to record location every 5 min from 3:00 AM to 11:00 PM. Geese were

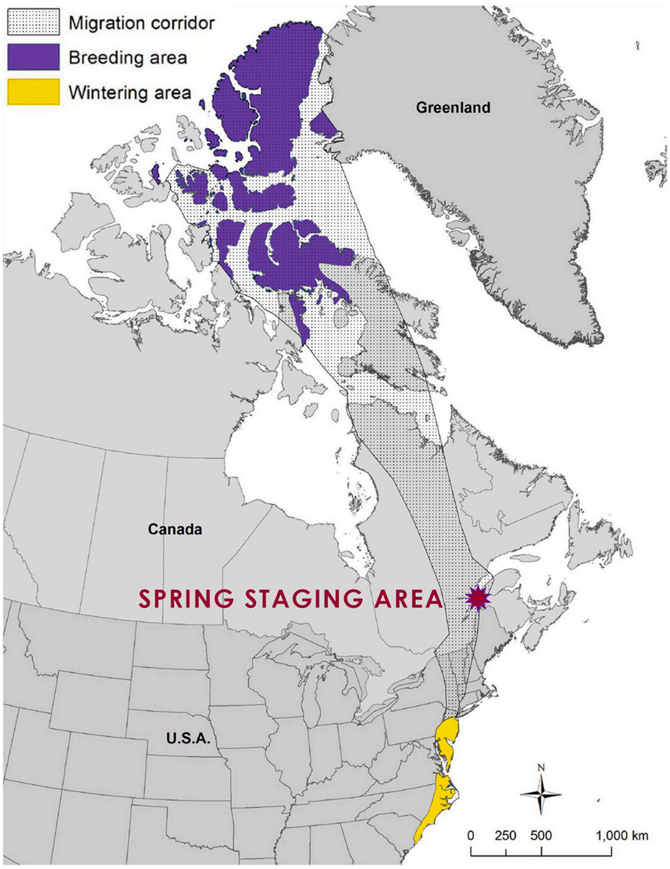

Fig. 1. Map of the breeding (purple), wintering (yellow) and staging areas (red star) of the migratory greater snow goose population. The hatched polygon represents the migratory flyway. This map was modified from Lefebvre et al., 2017. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

released together either immediately after handling when captures occurred during the day or the following morning to avoid disorientation when handling ended after dark. In 2020, special protective equipment was used when handling birds to avoid any cross-contamination between humans and geese (Frederick et al., 2021). All manipulations conducted in 2019 and 2020 were approved by the Committee of Animal Protection of our institution.

To compare goose body condition between years, we retrieved original data on geese collected in 1979 and 1980 by Gauthier et al. (1984), in 1989 and 1990 by Gauthier et al. (1992), and in 1999 and 2000 by Féret et al. (2003). In 1979 and 1980, geese were shot throughout the staging grounds under special scientific permit, stored frozen in plastic bags and weighed in the laboratory ($n = 91$ in 1979 and 84 in 1980). Between 1989 and 2000, geese were captured with baited canon nets at three sites along the St-Lawrence River. A random sample of females were killed by lethal injection, stored in plastic bags and frozen ($n = 38$ in 1989; 39 in 1990, 92 in 1999 and 148 in 2000). Geese were subsequently weighed to the nearest gram (except in 1990 where birds were weighed in the field, to the nearest 25 g) and culmen and tarsus measurements were taken in the laboratory. Fluid loss is possible but was likely minimal because carcasses were rapidly frozen after collection and weighed before thawing. Body masses from all years are thus comparable.

2.2. *Statistical analyses*

2.2.1. *Body condition*

To compare body condition among individuals, we needed a non-invasive measure of endogenous reserves that was independent of structural size. Following the procedure described in Féret et al. (2003), we ran a principal component analysis (PCA) on two skeletal measurements (culmen and tarsus lengths) and used the resulting first principal component (PC1) as a measure of relative body size. Loadings for the two variables were above 0.5 and the first axis explained over 50% of the overall variation. We then used the residuals of the regression between individual body mass and PC1 to which we added the average mass of the population as a measure of relative mass corrected for skeletal size. We validated that this index was a reliable indicator of endogenous reserves using a dataset of 90 females randomly sacrificed during captures in 2006, 2007 and 2008 and for which fresh abdominal fat was weighed (data from Legagneux et al., 2013). Our condition index was related to fat mass values ($F_{1,88} = 52.9$; $p < 0.001$; adjusted $R^2 = 0.37$).

We first assessed the potential effect of a reduction in hunting-related disturbance due to the COVID19 lockdown on overall body condition. Because geese gain approximately 10 g per day during spring staging, and because birds were captured on different dates in different years (Fig. A.1), we adjusted our condition index to take this daily mass gain into account. Thus, we adjusted individual condition to a single date near the end of staging (May 12th) using the average daily mass gain for all years pooled. We obtained the average daily mass gain by fitting polynomial regressions with mass adjusted for skeletal size as a response variable, day of year as a fixed effect and year as a random intercept. Candidate models were fitted up to the 5th degree, and we selected the most parsimonious of equivalent models (ΔAICc<2; see Fig. B.1 for selected date adjustment model) using Akaike Information Criterion (AICc; Burnham and Anderson, 2002). The resulting index provides a measure of body condition independent of skeletal size and capture date. We inferred hunting disturbance using three yearly metrics of hunting pressure in spring: total number of geese harvested in a hunting season ("harvest" from here on), number of active hunters and total number of hunting days. This is determined annually by wildlife agencies who conduct standard surveys among a large sample of hunters (data provided by M. Gendron, Environment and Climate Change Canada). We examined the relationship between body mass adjusted for structural size and our three metrics of hunting pressure (fixed effect) using separate linear mixed models with capture ID and year as random intercepts to account for the block structure of the data. Next, we compared overall body condition between years. We compared average body condition adjusted for size and date among years using a linear mixed model with year as a fixed effect and again capture ID as random intercepts.

Because disturbance could act on the rate at which geese gain mass during spring staging, we compared the rate of condition increase in 2020 to years with hunting for which data was available over a comparable period (2007, 2008, 2009, 2019; Fig. A.1). We fitted a linear mixed model with body condition index (mass adjusted for skeletal size only; see above) as the response variable. Year, date and their interaction were fitted as fixed effects and capture number as random intercepts. We fitted the fixed effect as a 3-level variable comparing 2020, 2019 and 2007–2009. The year 2019 was fitted as a separate level because goose body condition and weather conditions were similar to 2020 (see Section 3.2 and Fig. C.1 in the appendix) and we were thus interested in this specific contrast.

For all models described above, we tested and validated the assumptions of normality, homoscedasticity, non-collinearity among fixed effects, and independence of residuals. Linear mixed models were fitted using the `lmer` function of package `lme4` (Bates et al., 2015). All statistical analyses were conducted in the `R` statistical environment (version 4.0.1, R Core Team, 2020) and all estimates are reported with their 95% confidence intervals throughout.

2.2.2. *Habitat use*

We used locations of radio-marked geese at Île-aux-Oies and in the surrounding area to compare the use of the two main habitats used by

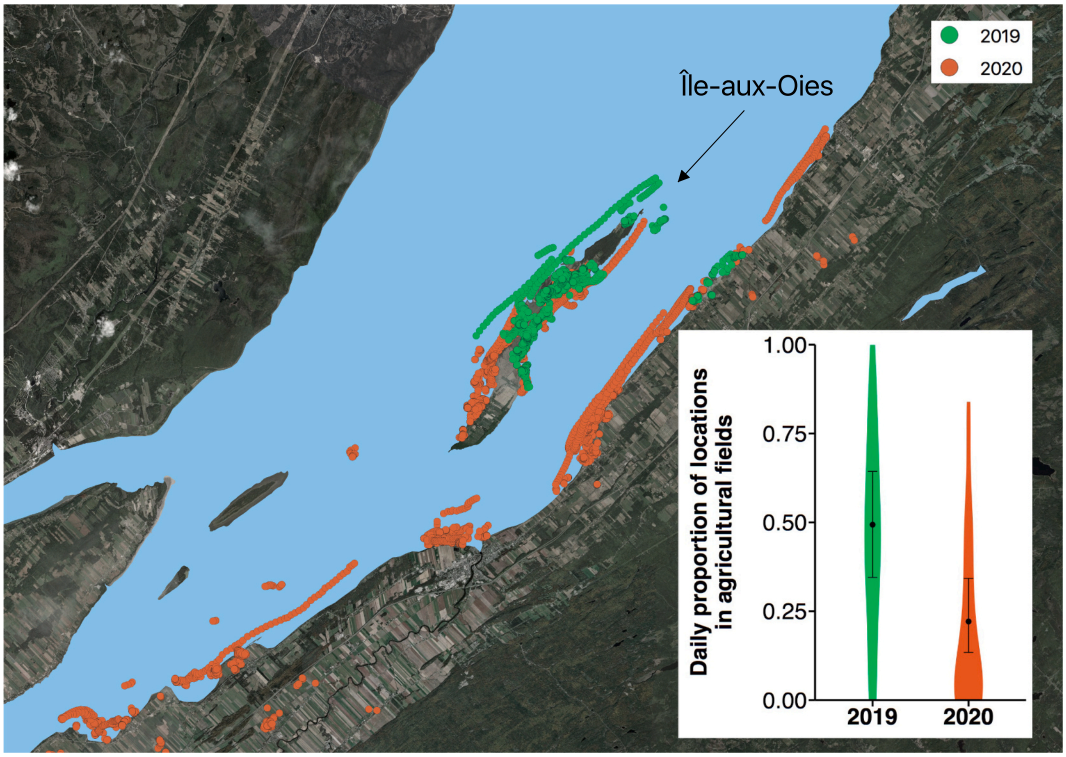

Fig. 2. Locations of the four GPS-collared snow geese tracked near the end of the staging period from May 6th to 24th in both 2019 (green dots) and 2020 (orange dots) in the St Lawrence estuary. All geese were captured and marked at Île-aux-Oies, which explains the larger concentration of dots there in 2019, the year of marking. Restricting the analysis to the Île-aux-Oies area only did not affect the proportion of locations in agricultural fields in either year. Window: average daily proportion of locations recorded in fields by the same individuals ($n = 4$) tracked in 2019 and 2020. Error bars are 95% CI and color shading represents the density distribution of individual data points. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

geese: tidal marsh areas and agricultural fields (Fig. 2). We classified agricultural fields and marshes in our study area by hand using the `Esri.WorldImagery` base map from package `mapedit` (Appelhans et al., 2020) in `R` (R Core Team, 2020). Location data was collected during the same period in both years, from May 6th to 24th, near the end of the staging period. We only considered locations from sunrise to sunset because geese do not use farmlands at night (Gauthier et al., 1988), and hunting is only permitted during the day. In addition, because locations taken during flight may not reflect habitat use on the ground, we removed them from the analysis. We computed the speed between each pair of consecutive points (distance covered divided by time elapsed between locations) and eliminated locations for which the average speed to the next point was above 10 km/h (376/10991, ~3%). We visually assessed our classification and there were few errors (~70 points, <0.7%).

We computed the proportion of locations in agricultural fields vs. in tidal marshes every day for the individuals tracked in both years ($n = 4$ individuals; 68 individual-days total over both years). The number of days considered ranges from 4 to 16 per individual, depending on the number of days individuals spent in the study area (Fig. 2) in each year. To compare the proportion of locations on land between years, we fitted a generalized linear mixed-model with a binomial distribution using Penalized Quasi-Likelihood to account for overdispersion using the `glmmPQL` function in the `MASS` package (Venables and Ripley, 2002) in R (R Core Team, 2020). The model was fitted with year and day of year (to account for potential temporal trends in habitat use) as fixed effects and bird ID as random intercepts to account for repeated measurements on individuals. Finally, we ran a second analysis with all collared birds ($n = 15$), but where individuals only contributed data for the year in which they were initially marked.

3. Results

3.1. Lockdown impacts on sources of disturbance

The travel restrictions imposed by the lockdown reduced overall hunting pressure and goose harvest in spring 2020 as we expected. Data on hunting activity showed a decrease of 54% in the number of active hunters, 32% in hunting days and 31% in geese harvested in 2020 compared to 2019 (Fig. 3A and Appendix D). Organized scaring activities aimed at chasing goose flocks from farmlands throughout the province were also affected due to the difficulty of recruiting staff during the lockdown. The number of scaring events in spring 2020 (1501 events) was 28% lower than in 2019 (2017) and 46% lower than in 2018 (2798) (Union des producteurs agricoles du Québec, unpubl. data).

3.2. Body condition

The body condition index of geese adjusted to May 12th was high in all springs without hunting despite some annual variation. Average condition was highest in 1979 and 1980, before the spring Conservation Harvest was implemented, and lowest in 1999 and 2000, the first two years following its implementation (Fig. 4). Average body condition in spring 2020 was higher than in all other years with a spring Conservation Harvest, apart from 2019 when body condition was similarly high (see Table 1; Fig. 4). Overall, we found a strong inverse relationship between the body condition of birds and the intensity of the Conservation Harvest (Fig. 3B and Appendix D). Body condition was negatively related with yearly spring harvest (Estimate = −0.009 [−0.012, −0.006] g/goose harvested).

Daily increase in body condition index in spring 2020 differed from recent years with a spring Conservation Harvest (2007–2009, 2019; Table 2, Fig. 5). On average, goose body condition in 2019 increased by

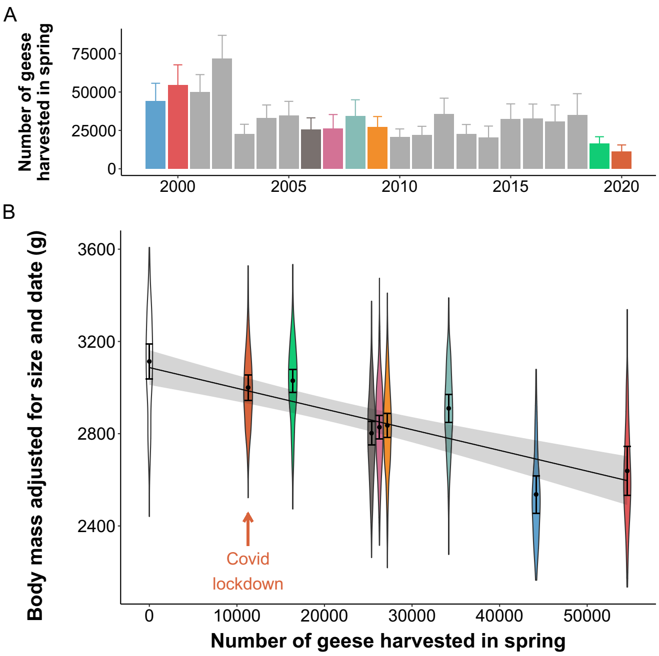

Fig. 3. A: Annual spring harvest of greater snow goose from 1999 to 2020. Error bars represent 95% confidence intervals. Colored bars represent years for which data on body condition is available. B: Spring body condition of geese at the end of the staging period in relation to annual spring harvest. Values at 0 harvest (white violin) correspond to years without a spring Conservation Harvest (before 1999). The black line represents the mean model predictions based on individual data points with its 95% CI (shaded; regression slope [95% CI]: −0.009 g/goose harvested [−0.012, −0.006], n = 3460). Black dots and error bars are the mean body mass with their 95% CI for each harvest level and color shading represents the density distribution of individual data points. Source of hunting statistics: Smith and Gendron (2020). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

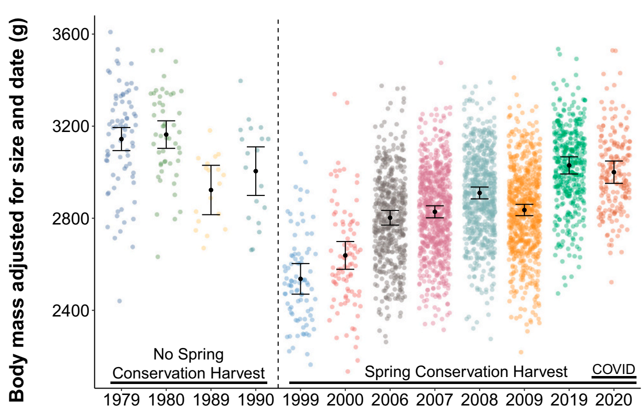

Fig. 4. Annual variation in greater snow goose body condition index during spring migratory stopover in Québec. Points are individual body masses corrected for skeletal size and adjusted to May 12th. The black dots and error bars represent average annual body mass with their 95% confidence intervals.

9.8 [2.4, 17.3] g/day, a value similar to 2007–2009 (11.3 [9.2, 13.8] g/day, Table 2). In contrast, there was no detectable increase in body condition during the same period in 2020 (−5.5 [−14.8, 3.8] g/day), suggesting that geese had reached an optimal body condition earlier in that year.

Table 1
Parameter estimates of the linear mixed model comparing adjusted body mass of greater snow geese among years. *Intercept* (*2020*) represents the average body condition (in g) in 2020. Other estimates represent the difference (in g) in average body condition with 2020. Estimates in bold are significantly different than 2020 ($n = 3460$).

Year	Estimate	95% CI
Intercept (2020)	3000	2953.7, 3046.1
1979	**143.9**	**76.8, 211.1**
1980	**163.4**	**88.8, 237.8**
1989	−77.3	−191.0, 36.8
1990	4.6	−107.3, 117.2
1999	**−463.5**	**−541.7, −384.9**
2000	**−361.5**	**−435.8, −287.9**
2006	**−197.9**	**−253.1, −142.6**
2007	**−172.0**	**−224.2, −119.2**
2008	**−90.2**	**−142.8, −38.2**
2009	**−164.3**	**−216.1, −112.5**
2019	29.5	−29.1, 87.5

Table 2
Parameter estimates of the linear mixed model testing the influence of year, date and their interaction on adjusted body mass of greater snow geese. *Date*(*2020*) is the average daily increase in body condition (g/d) in May 2020. The interactions *date : 2007–2009* and *date : 2019* represent differences in daily increase in body condition between 2020 and 2007–2009 or 2019, respectively. Significant effects are in bold. Model parameters other than effects of interest are in pale gray ($n = 2616$).

Effect	Estimate	95% CI
2020 (intercept)	3718.3	2465.6, 4970.9
2007–2009	−2374.5	−3680.1, −1104.5
2019	−2010.2	−3595.6, −424.7
Date (2020)	−5.5	−14.8, 3.8
Date * 2007–2009	**16.8**	**7.4, 26.6**
Date * 2019	**15.3**	**3.4, 27.2**

3.3. Habitat use

During the COVID19 lockdown, the relative use of agricultural fields by geese in the late staging period was reduced by 57% on average, as the proportion of locations in this habitat decreased from 0.49 [0.35, 0.63] in 2019 to 0.21 [0.12, 0.30] in 2020 (Fig. 2). Geese thus spent more time in agricultural fields during daytime in the 2 to 3 weeks preceding departure for migration in 2019 compared to 2020, and conversely less time in tidal marshes. Strikingly similar results were obtained when data from all GPS-marked individuals are analyzed (see Appendix E).

4. Discussion

We took advantage of the unplanned COVID19 lockdown and the ensuing reduction in hunting and scaring activities in southern Québec to opportunistically evaluate the impact of reduced disturbance on goose body condition and habitat use. By comparing body condition near the end of staging in 2019 and 2020 to historical information, we found that body condition in those two years was the highest since the implementation of the spring Conservation Harvest. However, our results suggest that body condition plateaued earlier in 2020 than in 2019, as it was already maximum at the onset of our captures at the beginning of May. This sets 2020 apart from 2019 where body condition was also high but increased throughout the capture period as observed in other years. Finally, geese spent less time in agricultural fields near the end of staging in 2020 compared to 2019. Taken together, our results suggest that the reduction of hunting- and scaring-related disturbance during the COVID19 lockdown allowed geese to build fat reserves faster and

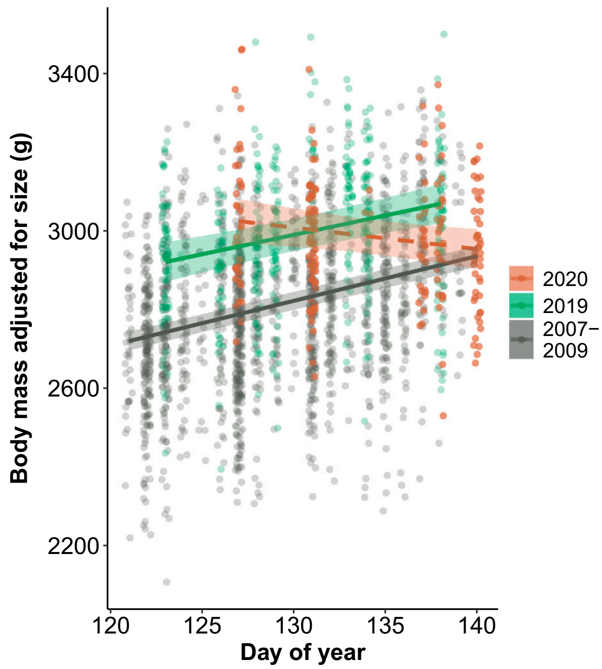

Fig. 5. Body condition index (mass corrected for body size) of greater snow geese in relation with date for 2019 (green), 2020 (orange) and years with a spring Conservation Harvest and sampling dates comparable to 2020 (2007–2009; gray). Lines are the mean model predictions with their 95% CI (shading) and represent the increase in goose body condition at the end of their migratory stopover in Québec. Full lines represent significant relationships and the dashed line a non-significant relationship (2020). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

reach an optimal body condition for their northward migration earlier than in previous years, which led to a change in habitat use near the end of staging.

4.1. Body condition

Body condition was particularly high in spring 2020, among the highest in our historical data and higher than all years with a spring Conservation Harvest, except 2019. Because of the known effect of disturbance on goose foraging behavior (Béchet et al., 2004; Klaassen et al., 2006; Nolet et al., 2016), the low hunting pressure in 2020 likely contributed to the high spring body condition of birds in that year and probably also in 2019. Indeed, even though harvest was lower in 2020 than in 2019, it was already moderate in the latter year, being 35% lower than the average harvest of the preceding decade (Fig. 3A). Previous studies showed that geese collected on the spring staging grounds in the first two years following the implementation of the spring Conservation Harvest (1999 and 2000), when hunting pressure was at its maximum, had considerably reduced fat and protein stores compared to years without hunting (Féret et al., 2003). Our results thus further reinforce previous conclusions that spring hunting affects dynamics of nutrient storage in this species by clearly showing that the body condition of geese at the end of the staging period is affected by the intensity of the spring hunting activity. Therefore, it is not surprising that body condition in spring 2020 was comparable to that observed before the implementation of the spring Conservation Harvest.

However, other factors than hunting disturbance can also affect body condition of spring-staging geese. One factor is weather conditions during spring staging, which may affect timing of snowmelt and the onset of plant growth in farmlands. For instance, the springs of 2019 and 2020 were both cool with a late snowmelt (Fig. C.1), conditions that generally benefit geese because plants grow more slowly and remain more nutritious (i.e. more protein and less indigestible fiber) for a longer period in spring (Bédard and Gauthier, 1989; Manseau and Gauthier, 1993). These conditions may thus also have contributed to the high body condition of geese in both 2019 and 2020. Presence of juveniles in spring may cause intra-family competition and interfere with foraging activity of their parents (Turcotte and Bédard, 1989). In spring 2019, there were very few juvenile birds in the population (2.5% of captured birds were juveniles) due to a widespread breeding failure of geese in 2018, whereas the opposite situation prevailed in spring 2020, with many juveniles in the population (22.1% of captured birds were juveniles). This factor may have facilitated fattening of geese in spring 2019 compared to 2020 and could explain why body condition at the end of the staging period was similar in both years despite a higher hunting pressure in 2019. An alternative explanation for the high condition of geese reached early in the season in 2020 could be that they arrived from the US wintering grounds already in high condition prior to the onset of the lockdown. However, observations of abdominal profiles of geese in 2020, a reliable index of goose body condition (Féret et al., 2005), allowed us to refute this explanation (Appendix F). Indeed, observations spanning the entire spring staging period (late-March to mid-May) revealed that geese arrived in Québec in low body condition and fattened considerably throughout the COVID19 lockdown period (Fig. F.1), which is a typical pattern for geese in spring (Gauthier et al., 1992).

4.2. Habitat use

The most likely explanation for the high body condition of geese reached earlier in 2020 than in any other year is improved foraging in farmlands early in the staging period, when the lockdown restrictions were most severe. Indeed, geese were likely able to complete longer, undisturbed foraging bouts and maximize their foraging efficiency in farmlands in early spring 2020 due to reduced disturbance (Béchet et al., 2004). Farmlands are a high-quality feeding habitat for geese because they feed on spilled grain and young shoots. These are more profitable food items than rhizomes, their primary food source in tidal marshes in spring, which are difficult and costly to extract from the ground (Bédard and Gauthier, 1989; Dokter et al., 2018; Pot et al., 2019). Nonetheless, farmlands undoubtedly remained a risky habitat for geese in 2020 because, unlike tidal marshes, hunting and scaring activity still occurred there, albeit at a reduced rate. This is why we expected that, if geese were able to complete their fattening earlier during the lockdown, they should reduce their time spent feeding in farmlands and spend more time resting in the tidal marshes near the end of staging. This pattern is exactly what we observe. Indeed, contrary to 2019 when geese heavily used farmlands and continued to gain condition until the end of staging, in 2020 they reduced considerably their use of farmlands after reaching a high body condition. It is also possible that, as travel restrictions within Québec started to be lifted in May, more hunting activity took place at the end of staging than at the beginning. This could have further encouraged geese to spend less time in farmlands and more time in marshes in late spring. Unfortunately, we do not have data on the temporal pattern of hunter activity in spring to test this idea. In summary, the high body condition of birds reached early in spring 2020 may have shifted the trade-off between food acquisition in a risky habitat (agricultural fields) and safety (natural marshes) at the end of staging, leading to the observed reduction of time spent in the former habitat.

4.3. Limitations

The data presented in this study was not collected with the objective of comparing seasonal variations in body condition or habitat used by geese, and the effects uncovered here should therefore be interpreted cautiously. There is much inter-individual and inter-annual variation in goose body condition, likely influenced by factors such as weather conditions in winter and presence of young in the population. Because the COVID19 lockdown is a punctual event, its effect is partly confounded with the year effect. Moreover, it is also possible that geese have habituated to hunting activity in spring since its implementation 20 years ago and have modified their behavior accordingly. However, the clear relationship between body condition and hunting pressure shown in our results supports the conclusion that the lockdown-related reduction in hunting and scaring disturbance affected dynamics of nutrient storage in spring-staging snow geese.

Start of field work was delayed in 2020 due to the special authorizations required during the lockdown, which resulted in a reduction in the number of captures ($n = 6$ vs. 9–15 between 2006 and 2019) and slightly later capture dates. There was thus little overlap in dates between 2020 and some other years with body condition data (e.g. 1999, 2000 and 2006; Fig. A.1), making the comparison between these years challenging. To account for this, we restricted the analysis on body condition increase to years with similar capture dates and we only compared overall body condition after adjusting for the effect of sampling date.

In spring 2019, tracked geese had recently been fitted with GPS-GSM collars for the period considered in our habitat use analysis. While we excluded the first day after collars were fitted from our analysis, collars may affect behavior in the first few weeks after being fitted on a bird, for example by increasing preening or head-shaking to get rid of the collar (Kölzsch et al., 2016). Still, this should have little impact on the habitat use pattern of individuals in this gregarious species because they mostly commute between marshes and farmlands in large groups. Moreover, restricting the analyses to only birds tracked in both 2019 and 2020 or using all birds yielded identical results, suggesting that our habitat use data were robust.

Data collected in the upcoming years will provide the opportunity to revisit the conclusions of this paper with a before-after impact design (Osenberg and Schmitt, 1996). According to the mechanisms proposed here, if disturbance due to hunting and scaring increases in the future relative to 2020, foraging efficiency in agricultural land should decrease and lead to a new reduction in body condition.

5. Conclusion

The overabundance of snow geese has been shown to negatively affect plant communities through overgrazing in several regions (Jano et al., 1998), as well as other arctic-nesting species through apparent competition (Lamarre et al., 2017). These effects played an important role in the decision of liberalizing hunting regulations to limit the growth of this population (Lefebvre et al., 2017). Moreover, goose overabundance was the source of important conflicts with farmers, who suffer depredation losses to geese in Québec. Following the establishment of the special spring Conservation Harvest in 1999, production of young was reduced, and population growth stopped (Lefebvre et al., 2017). Taking advantage of a release in hunting pressure associated with the COVID19 lockdown in 2020, our results, combined with long-term data on harvest and body condition, show that spring hunting activity still negatively impacts the body condition of spring staging geese twenty years after its implementation. Our study provides useful insights for the management of this overabundant population. Indeed, the high body condition achieved by geese due in part to reduced hunting activity during the COVID19 lockdown may improve reproductive success and lead to high recruitment of young, thereby fueling additional population growth. At a broader level, our study further emphasizes that sustained human disturbance during a critical period of the life cycle, i.e. spring staging, interferes with the nutrient storage dynamics of a long-distance migrant even after being exposed to these sources of disturbance for more than two decades. This suggests no or little long-term habituation, which may have consequences for the reproduction and ultimately the population growth of species exposed to such disturbances.

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CRediT authorship contribution statement

Frédéric LeTourneux: Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Visualization **Thierry Grandmont**: Conceptualization, Writing – Review & Editing, Visualization **Frédéric Dulude-de Broin**: Conceptualization, Methodology, Formal Analysis, Investigation, Writing – Review & Editing, Visualization **Marie-Claude Martin**: Investigation, Resources **Josée Lefebvre**: Writing – Review & Editing **Akiko Kato**: Resources, Writing – Review & Editing **Joël Bêty**: Conceptualization, Writing – Review & Editing **Gilles Gauthier**: Conceptualization, Writing – Review & Editing, Supervision **Pierre Legagneux**: Conceptualization, Methodology, Investigation, Writing – Review & Editing, Visualization, Supervision, Project Administration, Funding acquisition.

Declaration of competing interest

The authors declare they have no known competing interests, financial or otherwise that have influenced the contents of this paper.

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