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Harvest, Survival, and Abundance of Midcontinent Lesser Snow Geese Relative to Population Reduction Efforts

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ABSTRACT We assessed the effectiveness of an extensive and unprecedented wildlife reduction effort directed at a wide-ranging migratory population of geese. Population reduction efforts that targeted several populations of light geese (greater snow geese [*Chen caerulescens atlantica*], lesser snow geese [*C. c. caerulescens*], and Ross's geese [*C. rossii*]) began in 1999 in central and eastern North America. Such efforts were motivated by a broad consensus that abundance of these geese was causing serious ecological damage to terrestrial and salt marsh ecosystems in central and eastern parts of the Canadian Arctic and subarctic regions along Hudson Bay. Starting in February 1999, special conservation measures (or, in the U.S., a conservation order) were added to the respective federal regulations that permitted hunters to take snow geese (in parts of Canada and the U.S.) and Ross's geese (in parts of the U.S.) during specified harvest periods outside of the hunting season. These measures were accompanied by increase or removal of daily kill and possession limits and by permissions to use previously prohibited equipment for hunting these species in certain regions of the continent. The intent was to reduce adult survival through increased hunting mortality, which was judged to be the most cost-effective approach to reversing population growth. Our principal goal was to assess the effectiveness of reduction efforts directed at the midcontinent population of lesser snow geese, which was thought to be the most serious threat to arctic and subarctic ecosystems of the 3 light goose populations. Our multiple objectives included the estimation and detection of change in the response measures of total annual harvest, harvest rate, survival rate, and abundance, using the 1998 hunting period (defined as 1 Aug 1998 to 31 Jul 1999) as a point of reference. We used information about hunter recoveries of leg-banded snow geese and estimates of regular-season harvest to estimate 1) conservation-order harvest and total annual harvest, 2) geographic and temporal distribution of recoveries by age class, 3) survival and recovery probability, and 4) abundance of snow geese each August using Lincoln's (1930) method. We also modeled population growth to infer the form of population response to management efforts. Toward that end, we also proposed a method of estimating conservation-order harvest and tested for differences in band-reporting rate between Canada and the United States. Overall, the balance of evidence favored the conclusion that the midcontinent population has continued to grow during the conservation order, although perhaps at a reduced rate. We suggest that annual rate of population growth ($\hat{\lambda}$), derived from estimates of annual population size in August, likely provides the most reliable inference about change in the midcontinent population. There was a decline in annual survival probability between these 2 periods from about 0.89 to about 0.83 among snow geese from the southern-nesting stratum (south of 60°N latitude), thought to compose about 10% of the midcontinent population. However, we detected no change in the much larger northern-nesting stratum (north of 60°N latitude), where annual survival remained at about 0.87 from 1989 to 2006. Thus, the conclusion that this population continued to increase during the conservation order was largely consistent with the finding that a weighted-survival probability for midcontinent snow geese essentially did not change between the period preceding (1989–1997) and during (1998–2006) the conservation order. Consistent with high survival rates were low harvest rates, which increased from 0.024 during 1989–1997 for northern geese to only 0.027 during 1998–2006 and from 0.031 to only 0.037 for southern geese. Despite the initial increase associated with the conservation order, harvest rates declined during the conservation order for geese from both strata. We suggest that the higher harvest rate evident for

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southern geese was related to their earlier fall migration and thus earlier exposure to harvest pressure. Migration by more abundant northern geese was later and resulted in a higher ratio of geese to hunters. Additionally, there was more harvest of southern geese in areas north of the Canadian prairies than there was of northern geese. Total annual harvest increased due to the conservation order but failed to exceed 0.75 million adults in any year during the assessment from 1989 to 2006. Harvest of both age classes exceeded 1 million in only 2 of 9 annual harvest periods since the conservation order started. These lower-than-expected harvests of adult snow geese combined with their low harvest rates of ≤ 0.048 during the conservation order suggested an August population size in excess of 15 million adult snow geese since 1998. We suggest that abundance of midcontinent snow geese was seriously underestimated in the past, and that this underestimate may have contributed to an overconfidence with which suggested harvest levels could achieve a goal of reduced survival and population reduction. Overall, all 3 populations of light geese now exceed numbers present when the conservation order was initiated. We are confident that the abundance and population growth rate of midcontinent snow geese (as well as by Ross's and greater snow geese) currently exceeds the ability of existing numbers of hunters to exert harvest pressure that is necessary to impose sufficient additive mortality and thus effectively influence population growth. It remains unknown how much more or how much longer such populations can increase towards carrying capacity, which we assume to be determined by the standing crop of arctic foods that they exploit, before density dependence can measurably slow the population growth rate. Estimation of carrying capacity in the large northern nesting stratum is among the key research needs that we propose. The situation that has emerged requires a review of perspectives about impacts of midcontinent lesser snow geese in the arctic, whether initial goals behind population management are still relevant, and whether alternative options from the initial array of management tools should be exercised.

KEY WORDS arctic ecosystems, band-recovery models, harvest management, midcontinent lesser snow geese, population dynamics, population growth, Ross's geese, survival.

Récolte, Survie et Abondance de la Petite Oie des Neiges du Milieu du Continent en Relation avec les Efforts de Réduction de la Population

RÉSUMÉ Nous avons évalué l'efficacité d'un effort étendu et sans précédent de réduction d'une espèce sauvage, une population migratrice d'oies occupant une large étendue géographique. Les efforts de réduction de populations ciblant plusieurs populations d'oies blanches (grande oie des neiges, *Chen caerulescens atlantica*, petite oie des neiges, *C. c. caerulescens*, et oie de Ross, *C. rossii*) ont débutés en 1999 dans le centre et l'est de l'Amérique du Nord. Ces efforts étaient justifiés par un consensus élargi à l'effet que ces oies causaient des dommages écologiques aux écosystèmes terrestres et de marais salés dans les régions centrales et orientales de l'Arctique Canadien ainsi que dans les régions subarctiques le long de la Baie d'Hudson. À partir de 1999, des mesures de conservation spéciales (décret de conservation aux É.U.) furent ajoutées aux règlements fédéraux respectifs qui permettaient aux chasseurs de récolter des oies des neiges (dans certaines régions du Canada et des É.U.) et des oies de Ross (dans certaines régions des É.U.) pendant des périodes de récolte spécifiques, hors de la saison de chasse. Ces mesures étaient accompagnées d'une augmentation ou de l'élimination des limites de prises quotidiennes et de possession, ainsi que l'autorisation d'utiliser des engins de chasse précédemment prohibés pour la chasse de ces espèces dans certaines régions du continent. L'intention était de réduire la survie des adultes par l'entremise d'une augmentation de la mortalité par la chasse, approche jugée comme étant la plus efficace pour inverser la croissance de la population. Notre objectif principal était d'évaluer l'efficacité des efforts de réduction dirigés vers la population de la petite oie des neiges du milieu du continent, qui était considérée come étant la plus grande menace aux écosystèmes arctiques et subarctiques des 3 populations d'oies blanches. Les multiples objectifs de ce manuscrit incluent l'estimation et la détection de changements dans les mesures de récolte annuelle totale, de taux de récolte, de taux de survie et d'abondance, utilisant la période de chasse de 1998 (définie comme étant du 1 août 1998 au 31 juillet 1999) comme point de référence. Nous avons utilisé de l'information sur les retours, par les chasseurs, de bagues d'oies des neiges ainsi que des estimés de la récolte durant la saison régulière pour estimer: (1) la récolte pendant les périodes du décret de conservation et la récolte annuelle totale, (2) la distribution temporelle et géographique des retours de bagues par classe d'âge, (3) la survie et la probabilité de retour de bague et (4) l'abondance des oies des neiges à chaque mois d'août en utilisant la méthode de Lincoln (1930). Nous avons aussi modélisé la croissance de la population afin de déduire la forme de la réponse de la population aux efforts de gestion. À cette fin, nous avons aussi proposé l'utilisation d'une méthode pour estimer la récolte pendant les périodes couvertes par le décret de conservation et avons testé pour des différences dans les taux de signalement de bagues entre les États-Unis et le Canada. Dans l'ensemble, l'évidence suggère que la population du milieu du continent a continué de croître durant la période du décret de conservation, mais possiblement à un taux moins élevé. Nous suggérons que le taux de croissance de la population, $\hat{\lambda}$, estimé à partir des estimés de taille de population annuelle en août, prodigue probablement les inférences les plus fiables sur les changements dans la population du milieu du continent. Il y a eu un déclin de la probabilité de survie annuelle entre ces deux périodes, d'environ 0,89 à environ 0.83, pour les oies des neiges nichant dans la strate sud (sud de la latitude 60°N) et qui représentent environ 10% de la population du milieu du continent. Par contre nous n'avons détecté aucun changement dans la plus imposante strate nordique (nord de la latitude 60°N) où la survie annuelle est demeurée aux environs de 0.87 pour la période 1989 à 2006. La conclusion que cette population a continué d'augmenter pendant la période du décret de conservation concorde avec le résultat qui indique que la probabilité de survie pondérée pour l'ensemble de la population du milieu du continent n'as pas changé entre la période précédent (1989–1997) et celle durant (1998–2006) le décret de conservation. Les taux de survie élevés concordaient avec de faibles taux de récolte, qui ont augmenté de 0.024 pendant 1989–1997 pour les oies de la strate nord à seulement 0.027 pendant 1998–2006, et de 0.031 à seulement 0.037 pour les oies de la strate sud. Malgré une augmentation initiale associée au décret de conservation, les taux de récolte ont déclinés pendant la période couverte par le décret de conservation dans les deux strates. Nous suggérons que les taux de récolte plus élevés pour les oies de la strate sud sont dus à leur migration automnale plus hâtive, ce qui les exposerait plus tôt à la pression de chasse. La migration des oies de la strate du nord, plus abondantes, avait lieu plus tard et résultait en un ratio d'oies par chasseurs plus élevé. De plus, il y avait une plus grande récolte d'oies de la strate sud dans les secteurs au nord des prairies Canadiennes que pour les oies de la strate nord. La récolte annuelle totale a augmenté suite au décret de conservation mais n'as excédé 0.75 million d'adultes dans aucune des années utilisées dans l'évaluation, soit de 1989 à 2006. La récolte des deux classes d'âge à dépassé 1 million pour seulement 2 périodes de récolte annuelles sur 9 depuis la mise en place du décret de conservation. Cette récolte plus faible que prévue d'oie des neiges adulte et le faible taux de récolte de $\leq$ 0.048 pendant la période du décret de conservation laisse croire que la population, mesurée au mois d'août, aurait été de plus de 15 millions d'adultes depuis 1998. Nous suggérons que l'abondance de la population d'oie des neiges du milieu du continent a été sérieusement sous-estimée dans le passé et que cette sous-estimation pourrait avoir contribué à un sentiment de sur-confiance envers le fait que les niveaux de récolte pourraient mener à l'atteinte de l'objectif de diminution de la survie et réduction de la population. Les 3 populations d'oies blanches ont maintenant des populations plus grandes que lors de la mise en place du décret de conservation. Nous somme convaincus que l'abondance et le taux de croissance actuel de la population d'oie des neiges du milieu du continent (ainsi que l'oie de Ross et la grande oie des neiges) dépasse la capacité des chasseurs actifs d'exercer une pression de récolte suffisante pour augmenter la mortalité additive à un niveau qui influencerait effectivement la croissance de la population. Nous ne savons toujours pas pendant combien de temps ces populations peuvent continuer de croître et approcher la capacité de support, que l'on pense déterminée par la population sur pied des plantes arctiques qu'elles exploitent, avant que des effets densité-dépendants ralentissent le taux de croissance de la population de façon mesurable. L'estimation de la capacité de support de la grande strate du nord est un des besoins clés en recherche que nous proposons. La situation qui émerge requière une revue des perspectives concernant les impacts des oies des neiges du milieu du continent dans l'Arctique, si les objectifs initiaux de gestion de la population sont encore pertinents et si d'autres options à partir de l'ensemble initial d'outils de gestion doivent être exercées.

Aprovechamiento, Supervivencia y Abundancia del Ganso Blanco del Continente Medio Relativo a los Esfuerzos Realizados para Reducir a la Población

RESUMEN Investigamos la efectividad de una iniciativa de disminución de vida silvestre bastante extensiva y sin antecedentes, dirigida a una población migratoria de gansos blancos de un amplio rango de distribución. En 1999, se iniciaron esfuerzos de disminución de poblaciones dirigidos a varias poblaciones de gansos claros (*Chen caerulescens atlantica*, *C. c. caerulescens*, y *C. rossii*) en las regiones centrales y del este de Norte América. Estos esfuerzos fueron motivados por el amplio consenso sobre la noción de que la abundancia de estos gansos estaba causando graves daños ecológicos a ecosistemas terrestres y humedales salobres en las regiones centrales y del este del Ártico Canadiense y las regiones sub-árticas a lo largo de la Bahía Hudson. Medidas especiales de conservación (definidas en E.E.U.U. como una "orden de conservación") fueron añadidas en Febrero de 1999, a las regulaciones federales respectivas, las cuales les permiten a los cazadores cazar gansos blancos (en partes de Canadá y E.E.U.U.) y gansos de la especie *C. rossii* (en partes de E.E.U.U.) durante periodos específicos de cosecha fuera de la temporada de cacería regular. Estas medidas fueron acompañadas por un aumento y/o remoción de límites de posesión y matanza diaria, al igual que permisos para utilizar equipo prohibido anteriormente para la cacería de estas especies en ciertas regiones del continente. La intención era disminuir la supervivencia de adultos por medio de un aumento en la tasa de mortalidad como resultado de la cacería, la cual fue designada como la forma más rentable para poner en marcha atrás el crecimiento poblacional. Nuestra meta principal fue asesorar la efectividad de los esfuerzos de disminución dirigidos a las poblaciones de *C. c. caerulescens* en el continente medio, la cual, de las tres poblaciones de gansos blanco, se considera que presenta la amenaza más seria a los ecosistemas árticos y sub-árticos. Los objetivos múltiples de este artículo incluyen la estimación y detección de cambios en las medidas de respuestas de cosecha anual total, tasa de cosecha, tasa de supervivencia, y abundancia, utilizando el periodo de cacería de 1998 (definido como el 1 de Agosto 1998 al 31 de Julio 1999) como el punto de referencia. Utilizamos información sobre individuos de gansos blancos anillados en una pata que fueron recuperados por cazadores y valores estimados de cosechas durante la temporada de cosecha regular, para estimar (1) cosecha durante la orden de conservación y la cosecha anual total, (2) distribución geográfica y temporal de individuos recuperados por clase de edad, (3) probabilidades de supervivencia y recuperación, y (4) abundancia de gansos blancos para cada mes de Agosto utilizando el método de Lincoln (1930). También modelamos el crecimiento poblacional para realizar inferencias sobre la forma de la respuesta poblacional a las iniciativas de manejo. Para este fin, también proponemos metodología para estimar la cosecha durante la orden de conservación y realizamos pruebas para determinar si existen diferencias entre tasas de reportaje de anillos entre Canadá y E.E.U.U. En conjunto, la evidencia favorece la conclusión de que la población del continente medio ha continuado de crecer durante la orden de conservación, aunque tal vez a una tasa más reducida. Sugerimos que la tasa anual de crecimiento poblacional, $\hat{\lambda}$, estimada a partir de valores estimados de tamaño poblacional anual en Agosto, probablemente proporcionan el nivel de inferencia más confiable sobre cambios de la población del continente medio. Tuvimos una disminución en la probabilidad de supervivencia anual entre estos dos periodos, desde alrededor de 0.89 hasta alrededor de 0.83 entre gansos blancos del estrato de anidamiento sureño (sur de 60°N latitud), los cuales se consideran que componen alrededor de 10% de la población del continente medio. No obstante, detectamos que en el estrato de anidamiento norteño (norte de 60°N latitud), cuya población es mucho más grande, no hubieron cambios, y supervivencia permaneció a valores alrededor de 0.87 desde 1989 hasta 2006. En consecuencia, la conclusión de que esta población continúo aumentando durante la orden de conservación es bastante consistente con nuestro descubrimiento que una probabilidad de supervivencia ponderada para los gansos blancos del continente medio esencialmente no cambio entre el periodo precedente (1989–1997) y durante (1998–2006) la orden de conservación. Las tasas altas de supervivencia resultaron consistentes con tasas de bajas cosecha, las cuales aumentaron de 0.024 durante 1989–1997 para gansos norteños a solo 0.027 durante 1998–2006, y de 0.031 a solo 0.037 para gansos sureños. A pesar del aumento inicial asociado con la orden de conservación, tasas de cosecha disminuyeron durante la orden de conservación para gansos de ambos estratos. Sugerimos que las tasas de cosecha elevadas que fueron evidentes en gansos sureños estaban relacionadas a su época de migración más temprana durante el otoño, y por ende, estos fueron expuestos a una presión de cosecha más temprano. La migración de los gansos norteños más abundantes se realizo después y resulto en una proporción más alta de gansos a cazadores. Adicionalmente, se cosecharon más gansos sureños en regiones ubicadas al norte de las praderas de Canadá que se cosecharon gansos norteños. La cosecha total anual aumento a causa de las acciones de conservación, pero falló en exceder los 0.75 millones de adultos para cualquier año al que este fue asesorado, del 1989 al 2006. La cosecha de ambas clases de edades excedió 1 millón para solo 2 de los 9 periodos de cosecha desde que la orden de conservación inició. La combinación de una cosecha de adultos de ganso blanco por debajo de lo esperado y las bajas tasas de cosecha de ≤ 0.048 durante la orden de conservación nos indican que hemos tenido un exceso de 15 millones de gansos blancos sobre el tamaño poblacional para el mes de Agosto desde 1998. Sugerimos que la abundancia de gansos blancos del continente medio fue seriamente subestimada en el pasado, y que esta subestimación posiblemente contribuyo al exceso de confianza que se tuvo de que los niveles de cosecha sugeridos podrían lograr los objetivos de disminuir supervivencia y reducir la población. En general, las tres poblaciones de gansos blancos en este estudio ahora exceden las cantidades presentes cuando la orden de conservación inició. Estamos confidentes de que la abundancia y la tasa de crecimiento poblacional del ganso blanco del continente medio (al igual para *C. c. atlántica* y *C. rossii*) actualmente exceden la presión de cosecha que puede ejercer la cantidad de cazadores existentes requerida para imponer niveles suficientes de mortalidad aditiva, y por ende, influir efectivamente niveles de crecimiento poblacional. Todavía no sabemos que tanto mas podrían aumentar dichas poblaciones hacia la capacidad de carga, ni por cuanto más tiempo, lo cual presumimos que se podría determinar basándose en la cantidad existente de fuentes alimenticias en el ártico que ellos puedan explotar, antes de que la dependencia de densidad pueda reducir la tasa de crecimiento poblacional. La estimación de la capacidad de carga del amplio estrato de anidamiento ubicado en el Norte es justo uno de los objetivos claves de investigación que proponemos. La situación que tenemos antemano requiere de un repaso de las perspectivas sobre los impactos de *C. c. caerulescens* del continente medio, determinar si los objetivos de manejo de poblaciones iniciales todavía son relevantes, y ver si debemos optar por opciones alternativas que no son parte del conjunto inicial de herramientas de manejo.

Contents

INTRODUCTION

Population management goals frequently include attainment of a desired abundance or, for exploited populations, a sustainable level of harvest (Williams et al. 2001). The practice of wildlife management has historically included efforts to manipulate population size either to enhance or to reduce abundance of a species (Giles 1971). Although a common issue for wildlife management, species overabundance is a new dilemma for conservation biologists. It had received little attention from the conservation biology community (Garrott et al. 1993) perhaps because actions required to reduce populations often are either lethal or highly intrusive (e.g., culls, relocation, contraception).

Designation of a species as overabundant is inherently difficult because it often rests on subjective principles of what determines properly functioning ecosystems as well as socio-economic considerations. Caughley (1981) recognized 4 categories to which the term overabundance could refer in an animal population: 1) when animals threaten human life or livelihood, 2) when animals depress the densities of favored species, 3) when animals are too numerous for their own good, and 4) when their numbers cause ecosystem dysfunction. There are now many examples of native and exotic species that have increased in abundance and distribution to the point where they match ≥1 of Caughley's categories and are viewed as overabundant. Among native species with populations that had expanded to overabundant levels, most are generalists that have benefited from anthropogenic modifications of their habitats leading to reduced levels of predation, increased protection through the establishment of refuges, or increased access to agricultural foods. Although often controversial to the general public and even within the wildlife management and conservation communities, Garrott et al. (1993) implied that goals of both communities can be similar and recommended that conservation biologists confront the sensitive issues of controlling and manipulating populations of native species to reverse negative effects of overabundance.

Waterfowl management in North America has faced challenges of species overabundance for the first time at large scales within the last decade and a half. Traditionally, waterfowl managers have focused their efforts on maintaining or enhancing population growth, rather than population reduction. This philosophy has been confronted by rapid increases in abundance of many North American goose populations, which motivated a seminal paper by Ankney (1996). Ankney (1996) challenged the waterfowl management community to consider appropriate population levels and to expand thinking about short-term population control of geese in the interests of long-term conservation. The challenge of exponential growth in North America by snow geese (*Chen caerulescens*) and Ross's geese (*C. rossii*), and indications of density-dependent effects on arctic and subarctic habitats, motivated review and deeper analysis by the Arctic Goose Habitat Working Group of population growth in these species (Batt 1997, 1998; Moser 2001).

The first review, summarized by Batt (1997), focused on overabundance of lesser snow geese (*C. caerulescens caerulescens*, hereafter snow geese) and led to a prescription for conserving arctic ecosystems that included recommendations for increased harvest to reduce population density on arctic nesting areas. Specific recommendations related to population management that were to be implemented under an Arctic Goose Management Initiative (Batt 1997:118–119) included 1) "proactive population reduction measures to reduce midcontinent white goose populations to a level of about 50% of current numbers by the year 2005," 2) "population growth rate be reduced to an annual level of between 0.85 and 0.95 . . . from the current growth rate of about 1.05," and 3) "harvest rate should be increased to about 3 times the current level." In 1997, harvest was about 0.73 million midcontinent snow geese (see below), so the de facto harvest goal was 2.2 million annually.

These recommendations were based largely on scenarios about the assumed interplay between harvest rate and survival probability with resulting population projections conducted by Rockwell et al. (1997), who used up-to-date information at the time of their analyses. Because of incomplete information from the entire breeding range of midcontinent snow geese in Canada's central and eastern arctic and subarctic around southern Hudson Bay, population analyses by Rockwell et al. (1997) were based on assumptions about annual rate of population change (λ) of 1.05 (i.e., approx. 5% per yr). This growth rate was inferred from winter counts of light geese conducted in the midcontinent and also projected from data about recruitment and survival gathered during 1973–1984 from the snow goose colony at La Pérouse Bay, Manitoba. Rockwell et al. (1997:83), although careful to note that these estimates "may not be applicable to the entire midcontinent population," concluded that they still seemed "generally applicable."

Assuming an adult-survival probability of 0.88 for the midcontinent population (estimated by Francis et al. (1992) from southern-nesting snow geese captured along south Hudson Bay), Rockwell et al. (1997) predicted that reductions in probability of adult survival to between 0.71 and 0.73 would result in a declining midcontinent population of snow geese with $\lambda = 0.85$. Implicit in their analysis was that, for population stationarity of $\lambda \approx 1.0$, annual adult survival would need to decline to approximately 0.84; for $\lambda \approx 0.95$, annual adult survival would need to be approximately 0.795. Further assuming full controllability (cf. Williams et al. 1996) at increasing harvest and kill rates, and that all harvest of midcontinent snow geese was additive to natural mortality (i.e., in the absence of harvest), Rockwell et al. (1997) predicted that harvest necessary to achieve a survival rate of 0.795 required a 3-fold increase from average harvest estimated during 1985–1994 (i.e., from approx. 305,000 adults and young to approx. 915,000 adults and young annually). It was thought that 3–7 years of such increased harvest would reduce the midcontinent population to 50% of its level (at the time of analysis).

Subsequently, Cooke et al. (2000) conducted updated analysis of survival and recovery rates of midcontinent snow geese marked with legbands in arctic Canada. In addition, Cooke et al. (2000) reviewed and challenged several assumptions underpinning the model constructed by Rockwell et al. (1997). Cooke et al. (2000) pointed out that annual adult survival rate (>0.90) was higher than assumed (0.88) and doubted that kill rates and harvest rates could be high enough to affect population growth sufficiently. Using updated estimates of these parameters, Cooke et al. (2000) suggested that total harvest would need to be between 1.5 and 3.4 million snow geese to result in an annual negative population change corresponding to $0.85 \leq \lambda \leq 0.95$, about 5–10 times contemporary harvest. Addressing controllability of harvest (i.e., harvest response to changes in regulations; cf. Williams et al. 1996), Rockwell and Ankney (2000:34) were "confident that, given the opportunity, hunters can easily exceed a revised target harvest of 1.41 million snow geese, especially in the first several years of this endeavor."

Snow and Ross's geese (collectively referred to as light geese) in the midcontinent region are managed in aggregate. They share similar distributions, life histories, and probabilities of harvest and are difficult to differentiate when in large aggregations during aerial monitoring programs or winter counts, or more generally by hunters (Alisauskas 2001). Waterfowl managers responded to rapidly increasing abundance of light geese by incrementally liberalizing hunting regulations during regular seasons from 1989 to 1997 (Alisauskas et al. 2006*a*). For example, Central and Mississippi Flyway states extended their regular seasons for hunting light geese to 10 March in 1996 (the last date allowable under the Migratory Bird Treaty [1916] between Canada and the United States), as well as increasing possession limits to 3–4 times the daily harvest limit allowable per hunter. However, continued growth of these goose populations, increased knowledge regarding light goose degradation of ecosystems, and growing agricultural depredation concerns (Abraham and Jefferies 1997) prompted additional action, as recommended under the Arctic Goose Management Initiative (Batt 1997). Due to concern for arctic ecosystems, the Canadian Wildlife Service and United States Fish and Wildlife Service implemented new regulations in 1999, under articles of the 1916 Migratory Bird Convention, specifically intended to reduce population growth of midcontinent light geese. These regulations allowed the take (harvest) of snow geese and Ross's geese, under certain conditions, with several new methods (e.g., unplugged shotguns, electronic calls, no daily harvest or possession limit) and outside the traditional hunting framework period (1 Sep to 10 Mar).

We focused specifically on an assessment of response in survival probability of adult snow geese, because that was a key objective of range-wide management efforts. We considered juvenile survival to be a component of recruitment to adulthood and suggest that it merits full but separate treatment elsewhere with other components of recruitment, including fecundity and breeding probability. Thus, our objectives were to 1) estimate annual harvest of midcontinent snow geese since 1988, both during the regular season and resulting from the conservation order in the United States or from spring conservation harvest in Canada, 2) assess whether annual survival was negatively related to annual harvest of snow geese, 3) determine whether probability of annual survival had declined since initiation of additional harvest opportunities starting in 1998–99, and 4) evaluate evidence that either population abundance or annual rate of growth of midcontinent snow geese had declined.

STUDY AREA

Our goals in selecting data for survival estimation were to include sufficient information both before and after the beginning of concerted efforts to reduce the midcontinent population of lesser geese that began in 1998 and 1999 and to represent the known range of its nesting distribution. This population nested in Canada's central and eastern arctic with the largest known aggregations in areas adjacent to Queen Maud Gulf, eastward to the Great Plain of the Koukjouak on southwest Baffin Island, as well as north, west, and south of Hudson Bay (Fig. 1; Cooke et al. 2000, Kerbes et al. 2006). This latitudinal range of snow goose nesting was accompanied by great variation in climate, nesting chronology, habitat quality, and migration distance to midcontinent wintering areas, all of which may have caused

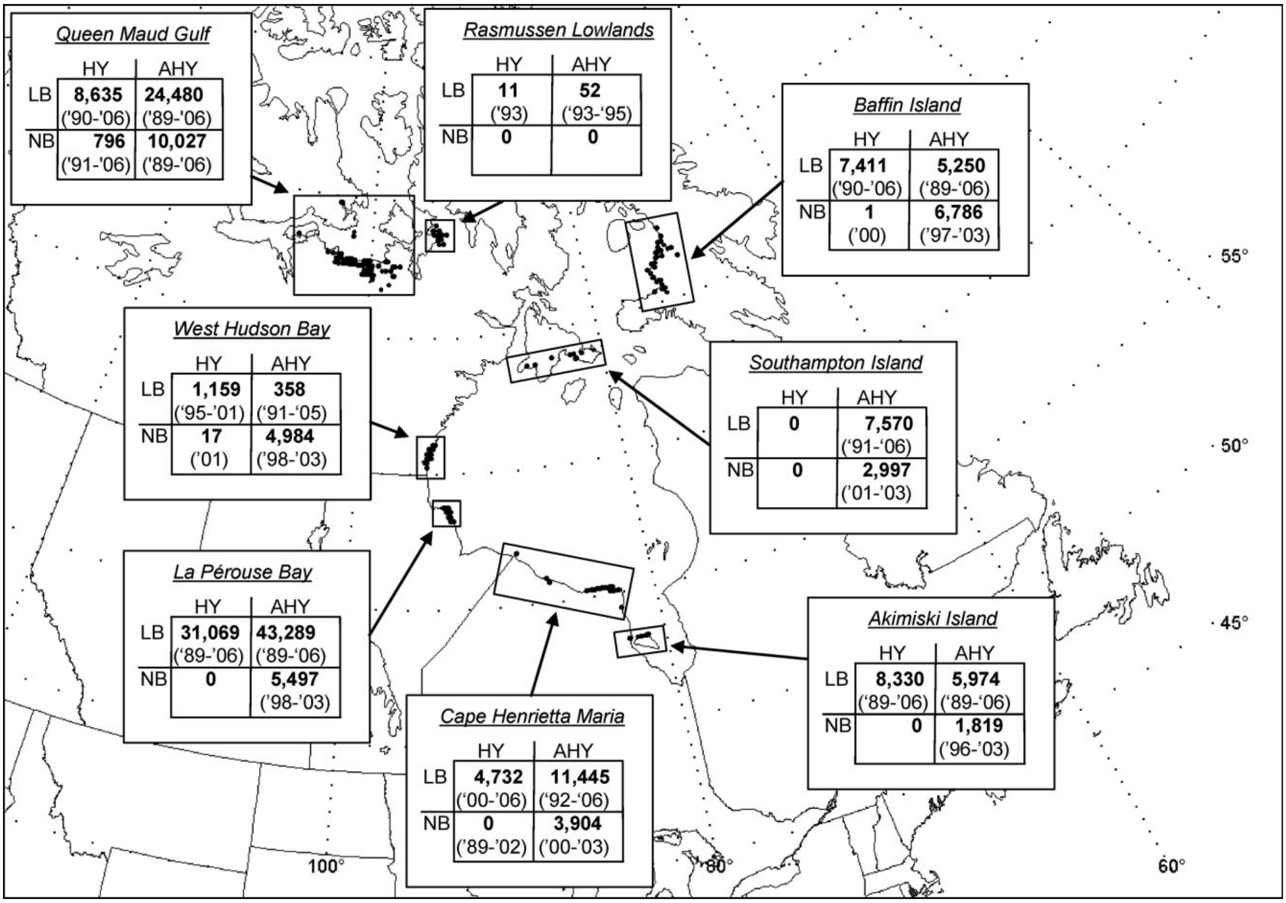

Figure 1. Distribution of marking effort for midcontinent snow geese in Canada's central and eastern arctic and subarctic, 1989–2006. Shown are numbers of juveniles (HY, hatch year, i.e., <1 year old) and adults (AHY, after-hatch year, i.e., >1 year old) marked with legbands only (LB) or with legbands and neckbands (NB); below each quantity is the range of calendar years during which marking occurred at each region.

range-wide variation in nonhunting and possibly hunting mortality. Despite this wide latitudinal distribution (Fig. 1), Kerbes et al. (2006) estimated that nesting areas north of 60°N latitude contained 90% of breeding midcontinent snow geese in 1997–1998 compared to 10% along southwest Hudson Bay in Manitoba and Ontario (Fig. 2). Our term midcontinent snow geese includes geese traditionally defined by North American waterfowl managers as the Midcontinent Population and Western Central Flyway Populations of light geese, based on their winter distributions. We believe that breeding-area affiliations are more biologically meaningful than those during winter, but readers should note that our treatment includes geese of both of these previously defined management populations.

METHODS

Migration and Recovery Phenology and Distribution

We reviewed marking and recovery information from the Bird Banding Laboratory for lesser snow geese (blue, white, and intermediate phases, i.e., American Ornithologist Union [AOU] codes of 1690–1695) marked in June, July, or August in the Canadian arctic east of 110°W longitude and between 53°N and 71°N latitude from 1989 to 2006. Banding origin initially was classified into 8 distinct regions (Fig. 1) until 1995, after which data from Rasmussen Lowlands (Table 1) were combined with Queen Maud Gulf data.

As a first step, we summarized banding data (Fig. 1) according to banding origin, whether geese were marked in their hatch year (HY, i.e., as juveniles) or after-hatch year (AHY, as adults) and whether they were marked with legbands only (LB) or with legbands and neckbands (NB). We included birds marked with reward bands from 2003 to 2005 in analyses for survival estimation; however, we did not use reward bands for population estimation using Lincoln's method (see below). Note that marking effort was disproportionately focused in the southern stratum (Table 1); southern snow geese constituted an average of 65% of the banded sample per year although they composed only 10% of the midcontinent population (Fig. 2).

For recovery data, we considered only those marked birds that were shot, retrieved, and reported by hunters (i.e., "How" code = 01) to the Bird Banding Laboratory from this sample of banded birds. We considered both LB and NB snow geese for determining harvest distribution (Fig. 3). Following analyses about timing of migration by geese from these areas, we stratified banding and recovery data by northern and southern nesting origin (see below). We summarized percentage of recoveries of snow geese banded in each stratum by United States state or Canadian province. We defined hunting periods from 1 August

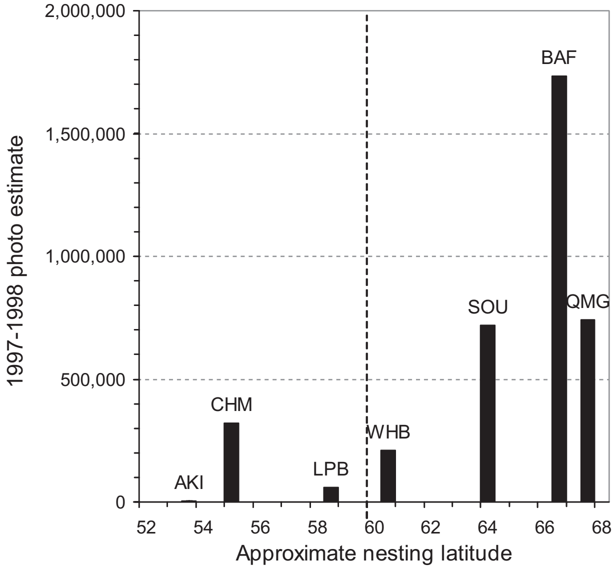

Figure 2. Variation in abundance of midcontinent snow geese known to have nested in specific regions of Canada's central and eastern arctic and subarctic (1997–1998), shown by latitude. Regions include Akimiski Island (AKI), Cape Henrietta Maria (CHM), La Pérouse Bay (LPB), Southampton Island (SOU), Baffin Island (BAF), Queen Maud Gulf (QMG), and West Hudson Bay (WHB). Estimates based on aerial photography and photo-interpretation and do not include nonnesting geese (Kerbes et al. 2006).

to 31 July (e.g., we defined the 1989 hunting period as 1 Aug 1989 to 31 Jul 1990). Any recoveries in August from northern Canada would properly be assigned to a hunting period after the main banding period during July and August in northern Canada.

We modeled variation in timing of harvest for snow geese with different origins using general linear models with PROC GLM (SAS 2003). The response variable was Julian date that marked geese were harvested (D), with origin (O = 7 regions with Queen Maud Gulf [QMG], and Rasmussen Lowlands [RAS] pooled, Table 1), marker type (M = legband vs. neckband), and age when killed (A = AHY vs. HY) as class variables, recovery latitude (L) as a covariate, and recovery period (Y) as a trend covariate. Thus, the full model included main effects and interactions among class variables {L, O, A, M, Y, O × A, O × M, A × M}. To exclude birds that had reached terminal wintering areas, we used only fall recoveries from Canada (north of 49°N latitude) and the northern United States (between 39°N and 49°N). We expected that during southward migration (i.e., before 1 Jan), recovery date would be negatively related to recovery latitude. Before analysis, we rescaled Julian date of recovery so that 1 January = 1 and dates preceding 31 December in the same hunting period were negative. Thus, band recovery dates in this set of analyses could range from −151 (1 Aug) to 212 (31 Jul). We developed 16 submodels for each set of recoveries (2,854 from Canada and 1,613 from the northern U.S.) based on variables in the full model, and we assessed the relative support for candidate models using Akaike Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002).

We assessed recovery distribution of adult geese from different banding areas after stratifying recoveries according to whether they were harvested during 1) regular seasons before initiation of the conservation order (Pre: 1989–1997), 2) regular seasons after initiation of the conservation order (Post: 1998–2006), or 3) the conservation-order harvest in the United States and spring harvest in Canada (Con: 1998–2006). This stratification allowed an evaluation of temporal changes in spatial distribution of recoveries during regular-season harvest (Pre: 1989–1997 vs. Post: 1998–2006), comparison of spatial distribution of recoveries both between regular-season harvest (Post: 1998–2006) and conservation-order or spring harvest (Con: 1998–2006), and an estimate of proportional recoveries during regular-season harvest (Post: 1998–2006) vs. conservation-order or spring harvest (Con: 1998–2006). We also examined differences in timing and location of recoveries between adult and juvenile geese to

Table 1. Numbers of adult (>1 year old) midcontinent lesser snow geese marked, 1989–2006, with legbands only (including reward and control bands) in 8 regions of Canada's central and eastern arctic and subarctic.

	Southern stratum				Northern stratum						
Year	Akimiski Island	Cape Henrietta Maria	La Pérouse Bay	Total	Baffin Island	Queen Maud Gulf	Rasmussen Lowlands	Southampton Island	West Hudson Bay	Total	Contribution of southern geese to banded sample (%)
1989	8	0	1,191	1,199	5	796	0	0	0	801	60
1990	2	0	1,650	1,652	46	580	0	0	0	626	73
1991	0	0	1,981	1,981	35	279	0	24	3	341	85
1992	0	3	3,295	3,298	36	549	0	0	0	585	85
1993	0	0	2,397	2,397	0	267	5	0	0	272	90
1994	0	216	1,512	1,728	0	769	32	0	0	801	68
1995	185	0	870	1,055	0	601	15	0	55	671	61
1996	438	0	0	438	0	155	0	0	0	155	74
1997	457	0	0	457	35	1,132	0	0	24	1,191	28
1998	705	0	1,777	2,482	10	2,181	0	0	37	2,228	53
1999	674	0	1,945	2,619	79	1,450	0	0	2	1,531	63
2000	456	1,129	7,657	9,242	63	1,378	0	0	0	1,441	87
2001	541	1,238	4,213	5,992	77	1,255	0	88	37	1,457	80
2002	582	1,066	3,778	5,426	64	1,673	0	1	0	1,738	76
2003	213	1,597	2,364	4,174	1,095	2,897	0	1,604	0	5,596	43
2004	579	2,003	3,667	6,249	791	3,356	0	1,799	0	5,946	51
2005	482	2,021	2,798	5,301	1,816	3,168	0	1,998	200	7,182	42
2006	652	2,172	2,195	5,019	1,098	1,994	0	2,056	0	5,148	49
Total	5,974	11,445	43,290	60,709	5,250	24,480	52	7,570	358	37,710	$\bar{x} = 65$

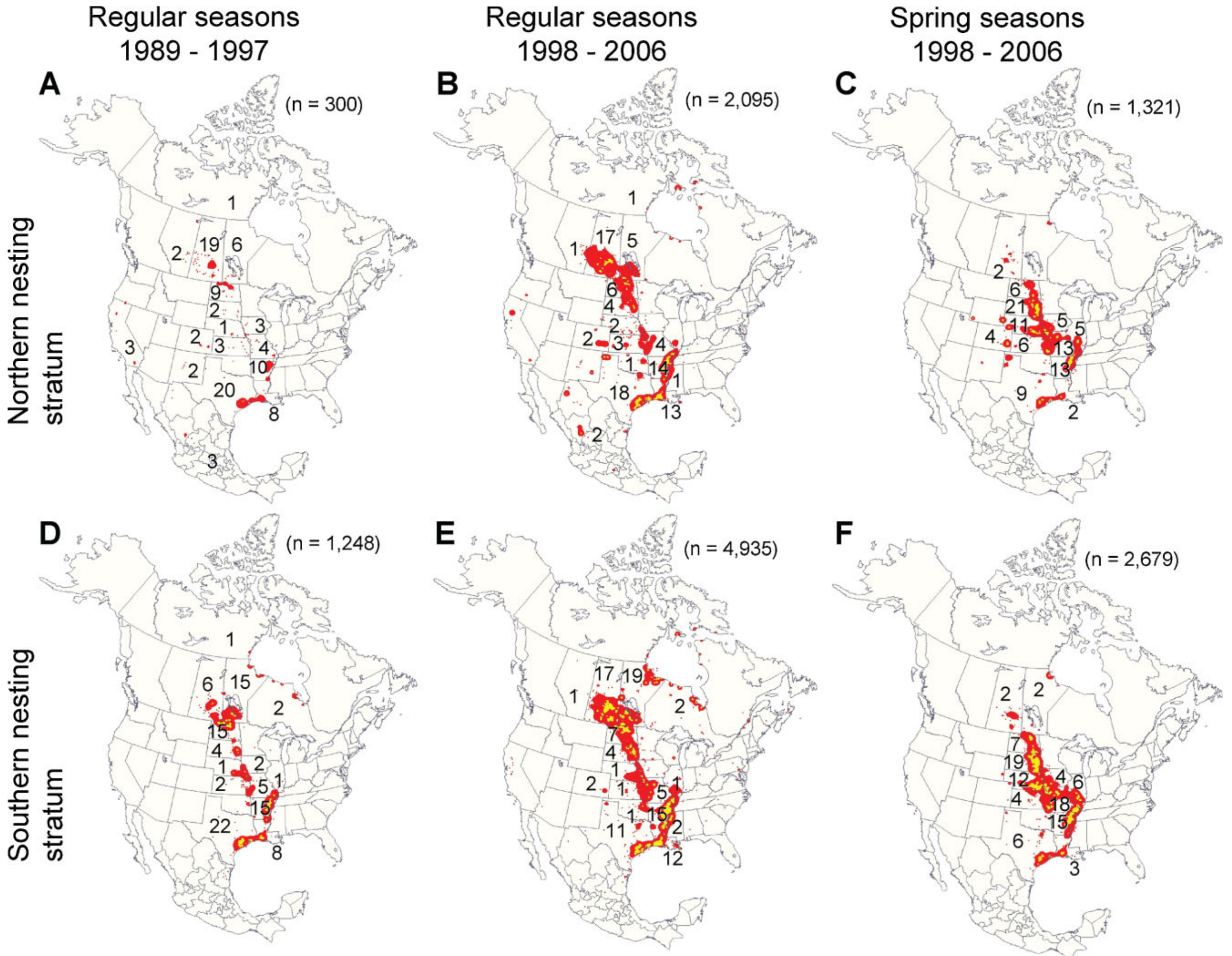

Figure 3. Harvest distribution of midcontinent snow geese marked in Canada's central and eastern arctic from 1989 onward. We summarized recoveries (*n*) by banding origin either north (Northern nesting stratum A, B, C) or south (Southern nesting stratum, D, E, F) of 60°N latitude and by timing of recoveries during (A and D) regular seasons, 1989–1997, (B and E) regular seasons 1998–2006, or (C and F) the conservation-order harvest 1998–2006. Numbers shown for each state, province, or Mexico are percentage of all recoveries for each summary. Density of recoveries/10,000 km^2 is shown as cream (<5), red (5–50), or yellow (>50).

understand whether the conservation order was properly directed at adult geese, the object of population reduction efforts.

Harvest During Regular Seasons compared to Conservation-Order or Spring Harvest

Periods of allowable harvest and harvest regulations for light geese have been reviewed by Kruse et al. (2009). A number of changes in harvest regulations for light geese have been implemented in the last few years, particularly since the 1998 harvest period, that required estimation of harvested light geese separately for regular seasons and conservation-order or spring harvest. Harvest under special provisions (e.g., use of electronic calls and increased bags during the regular season) and the conservation-order (i.e., harvest outside the regular season) were initiated in the United States during the 1998 harvest period (i.e., in Feb 1999) but varied by state. Special-provision harvest occurred in 9 states during the 1998 harvest period, 4 states during the 1999 harvest period, and 1 state during the 2000 and 2001 harvest periods. Conservation-order harvest occurred in 11 states in 1998, 17 states in 1999, and during each harvest period thereafter in 18 states. In Canada, a spring-conservation harvest was initiated during the 1998 harvest period (Moser and Duncan 2001).

Harvest was estimated separately in Canada by the Canadian Wildlife Service (CWS; Gendron and Collins 2007) and in the United States by the United States Fish and Wildlife Service (USFWS). From the early 1950s until the 2001 regular hunting season, regular-season harvest in the United States was estimated by USFWS using the Mail Questionnaire Survey (MQS) of Federal Duck Stamp purchasers. A separate survey of hunters, called the Migratory Bird Harvest Information Program (HIP), was initiated in 1999 (Harvest Surveys Section 2003) using an approach whereby United States hunters were stratified and selected for sampling based on questions answered at the time of license purchase about their harvest the previous year. Mail Questionnaire Survey and HIP sampling overlapped during the 1999–2001 hunting seasons, but we used MQS estimates for 1989–1998 and HIP estimates for 1999–2006 regular-season harvests.

Preliminary work (Johnson et al., in press) has suggested that past estimates of harvest of all waterfowl in the United States have been biased high possibly due to 1) prestige or memory bias (i.e., a possible tendency of sampled hunters to inflate individual harvest reported during sampling), and 2) use of arithmetic means for estimation of seasonal hunter harvest when the distribution of data is Poisson. In the case of snow goose harvest from the Central and Mississippi Flyways, bias adjustment resulted in estimates of harvest that were $\bar{x} = 58.9\%$ of previous HIP estimates for 1999–2006 (Johnson et al., in press; Fig. 4).

We used specific dates of each hunting period in each state (Kruse et al. 2009) to assign United States recoveries to either 1) regular seasons, 2) special provisions within regular seasons, or 3) conservation-order harvest. The sampling frame for estimation of regular-season harvest included special-provision harvest (P. Padding, USFWS, personal communication). We considered any band recoveries that occurred in Canada from 1 January to 31 May from 1999 onwards as spring-conservation harvest. Additionally, U.S. harvest outside of the regular season was estimated by each state, but the harvest estimate was of number of light geese (i.e., Ross's and snow geese in aggregate) without an estimate of the age ratio in that portion of the harvest.

We estimated annual harvest during regular seasons for adults ($\hat{H}_i^{\text{AHY}}$) and juveniles ($\hat{H}_i^{\text{HY}}$), for each country separately. For example, Canadian harvest of adult snow geese in each year i was

$$H_i^{\text{AHY,REG,CAN}} = H_i^{\text{REG,CAN}}\left(1 - \frac{\hat{a}_i^{\text{CAN}}}{1 + \hat{a}_i^{\text{CAN}}}\right) \tag{1}$$

where $\hat{a}_i^{\text{CAN}}$ is age ratio (juvenile/adult) of snow geese harvested in Canada in year i. We obtained age-ratio data from the Species Composition Survey in Canada (Gendron and Collins 2007) and from the Parts Collection Survey in the United States (Kruse et al. 2009).

An estimate of total harvest of snow goose adults was required because the objective of management action was to reduce population size of midcontinent snow geese through increased harvest of adult geese (see Rockwell et al. 1997). We used an approach similar to that of Alisauskas et al. (2006*a*) for estimation of adult snow goose harvest during the: 1) regular season, 2) special provisions, and 3) United States conservation-order plus spring harvest in Canada. In short, the approach of Alisauskas et al. (2006*a*) was to estimate proportion of band recoveries in each of those respective portions (i.e., regular season vs. conservation order) of hunting periods and then to apply those proportions as weights to harvest estimates of adult and juvenile geese taken during the regular season. For example, if $\hat{R}_i$ is harvest estimated during the regular season in year i, it is composed of traditional harvest, $\hat{R}_i^{\text{trad}}$, and that from special provisions, $\hat{R}_i^{\text{spec}}$,

$$\hat{R}_i = \hat{R}_i^{\text{trad}} + \hat{R}_i^{\text{spec}} \tag{2}$$

but does not include conservation-order harvest in the United States or spring harvest in Canada, C_i. In conjunction with R_i, we used bands recovered during regular season, r_i, and those recovered during conservation-order and spring harvest, c_i, to estimate $\hat{C}_i$ (Alisauskas et al. 2006*a*, 2009). Specifically, Alisauskas et al. (2009) postulated that

$$\frac{\hat{C}_i}{\hat{R}_i} = \frac{c_i \hat{\rho}_{c_i}^{-1}}{r_i \hat{\rho}_{r_i}^{-1}} \tag{3}$$

where $\hat{\rho}_{c_i}$ and $\hat{\rho}_{r_i}$ are estimates of band-reporting rate during conservation-order and regular seasons, respectively. If band reporting rates are equal between spring harvest and regular seasons, such that $\hat{\rho}_{c_i} = \hat{\rho}_{r_i}$, then these cancel and, following rearrangement, equation 3 simplifies to the estimator

$$\hat{C}_i = \frac{c_i}{r_i}\hat{R}_i \tag{4}$$

Essentially, we can estimate conservation-order harvest from regular-season harvest, weighted by the quotient of band recoveries in respective periods of harvest, assuming equal within-year reporting rates for regular-season and conservation-order harvest intervals. Thus, we estimated annual harvest of midcontinent snow goose adults in year i, $\hat{H}_i$, as

$$\hat{H}_i = \hat{R}_i + \hat{C}_i \tag{5}$$

We tested the assumption that $\hat{\rho}_c = \hat{\rho}_r$ using reward bands of \$10, \$20, \$30, \$50, or \$100 value and control bands of \$0 value applied to 24,518 snow geese and 10,509 Ross's geese from 2003 to 2005 (Table 2). We used PROC NLMIXED (SAS 2003) to build multinomial models to estimate band-reporting rates, $\hat{\rho}_j$, and harvest probabilities, $\hat{h}_{ij}$, for population i (i.e., Ross's goose, northern snow goose, or southern snow goose) from direct recoveries during season j (i.e., regular or conservation-order season) as detailed by Zimmerman et al. (2009). We assumed the number of band recoveries, N_i, was distributed as Multinomial(N_i; $h_{ij} \times \rho_j$), allowing an interaction between harvest rate and band reporting rate. We used AIC$_\text{c}$ (Burnham and Anderson 2002) to compare models that: 1) structured ρ by season and h by season and population (i.e., 8 parameters: ρ_c, ρ_r, $h_{\text{Ross's},r}$, $h_{\text{Ross's},c}$, $h_{\text{Lesser north},r}$, $h_{\text{Lesser north},c}$, $h_{\text{Lesser south},r}$, $h_{\text{Lesser south},c}$); 2) structured ρ and h by season (i.e., 4 parameters: ρ_c, ρ_r, h_r, h_c); 3) had constant ρ between seasons, but different h by

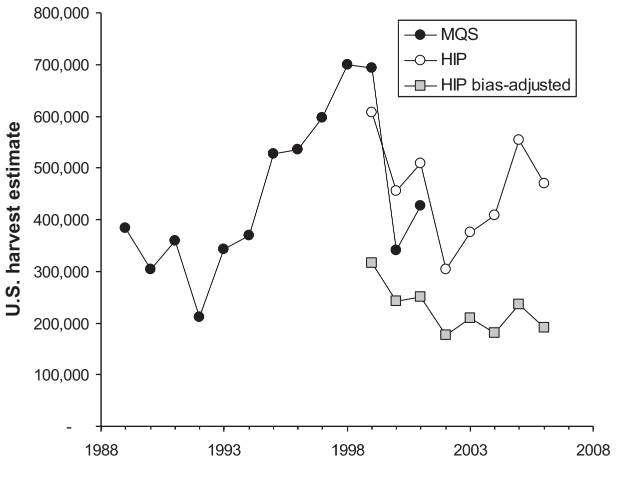

Figure 4. Estimates for harvest of snow geese during the regular season in the Central and Mississippi Flyways, 1989–2006. Estimates (Kruse 2009) from the Mail Questionnaire Survey (MQS) and Harvest Information Program (HIP) generally show correspondence during years when both methods were used (1999–2001). Also shown are preliminary estimates adjusted for bias (P. Padding, United States Fish and Wildlife Service, personal communication, cf. Johnson et al., in press).

Table 2. Numbers of adult (>1 year old) Ross's geese and midcontinent lesser snow geese marked, 2003–2005, with reward or control legbands in Canada's central and eastern arctic and subarctic.

		Snow geese	
Reward value ($)	**Ross's geese**[a]	**North**[b]	**South**[c]
0	5,850	7,552	4,717
10	1,165	1,508	942
20	1,166	1,509	945
30	1,168	1,510	945
50	1,162	1,508	939
100	1,162	1,507	936
Total	10,509	15,094	9,424

[a] Queen Maud Gulf, West Coast Hudson Bay.

[b] Baffin Island, Queen Maud Gulf, Southampton Island.

[c] Cape Henrietta Maria, La Pérouse Bay.

season and population (i.e., 7 parameters: $\rho.$, $h_{\text{Ross's},r}$, $h_{\text{Ross's},c}$, $h_{\text{Lesser north},r}$, $h_{\text{Lesser north},c}$, $h_{\text{Lesser south},r}$, $h_{\text{Lesser south},c}$); and 4) had constant ρ, but season-specific h (i.e., 3 parameters: $\rho.$, h_r, h_c). We used a logit link for all parameters and included dollar value as an individual covariate in all models, with the assumption that all recovered $100 reward bands were reported (Nichols et al. 1991, Royle and Garretson 2005, Zimmerman et al. 2009).

Estimation of Survival and Recovery Probabilities

The immediate goal of management action for population reduction of midcontinent snow geese was to reduce survival of adults through increased harvest; hence, our main focus was on adult (AHY) geese for estimation of survival. Specifically, we used a model-based approach to test the hypothesis that survival probability declined with the start of efforts directed at population reduction through enhanced opportunities to kill midcontinent snow geese.

Adult snow geese were marked with legbands (including some with reward bands during 2003–2005,) each year from 1989 onward at QMG (Zimmerman et al. 2009; Table 1). Except for La Pérouse Bay (LPB), all other areas had very few snow geese marked only with legbands before 1999, when special-harvest provisions (conservation order in the U.S. or spring conservation harvest in Canada) for increased kill of snow geese were initiated. Geese marked with neckbands generally show markedly reduced survival (Alisauskas and Lindberg 2002, Alisauskas et al. 2006*a*, but see Menu et al. 2000), so we considered only snow geese that were marked solely with legbands during June–August from 1989 onward.

Most marking of snow geese before the start of management efforts toward population reduction in the 1998 season was restricted largely to LPB (first sampled in 1969) and QMG (first sampled in 1949), at least since 1988 (Table 1). Appreciable and uninterrupted marking of snow geese using only legbands started in 1995 on Akimiski Island (AKI), in 2000 at Cape Henrietta Maria (CHM), and in 2003 on Baffin (BAF) and Southampton (SOU) Islands. The availability of data from a much greater geographic area during 2003–2006 (Table 1) permitted the test of important assumptions that survival and recovery estimates from QMG and LPB data were representative of snow geese from respective northern and southern strata of nesting distribution (Table 1).

This unbalanced sampling offered 2 general approaches for estimation of survival and recovery probabilities. First, analysis could have been restricted to 67,770 geese marked only at LPB and QMG starting in 1989, which would have provided 9 years of information before the 1998 season in which spring harvest began (Feb 1999) and 9 years of information after. This approach would have reduced model complexity but possibly sacrificed precision in estimation because information from an additional 30,649 marked birds from 6 other areas would have been forfeited (Table 1). Alternatively, analysis could proceed with all 98,419 snow geese marked since 1988; increased sample size (by approx. 45%) would undoubtedly improve the apparent precision of estimates. However, inclusion of information from other areas increases model complexity and could bias estimates if modeling was done without proper stratification by geographical origin.

We were interested in optimizing the use of all information balanced against a parsimonious modeling approach, so we used the 2-step approach to stratify reference areas according to similarity of survival probability. We used our finding of differences in fall migration phenology between northern and southern breeding strata of midcontinent snow geese (see the Results Section) as a starting point for testing whether respective stratification of survival probabilities was justified. First, we modeled survival and recovery probabilities among all banding areas during 2003–2006 to test whether there was spatial variation among arctic areas in which geese were marked. Second, depending on spatial variation from this more recent data set, we integrated it with the 1989–2006 data from QMG and LPB, with which there was overlap.

For both steps, we estimated survival probability ($\hat{S}$) and recovery probability ($\hat{f}$) using the models of Brownie et al. (1985) as implemented in Program MARK (White and Burnham 1999). Specifically, S_i is defined as the probability that a goose alive at the time of banding in August of year i will survive 1 year to the time of next banding in August of year $i + 1$, and f_i is defined as the probability that a goose alive at the time of banding in year i will be shot and its band reported within a year of being banded (i.e., during the next hunting season). As noted above, we used bands that had no toll-free number inscribed (i.e., address only, applied 1989–1998), bands that had a toll-free number (applied 1997–2006), and bands that had a reward (applied 2003–2005). We compared $\hat{S}_i$ estimated with $\hat{f}_i$ ignoring band inscription type against $\hat{S}_i$ with $\hat{f}_i$ structured by band type (Doherty et al. 2002). We found inferences about variation in $\hat{S}_i$ to be identical despite a slight average bias in $\hat{S}_i$ of -0.012 and bias in 95% CI($\hat{S}_i$) of -0.004 if we ignored band type (R. Alisauskas, Environment Canada, and G. Zimmerman, United States Fish and Wildlife Service, unpublished data). Thus, band type was ignored in later analyses.

We used an information-theoretic approach (Burnham and Anderson 2002) to select from a set of competing candidate models that addressed sources of spatial and temporal variation in both $\hat{S}$ and $\hat{f}$. We based model selection on Akaike's Information Criterion (AIC) with adjustments for overdispersion and small sample size (i.e., QAIC_c). We used median $\hat{c}$ tests in Program MARK (Cooch and White 2009) on global models $\{S(g * t), f(g * t)\}$ (t denoting annual variation and g denoting reference area) for estimation of the variance inflation factor, $\hat{c}$, to account for overdispersion. Following Burnham and Anderson's

(2002) rule of thumb, we considered models with ΔQAIC$_c$ <2.0 as having substantial empirical support. Where >1 model was supported by the data, we used model-averaging (Burnham and Anderson 2002) for inference about temporal variation and spatial differences in annual survival of adult snow geese. To facilitate model comparisons, we computed QAIC$_c$-based model weights, which sum to unity and provide a measure of the weight of evidence in favor of a particular model, given the data (Burnham and Anderson 2002).

Six reference areas, 2003–2006.—Input data were recovery matrices from each of 6 regions (Appendix A). Our candidate set for this analysis included models that recognized additive or multiplicative effects of time and banding location on both survival and recovery probabilities, as well as models that assumed constancy or no regional differences in these parameters. Because our aim in this analysis was to evaluate the specific prediction that survival estimates from QMG and LBP represented those of northern and southern nesting areas, respectively, we also considered 6 additional models (denoted $\{S(\mathrm{NS})\}$ with respect to survival) in which survival probability was structured according to northern and southern strata. Specifically, these models contrasted survival probability estimated from the 3 northern reference areas (QMG, BAF, and SOU) with that estimated based on data from the 3 southern reference areas (LPB, CHM, and AKI). Two of these models also recognized annual variation in survival, with and without interaction (i.e., $\{S(\mathrm{NS} * t)\}$ and $\{S(\mathrm{NS} + t)\}$, respectively). Alternative parameterizations for recovery probability for the north–south models included additive effects of stratum and time $\{f(\mathrm{NS} + t)\}$, additive effects of area and time $\{f(g + t)\}$, and simple differences among strata $\{f(\mathrm{NS})\}$. In total, 31 models comprised the candidate set for this analysis.

North vs. south stratum, 1989–2006.—We constructed an input file formatted as a recovery matrix for AHY snow geese marked with legbands (including reward and plastic tarsal bands, but not neckbands) either in the north or south stratum of nesting distribution, and then shot, retrieved, and reported to the Bird Banding Laboratory by hunters (Appendix B). We considered 52 models that represented various effects of time, region, and harvest regulations. Specifically, we included models representing additive and multiplicative effects of time (contrasting annual, e.g., $\{S(t)\}$, and linear trends in time, e.g., $\{S(T)\}$, with no time effect, e.g., $\{S(.)\}$) and area (north vs. south, e.g., $\{S(g)\}$, compared to no area effect, e.g., $\{S(.)\}$) on probabilities of both survival and recovery. We modeled a monotonic trend in the time series of survival in the design matrix of Program MARK by coding 1989 as "1" and incrementing each year in sequence and ending with 2005 as "17." We also modeled survival in relation to our estimates of adult snow goose harvest; covariate effects of harvest were expressed as either annual totals, H_i^{AHY}, or partitioned by regular, R_i^{AHY}, and conservation-order, C_i^{AHY}, harvest, as additive effects (e.g., $\{S(H)\}$ or $\{S(R + C)\}$). We modeled effects of harvest on survival by including a vector of annual estimates of total adult harvest in the design matrix parallel to the vector for survival probability in respective years. We considered models $\{S(\mathrm{CO})\}$ in which survival probability was contrasted between the period 1989–1997, when there were no special provisions, conservation-order, or spring harvest; and 1998–2006, when these additional harvest opportunities were in effect.

Estimation of August Population Size

We broadened the focus on probabilities of annual recovery, $\hat{f}_i$, and harvest, $\hat{h}_i$, estimated from banding data from 1989 to 2006 to a longer period, 1971 to 2006, to provide historical context to more recent levels. We used these estimates in conjunction with annual harvest estimates described above, $\hat{H}_i$, to estimate size of the midcontinent population of AHY and HY snow geese at the time of banding (usually early Aug) when goslings are about 4–6 weeks old. We followed Boyd (1976) and Boyd et al. (1982) and used Lincoln's (1930) method to estimate population size. Recently, Otis (2006) applied the method to midcontinent mallards, as did Alisauskas et al. (2009) to 4 arctic goose populations, including midcontinent snow geese, for the period 1989–2004.

Lincoln's (1930) estimator is

$$\hat{N}_i = \frac{\hat{H}_i}{\hat{h}_i}. \tag{6}$$

We estimated annual probability of harvest, $\hat{h}_i$, from probability of direct band recovery, $\hat{f}_i$, in Canada and the United States, and probability of band reporting, $\hat{\rho}_i$, using

$$\hat{h}_i = \frac{\hat{f}_i}{\hat{\rho}_i}. \tag{7}$$

Cooke et al. (2000) found no difference in direct recovery rates of snow geese marked with tarsal bands compared to metal legbands. So, we estimated direct recovery rate, in this case, using only normal metal legbands, tarsal bands, or control bands associated with reward band studies. We did not use geese marked with neckbands or reward bands to estimate direct recovery rates that we subsequently used for Lincoln's abundance estimator.

Alisauskas et al. (2009) summarized available historical estimates of $\hat{\rho}_i$ for 1989–2004, and provided justification for their use with geese harvested in the midcontinent region of North America. Although Boyd (1976) used $\hat{\rho}_i = 0.33$, citing Martinson and McCann (1966) and Henny (1967), Nichols et al. (1991) suggested that Henny and Burnham's (1976) estimate of $\hat{\rho}_{1972} = 0.39$ be modified to $\hat{\rho}_{1972} = 0.26$. Nichols et al. (1991) further estimated that $\hat{\rho}_{1987-1988} = 0.32 \pm 0.06$ (SE). Thus, we used $\hat{\rho}_{1971-1986} = 0.26 \pm 0.06$ (SE), $\hat{\rho}_{1987-1988} = 0.32 \pm 0.06$, $\hat{\rho}_{1989-1993} = 0.38 \pm 0.02$ (Nichols et al. 1995), $\hat{\rho}_{1994} = 0.514 \pm 0.077$, $\hat{\rho}_{1995} = 0.498 \pm 0.094$, $\hat{\rho}_{1996} = 0.491 \pm 0.069$, $\hat{\rho}_{1997} = 0.62 \pm 0.089$, $\hat{\rho}_{1998-2001} = 0.805 \pm 0.033$ (J. Dubovsky, USFWS, personal communication), $\hat{\rho}_{2002} = 0.719 \pm 0.034$ (Royle and Garretson 2005), and $\hat{\rho}_{2003-2006} = 0.80 \pm 0.08$ (see the Results Section). The increase in band-reporting rate was related to use of legbands engraved with a toll-free telephone number (Doherty et al. 2002). We estimated $\widehat{\mathrm{var}}(\hat{H}_i)$, $\widehat{\mathrm{var}}(\hat{h}_i)$, and $\widehat{\mathrm{var}}(\hat{N}_i)$ following Alisauskas et al. (2009).

Alisauskas et al. (2009) also noted that if there is heterogeneity in harvest rate of geese from different banding strata and the number of bands applied in each stratum is disproportionate to the abundance of geese in each stratum, Lincoln's estimator of $\hat{N}_i$ will be biased. The degree and direction of bias depended on the magnitude of differences in $\hat{h}_i$ and the difference between the proportions of bands applied in different strata and the proportions of geese represented by respective strata. Knowledge about the proportional contribution of geese from different strata allows bias correction in $\hat{N}_i$ stemming from heterogeneity in $\hat{h}_i$ (Alisauskas et al. 2009: equation 7). Thus, we estimated harvest rates using 2 approaches: 1) pooling recoveries from northern and southern breeding strata (see below), $\hat{h}_i$ from equation 7, and 2) stratifying harvest rates for each breeding stratum (north vs. south), weighting each by a measure of their respective contributions to the midcontinent population (0.9 for northern stratum, Kerbes et al. 2006) to calculate a weighted estimate as:

$$\hat{h}_i^{\text{corr}} = 0.9\hat{h}_i^{\text{north}} + 0.1\hat{h}_i^{\text{south}} \tag{8}$$

Consequently, we provide Lincoln estimates of abundance, $\hat{N}_i$, calculated from pooled harvest rates, $\hat{h}_i$, and of $\tilde{N}_i$ (i.e., bias-corrected abundance from use of appropriately weighted harvest rates, $\hat{h}_i^{\text{corr}}$, in the denominator of Lincoln's estimator [equation 6]).

Estimation of Population Growth Rate

To evaluate population growth rate, we evaluated time series for 2 abundance metrics: 1) an annual population estimate, $\hat{N}_i$ of midcontinent snow geese derived for each age class (HY and AHY) using Lincoln's method above; and 2) the midwinter index (Kruse 2009), or winter index (USFWS 2007), *W*, which is a count made of light geese in the Central and Mississippi Flyways (Cooke et al. 2000) that does not segregate age classes and includes both snow geese and Ross's geese. We estimated instantaneous population growth rate $\hat{r}$ over a given range of years as the slope from a linear regression (PROC REG; SAS 2003) of the log of population abundance on year. To derive unbiased estimates of regression parameters for analysis of population estimates $\hat{N}_i$ derived using Lincoln's method, we weighted each log-transformed estimate of abundance by $1/\widehat{\text{var}}(\ln(\hat{N}))$, which we approximated to first-order as $[\hat{N}^2/\text{var}(\hat{N})]$. We were unable to use weighted regressions for analysis of winter indices, *W*, because estimates of sampling variance were not available. To derive estimates of the finite rate of increase $\hat{\lambda}$ and $\text{var}(\hat{\lambda})$, we used the transformations $\hat{\lambda} = \text{e}^{\hat{r}}$ and $\text{var}(\hat{\lambda}) \approx \text{var}(\hat{r})\text{e}^{2\hat{r}}$ (sensu Ryding et al. 2007). If there is serial autocorrelation in the time series, then the estimated variance of $\hat{r}$ (and thus $\hat{\lambda}$) will be biased (Ryding et al. 2007). Preliminary analysis of our data indicated no significant serial correlation for either abundance metric.

We adopted several strategies to assess whether recent trajectories in abundance had changed in relation to population trajectories before the implementation of the conservation order in 1998. First, we estimated 95% CI($\hat{\lambda}$) for 4 periods: 1) 1971–2006 overall (i.e., all available years in our data), 2) 1971–1998 to represent the period overall before complete liberalization of harvest restrictions, 3) 1990–1998, and 4) 1998–2006. The latter 2 periods represent periods of equal duration (and thus of similar sample size) immediately before and after start of special-harvest initiatives in the season of 1998–1999, respectively. Second, we fit linear, quadratic, and cubic polynomials with PROC REG, as well as models for logistic and exponential growth using PROC NLIN (SAS 2003) to assess whether recent trajectories in various time series of $\hat{N}$ and *W* had changed in relation to those before 1998.

Finally, we used the R (2009) package strucchange (Zeileis et al. 2003) to test for the presence of breakpoints in our time series of abundance estimates. A breakpoint is defined as any point (i.e., year) where the slope of the linear relationship between the response and explanatory variables changes significantly before and after the breakpoint. We used both generalized fluctuation tests and *F* tests (Zeileis 2006); although both share a common null hypothesis of "no structural change" for a given time series, generalized fluctuation tests are suitable for various patterns of structural changes (i.e., allow for multiple breakpoints over a given time series). The generalized fluctuation tests fit a model (say, a simple linear regression model) to the given data and derive an empirical process that captures the fluctuation either in residuals or in estimates (we adopted an approach based on residuals). The idea that is common to all generalized fluctuation tests is that the null hypothesis of "no structural change" should be rejected when the fluctuation of the empirical process gets improbably large compared to the fluctuation of the limiting (random) process.

Two commonly used empirical fluctuation processes are 1) the cumulative sums of standardized residuals and 2) moving sums of standardized residuals. Using the cumulative sum process, the recursive residuals will have a zero mean up to a breakpoint and deviate from zero after it. For the moving-sum approach, the resulting empirical fluctuation process uses the sum of a fixed number of residuals in a data window whose size is determined by a bandwidth parameter and which is moved over the whole sample period. We determine the statistical significance of any fluctuation in the residual process by comparing observed fluctuations in the residual process against the null expectation of random fluctuations, which is known for a specified empirical fluctuation process (e.g., Weiner, random walk). The probability distributions for the cumulative and moving sum processes are discussed in Zeileis et al. (2003).

The *F*-test differs from the generalized fluctuation tests in that it is designed to test against a single-shift alternative hypothesis (i.e., a single breakpoint). We generated the *F*-statistic as the difference in residuals from the full model (where we estimate the coefficients in the subsamples, before and after the proposed breakpoint, separately), and the residuals from the restricted model, where we fit the parameters just once for all observations (i.e., without a breakpoint); see Zeileis et al. (2003) and Zeileis (2006) for details on significance testing with *F*-statistics.

In our breakpoint analysis, we used a minimal segment size of 4 (i.e., the minimal number of observations in each segment; i.e., grouping of consecutive years). We adopted this segment size as a compromise between having enough points to generate a meaningful linear model for a given segment, while allowing for a segment length short enough to accommodate changes in trajectory over a reasonable time scale. We used cumulative evidence over both types of tests to assess support for the hypothesis that population trajectory changed following the conservation order to a degree greater than expected by chance, given the degree of variation in the abundance data.

RESULTS

Migration and Recovery Phenology

We first focused on LPB and QMG banding locations because these had the largest sample sizes available both before and after

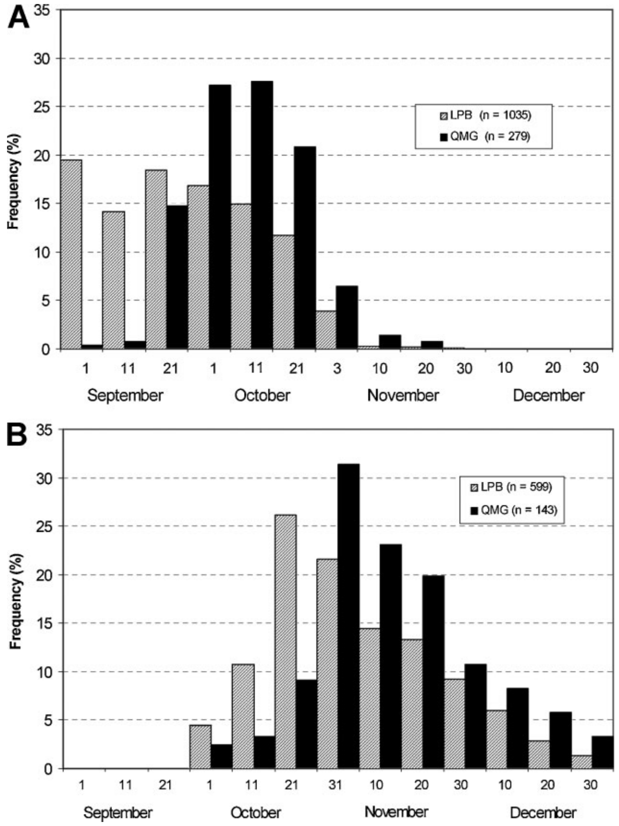

Figure 5. Temporal distribution of band recoveries of midcontinent snow geese marked near Queen Maud Gulf, QMG (solid), or La Pérouse Bay, LPB (stippled), and recovered in (A) Canada, or (B) northern United States north of 39°N latitude, date(s).

implementation of special harvest measures during the 1998 season. We estimated that the average date (±95% CI) of Canadian recoveries of adult snow geese during fall harvest (1989–2006) from LPB was 25 September ± 1.1 days, which was 15 days earlier than the average date for QMG adults (10 Oct ± 1.5 days, Fig. 5A). The same pattern was evident when we restricted analysis to northern United States recoveries reported between 39°N and 49°N latitude, although LPB geese were recovered only 8 days earlier (5 Nov ± 1.7 days) than QMG geese (13 Nov ± 3.3 days), on average (Fig. 5B).

These differences prompted us to evaluate sources of variation in migration and recovery phenology more fully by including the effects of neckband presence, origin of geese (7 regions with RAS considered as QMG, Table 1), and age using latitude of recovery as a covariate. Ranking of models was similar between Canadian and northern United States recoveries (Table 3); the best model in both sets included additive effects of latitude, origin, age, and year as a trend covariate {L, O, A, Y}, with model weights of 0.53 and 0.55, respectively. Mean dates of Canadian recoveries of geese from southern Hudson Bay were not different from one another, but these were considerably earlier than for geese marked north of 60°N latitude (Fig. 6). Differences in timing of recovery carried over into the northern United States, although differences between snow geese of northern versus southern origin were less clear. For example, geese from Baffin Island appeared to have caught up to those from southern Hudson Bay by the time that they were harvested during fall in North or South Dakota.

After accounting for differences in recovery dates for geese from different origins, parameter estimates for slopes of recovery date and latitude suggested that snow geese generally moved through Canada (between 66°N and 49°N latitude) during fall migration at a rate of 1° latitude every 4.8 ± 0.2 days, which is equivalent to approximately 25 km/day; the corresponding rate of average southward movement through the northern United States was 1° every 4.3 ± 0.25 days, or approximately 22 km/day. Adult geese were harvested 1.07 ± 1.08 days later than juveniles in Canada and 2.30 ± 2.11 days later in the United States; note that the 95% confidence interval included zero for Canadian, but not United States, recoveries despite presence of this age effect in the best models from candidate sets (Table 3). Geese were harvested an average of 0.19 ± 0.12 days/yr later in Canada, but 0.44 ± 0.18 days/yr later in the northern United States; in other words, this linear trend suggested that geese were harvested in Canada approximately 3.2 days later in 2006 than they had been in 1989, but were harvested approximately 7.4 days later in the United States. Finally, there appeared to be no effect of marker type (i.e., neckband presence) on timing of harvest after controlling for all other effects in either Canadian or northern United States recoveries.

Overall, timing of harvest for QMG snow geese was similar to all other geese nesting north of 60°N latitude, whereas timing of harvest for snow geese marked at LPB was representative of birds from nesting south of Hudson Bay (Fig. 6). The large differences in migration behavior, and possible differences in recovery and survival probabilities, precluded pooling of all data; instead, stratification into northern and southern breeding populations for further analysis seemed appropriate.

Distribution of Recoveries by Hunters

The large sample of band recoveries ($n = 10{,}190$) allowed tests of independence in harvest distribution between northern and southern origins of midcontinent snow geese at the fine scale of state and provincial jurisdictions (Fig. 3). Northern-nesting snow geese were recovered during 1989–1997 in greater proportions from Canada (28% vs. 24% of southern nesters) and from Mexico (3% vs. <1% of southern nesters), whereas southern nesters were recovered in greater proportions from the United States (75%) than were northern nesters (67%, $\chi^2_2 = 20.2$, $P < 0.001$).

Proportional distribution of regular-season recoveries among jurisdictions changed from the 1989–1997 period to the 1998–2006 period of special harvest measures for snow geese from both northern ($\chi^2_{32} = 49.0$, $P < 0.001$, Fig. 3A,B) and southern origins ($\chi^2_{32} = 379.6$, $P < 0.001$, Fig. 3D,E). In the case of northern-nesting geese, this change was a result of a slight eastward shift in harvest distribution from the Central to the Mississippi Flyway ($\chi^2_3 = 10.6$, $P = 0.014$), but distribution among countries remained unchanged ($\chi^2_2 = 0.9$, $P = 0.6$). For southern-nesting geese, differences were the result of eastward shifts in both Canada and the United States ($\chi^2_3 = 82.4$, $P < 0.001$), but also a proportional increase in Canadian recoveries from 24% to 39% and a decline in United States recoveries from 76% to 61% more recently ($\chi^2_2 = 140.4$, $P < 0.001$). These changes resulted

Table 3. Sources of variation in recovery dates (RDATE) of midcontinent lesser snow geese marked in Canada's central and eastern arctic recovered either in Canada ($n = 2{,}854$) or northern United States between 39° and 49° north latitude ($n = 1{,}613$), with respect to latitude of recovery (L), origin (O; 7 regions, NS, north vs. south stratum), age (A) when killed (HY, hatch year, i.e., <1 year old, or AHY, after hatch year, i.e., >1 year old), neckband presence (M; legband only vs. neckband), and year (Y) as trend covariate.

Recovery location	Model for RDATE	ΔAIC$_c$[a]	AIC$_c$ weight[b]	*K*[c]	R^2
Canada	{L, O, A, Y}	0.0	0.53	11	0.57
	{L, O, Y}	1.7	0.23	10	0.57
	{L, O, A, M, Y}	2.0	0.20	12	0.57
	{L, O, A}	7.0	0.02	10	0.57
	{L, O, A, M}	9.0	0.01	11	0.57
	{L, O}	9.7	0.00	9	0.57
	{L, O, A, M, O × A, O × M}	10.0	0.00	22	0.57
	{L, O, A, M, O × A, O × M, A × M, O × A × M}	10.5	0.00	23	0.57
	{L, O, A, M, O × A, O × M, A × M}	10.5	0.00	23	0.57
	{L, O, A, M, A × M}	11.1	0.00	12	0.57
	{L, O, A, M, O × M}	11.3	0.00	18	0.57
	{L, O, M}	11.4	0.00	10	0.57
	{L, O, A, M, O × A}	12.0	0.00	15	0.57
	{L, NS, A, M}	49.1	0.00	6	0.56
	{L}	285.0	0.00	3	0.52
	{O}	1,999.0	0.00	8	0.13
Northern United States	{L, O, A, Y}	0.0	0.55	11	0.47
	{L, O, A, M, Y}	1.3	0.29	12	0.47
	{L, O, Y}	2.5	0.16	10	0.47
	{L, O, A}	21.1	0.00	10	0.46
	{L, O, A, M, O × A}	22.6	0.00	15	0.47
	{L, O, A, M}	22.9	0.00	11	0.46
	{L, O, A, M, A × M}	23.2	0.00	12	0.46
	{L, O, A, M, O × M}	25.5	0.00	18	0.47
	{L, O, A, M, O × A, O × M}	27.5	0.00	22	0.47
	{L, O, A, M, O × A, O × M, A × M, O × A × M}	29.0	0.00	23	0.47
	{L, O, A, M, O × A, O × M, A × M}	29.0	0.00	23	0.47
	{L, O}	29.2	0.00	9	0.46
	{L, O, M}	29.8	0.00	10	0.46
	{L, NS, A, M}	29.9	0.00	6	0.46
	{L}	40.7	0.00	3	0.45
	{O}	951.1	0.00	8	0.04

[a] Difference between Akaike's Information Criterion (AIC$_c$) of the current model and the lowest observed value (14,337.98 for Canadian recoveries and 8,743.32 for Northern U.S.).

[b] Normalized Akaike (AIC$_c$) weight (Burnham and Anderson 2002).

[c] Number of parameters estimated.

from a shift of harvest distribution among countries between northern and southern geese during regular seasons 1998–2006 ($\chi^2_2 = 180.4$, $P < 0.001$) compared to 1989–1997. Specifically, a greater proportion of southern geese were recovered from Canada in 1998–2006 (39% vs. 24% of northern geese) compared to 1989–1997 (24% southern vs. 28% northern). Regarding the eastern shift in harvest from the Central to Mississippi Flyways that occurred during regular seasons from 1989–1997 to 1998–2006, the proportion of northern snow geese harvested in the Central Flyway declined from 57% to 50% ($\chi^2_3 = 10.6$, $P = 0.014$), and that of southern geese declined from 58% to 42% ($\chi^2_3 = 82.4$, $P < 0.001$).

Harvest outside of regular seasons was almost completely restricted to the United States, where 97% of both northern (98%, Fig. 3C) and southern snow geese (96%, Fig. 3F) were harvested during the conservation order (compared to 72% of northern geese during regular seasons [Fig. 3B], $\chi^2_2 = 337.0$, $P < 0.001$, and 61% of southern geese during regular seasons [Fig. 3E] $\chi^2_2 = 1{,}149.5$, $P < 0.001$). Northern and southern geese did not differ with respect to the proportional contributions of Canadian and United States harvest during conservation-order or spring harvest ($\chi^2_1 = 0.40$, $P = 0.526$). More conservation-order harvest occurred in the Central Flyway than in the Mississippi Flyway overall, with proportionally more northern geese harvested (60%) than southern geese (52%, $\chi^2_1 = 22.5$, $P < 0.001$). The states with the greatest conservation-order harvest were South Dakota (19–21% of conservation-order harvest), Missouri (13–18%), Arkansas (13–15%), and Nebraska (11–12%). Harvest in Canada during spring accounted for only 4% of harvest of southern geese and only 2% of northern geese outside of regular-season harvests. For example, it was estimated that spring harvest in Saskatchewan averaged only approximately 11,400 snow geese from 2003 to 2008 (M. Gendron, CWS, personal communication) with an average annual participation in that province's spring harvest by only 740 hunters.

Distribution of Recoveries by Age

There were 1,768 recoveries of adult and 363 recoveries of juvenile snow geese that were marked only with legbands in all banding regions, recovered during 1989–1997 regular seasons, and for which country of recovery could be determined. Of the adults, 20% were recovered in Canada, 80% in the United States, and 1% in Mexico from 1989 to 1997, compared to 32%, 67%,

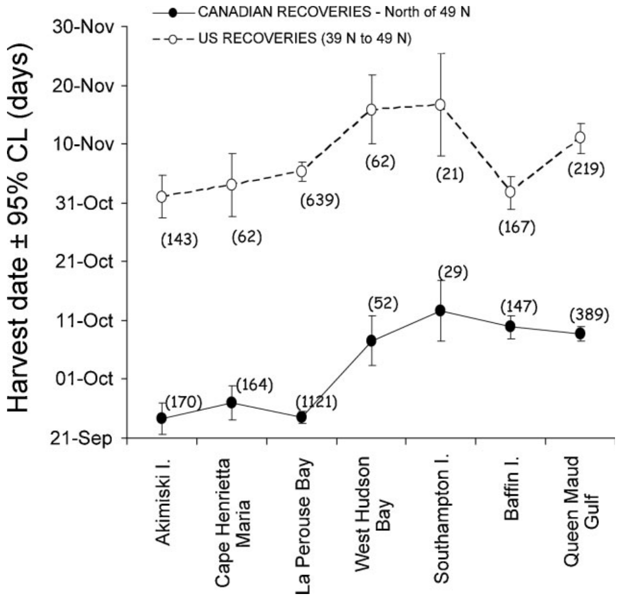

Figure 6. Mean (±95% confidence limits) recovery dates of midcontinent snow geese marked 1989–2006 ordered by most southerly to most northerly regions in Canada's central and eastern arctic and subarctic. Shown are mean dates for geese harvested in Canada and those harvested in the north central United States between 39°N and 49°N latitude.

and <1% of juveniles recovered in Canada, the United States, and Mexico, respectively (Canada vs. U.S.; $\chi^2 = 115.8$, df = 1, $P < 0.001$). As expected, Canadian harvest of snow geese from Canada's central and eastern arctic was composed of proportionally more juveniles than adults, compared to the United States harvest, as was also found for Ross's geese (Alisauskas et al. 2006*a*).

During the era of conservation-order or spring harvest from 1998 to 2006, there were 6,290 recoveries of adults and 1,158 recoveries of juveniles for which harvest could be assigned to either traditional or conservation-order–spring harvest. Of adults, 59% were recovered during regular seasons from 1998 to 2006 and 41% were recovered during conservation-order or spring harvest from 1998 to 2006, compared to 74% of juveniles during the regular season and 26% of juveniles during conservation-order or spring harvest ($\chi^2 = 102.9$, df = 2, $P < 0.001$). Thus, the conservation-order or spring harvest of snow geese had a proportionally greater influence on adults than on juveniles compared to harvest during regular seasons. Part of this difference was probably an outcome of proportionately fewer juveniles surviving regular seasons until they were available for spring or conservation-order harvest. Nevertheless, nontrivial numbers of juvenile birds were harvested during spring (see below), thereby buffering harvest pressure on adult geese.

Annual Harvest During Regular Seasons Compared to Conservation-Order or Spring Harvest

Comparisons of different models for band-reporting probability, $\hat{\rho}$, and harvest rate, $\hat{h}$, suggested that the best estimates were from model $\{\rho(.)\ h(\text{season} * \text{population})\}$, which treated band-reporting probability as equal between regular seasons and conservation-order harvest, regardless of whether there was an adjustment for band loss (Table 4). Model fit was clearly better when harvest rate was parameterized by population origin. We estimated $\hat{\rho}$ ± 95% confidence interval to be 0.83 ± 0.17, if we made no adjustment for band loss, and 0.80 ± 0.16 after adjustment (Table 5).

Overall, direct estimates of harvest rate from reward bands, adjusted for band loss, were low for both Ross's and northern snow geese ($\leq$3%) and almost as low for southern snow geese (approx. 4%). Note that most known Ross's geese nested in the northern stratum of snow goose nesting. However, vulnerability of Ross's geese during the conservation order relative to regular harvest ($\hat{v} = \hat{h}_c/\hat{h}_r$) was only 0.45 compared to 0.93 for northern snow geese and 0.71 for southern snow geese.

Because band-reporting probability was equal between regular seasons and conservation-order harvest, we used equations 4 and 5 for estimation of harvest during conservation-order take. After reaching a low of approximately 202,000 adults in 1993, harvest of midcontinent snow geese during the regular season (including special provisions in 1998 and 1999) increased almost steadily to approximately 561,000 adults in 1999 (Table 6, Fig. 7A). Regular-season harvest declined from 1999 each year in sequence until 2003 to reach approximately 327,000, after which any trend to 2006 was unclear.

Annual conservation-order harvest of adults was highly variable, ranging from approximately 103,000 in the inaugural year following the 1998 regular season, to approximately 349,000 adults following the 2001 regular season (Table 6). Since the implementation of measures to liberalize harvest in 1998 until 2006, annual regular-season harvest has averaged (±95 CI) approximately 404,000 ± 59,000 adults (ignoring sampling variation) and approximately 200,000 ± 48,000 juveniles during the regular season (including special provisions), compared to approximately 246,000 ± 57,000 adults and approximately 73,000 ± 12,000 juveniles during conservation-order or spring harvest.

Total harvest of snow geese since 1988 reached a maximum of approximately 749,000 adults in 2001 (Fig. 7A) and of 353,000 juveniles in 1998 (Fig. 7B). Estimates of total harvest of adult geese did not exceed 0.75 million and exceeded 0.7 million during only 4 harvest periods since 1998 (1999–2001, and 2005, Table 6). By comparison, total spring-harvest estimates from surveys conducted separately by individual states in the United States were 1.5 times to 3.0 times higher than estimates obtained using the band-recovery methods (Table 6), partially because state estimates did not distinguish between snow geese and Ross's geese during the conservation order.

Conservation-order harvest accounted for an average of about 37% of total annual harvest of adults and 28% of juveniles from 1998 to 2006. For total adult harvest, this proportion increased following initiation of the conservation order after the 1998 regular season until 2001, after which the contribution of conservation-order harvest leveled off and may have begun to decline (Fig. 8). Part of the initial increase in the importance of conservation-order harvest was an outcome of declines in regular-season harvest over the same interval (Table 6, Fig. 7). Annual conservation-order or spring harvest of either adult or juvenile geese marked in both northern and southern strata did

Table 4. Set of candidate models for estimation of band-reporting probabilities ($\hat{\rho}$) and harvest probabilities ($\hat{h}$) for Ross's geese and midcontinent snow geese marked, 2003–2005, as adults (AHY, after-hatch year, i.e., >1 year old) in Canada's central and eastern arctic and subarctic. Analyses were done without and with adjustment for band loss following Zimmerman et al. (2009). Estimation of parameters was either by season (regular vs. conservation-order) or by season and population (pop; Ross's geese, snow geese marked north of 60°N latitude, snow geese marked south of 60°N latitude).

Adjustment for band loss	Model	ΔAIC_c[a]	AIC_c weight[b]	K[c]
No	$\{\rho(.)\ h(\text{season} * \text{pop})\}$	0	0.73	8
	$\{\rho(\text{season})\ h(\text{season} * \text{pop})\}$	2	0.27	9
	$\{\rho(.)\ h(\text{season})\}$	35	0.00	4
	$\{\rho(\text{season})\ h(\text{season})\}$	37	0.00	5
Yes	$\{\rho(.)\ h(\text{season} * \text{pop})\}$	0	0.73	12
	$\{\rho(\text{season})\ h(\text{season} * \text{pop})\}$	2	0.27	13
	$\{\rho(.)\ h(\text{season})\}$	38	0.00	8
	$\{\rho(\text{season})\ h(\text{season})\}$	40	0.00	9

[a] Difference between Akaike's Information Criterion (AIC_c), reported by PROC NLMIXED, of the current model and the lowest observed value (SAS 2003).

[b] Normalized Akaike (AIC_c) weight (Burnham and Anderson 2002).

[c] Number of parameters estimated.

Table 5. Estimates (95% CI) of band-reporting probability ($\hat{\rho}$) and harvest probabilities ($\hat{h}$) for Ross's geese and midcontinent snow geese marked, 2003–2005, in Canada's central and eastern arctic and subarctic. Estimates shown are without and with adjustment for band loss following Zimmerman et al. (2009). Estimation of parameters was either by season (regular vs. conservation-order [CO]) or by season and population (pop; Ross's geese, snow geese marked north of 60°N latitude, snow geese marked south of 60°N latitude). Unless otherwise footnoted, estimates are from best models (Table 4).

		Ross's and snow geese		Ross's geese		Snow geese (north)		Snow geese (south)	
Adjustment for band loss	Season	$\hat{\rho}$	95% CL	$\hat{h}$	95% CL	$\hat{h}$	95% CL	$\hat{h}$	95% CL
No	Regular			0.020	0.004	0.014	0.003	0.023	0.005
	Conservation-order			0.009	0.002	0.013	0.003	0.016	0.004
	Combined[a]	0.833	0.166	0.029	0.005	0.027	0.004	0.039	0.007
Yes	Regular			0.021	0.005	0.015	0.003	0.024	0.005
	Conservation-order			0.009	0.002	0.014	0.003	0.017	0.004
	Combined[a]	0.804	0.162	0.030	0.005	0.029	0.005	0.041	0.007

[a] Ad hoc estimate taken as sum of estimates from regular and conservation-order harvest.

Table 6. Harvest estimates for adult (AHY, after-hatch year, i.e., >1 year old) or juveniles (HY, hatch year, i.e., <1 year old) midcontinent snow geese during the regular season and conservation-order or spring harvest. Harvest is for Central and Mississippi Flyway states in the United States and Canada (Saskatchewan, Manitoba, and Ontario). United States harvest during regular season includes harvest during Special Provisions and is based on Mail Questionnaire Survey (MQS) of federal duck stamp purchasers (1989–1998) or on Harvest Information Program (HIP, 1999–2006). Harvest during conservation-order or spring, C_i, is based on weighted proportion of recoveries in relation to harvest and proportion of recoveries during the regular season, R_i (equation 4 and Alisauskas et al. 2006*a*, 2009). Harvest estimated from state surveys during the conservation order includes adults and juveniles of Ross's and snow geese in aggregate from all states in the Central and Mississippi Flyways (Kruse et al. 2009).

	Regular season						Conservation-order or spring harvest		
Year, i	Central Flyway[a]	Mississippi Flyway[a]	Canada[b]	Harvest, R_i	Adult harvest, R_i^{ad}	Juvenile harvest, R_i^{juv}	Adult harvest, C_i^{ad}	Juvenile harvest, C_i^{juv}	Estimates from state surveys[a]
1989	286,271	97,277	125,248	508,796	259,323	249,473	0	0	0
1990	211,758	92,834	88,402	392,994	242,161	150,833	0	0	0
1991	248,107	110,743	91,093	449,943	231,030	218,913	0	0	0
1992	151,942	60,171	48,612	260,725	229,845	30,880	0	0	0
1993	270,284	71,843	73,527	415,654	201,491	214,163	0	0	0
1994	270,358	99,031	87,131	456,520	268,653	187,867	0	0	0
1995	336,306	191,426	94,208	621,940	389,174	232,766	0	0	0
1996	304,617	231,491	81,736	617,844	366,178	251,666	0	0	0
1997	358,886	239,018	132,652	730,556	421,515	309,041	0	0	0
1998	303,791	396,504	122,056	822,351	519,225	303,126	103,396	49,789	398,455
1999	417,588	302,278	130,576	850,442	560,862	289,580	187,309	57,916	643,470
2000	349,279	160,752	101,424	611,455	445,064	166,391	288,966	64,828	536,296
2001	300,586	226,716	126,840	654,142	396,770	254,159	349,383	96,822	749,349
2002	230,814	110,766	110,882	452,462	339,378	113,084	293,753	48,781	640,526
2003	216,493	186,862	136,328	539,683	326,489	213,194	199,034	81,998	805,583
2004	183,810	168,358	100,509	452,677	365,832	86,845	308,913	82,897	660,358
2005	253,437	219,699	95,998	569,134	393,639	175,495	326,187	74,248	793,073
2006	194,565	140,300	149,336	484,201	288,818	195,383	152,743	96,725	706,232

[a] Kruse et al. (2009).

[b] Includes harvest only from Saskatchewan, Manitoba, and Ontario (Gendron and Collins 2007).

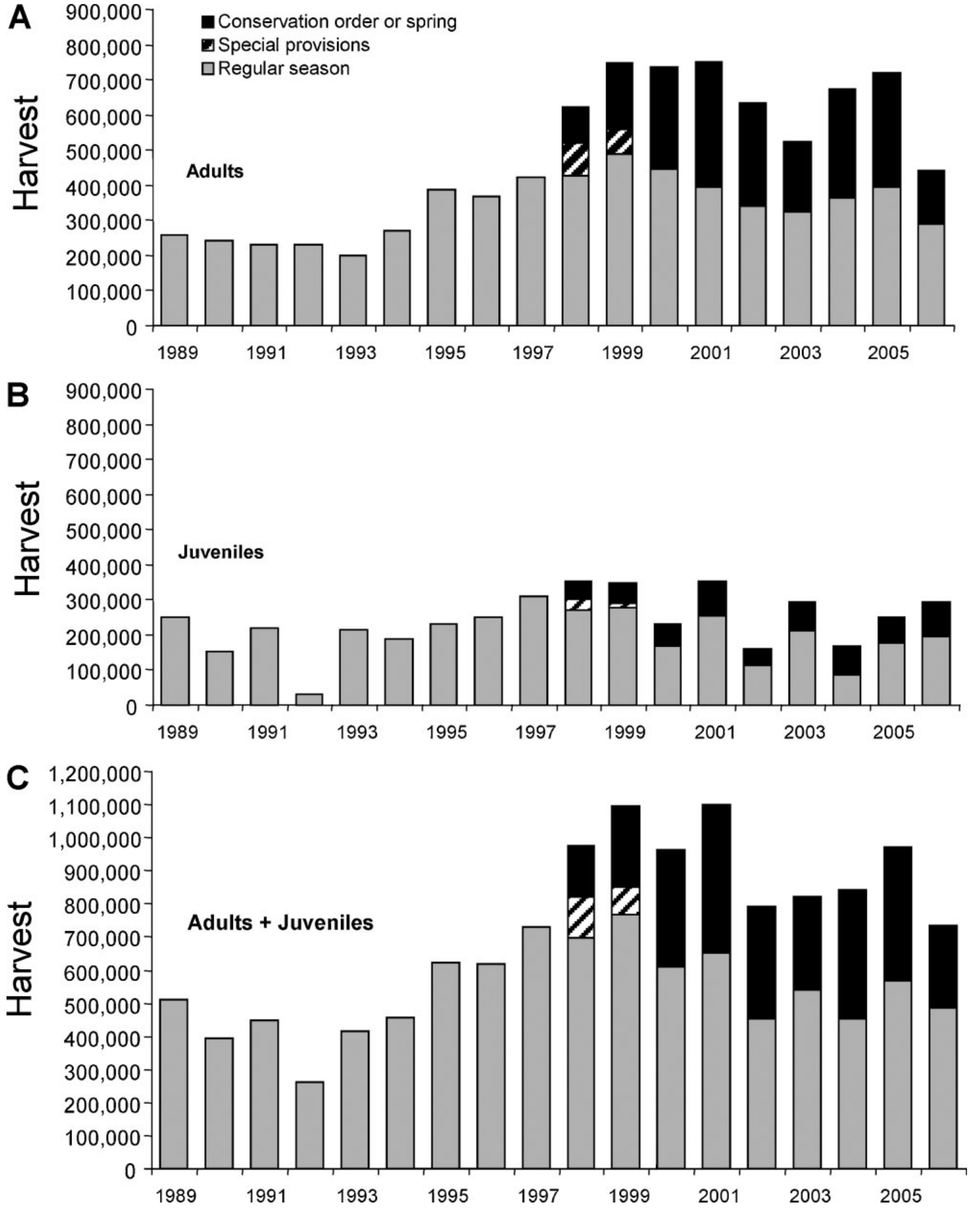

Figure 7. Harvest estimates of midcontinent snow geese harvested in Canada and United States as (A) adults, (i.e., >1 year old), (B) juveniles (<1 year old), or (C) shown with ages pooled during regular seasons (gray), special provisions (lines), or conservation-order and spring harvest (filled).

not exceed regular-season harvest in any year (Fig. 8A), despite declines during regular seasons after initiation of the conservation order. The proportion of adults harvested during the conservation order was greater than the proportion of juveniles (Fig. 8A). However, consistent with higher vulnerabilities of northern geese (Table 5), the proportion of northern adults harvested during the conservation order was somewhat higher than for southern adults (Fig. 8B), and this difference was even larger for juveniles from respective origin strata (Fig. 8C).

Estimates of Annual Survival and Recovery Probability

Six reference areas, 2003–2006.—Our survival analysis that involved 6 regions of Canada's central and eastern arctic was based on 44,415 adult snow geese banded during the period 2003–2006. Of these individuals, 2,268 were subsequently recovered by hunters (Appendix A). The number recovered from each banded sample over this period was 543 of 11,415 at QMG, 339 of 7,457 at SOU, 226 of 4,800 at BAF, 690 of 11,024 at LPB, 391 of 7,793 at CHM, and 79 of 1,926 at AKI (Appendix A).

Our estimate of the variance inflation factor for this analysis was $\hat{c} = 1.3674$. Model selection based on $QAIC_c$ indicated that the most parsimonious model $\{S(NS)\ f(g+t)\}$ was one in which survival probability was modeled as homogeneous within each of the 2 strata (northern and southern) but different between the 2 strata (Table 7). A north–south structure on survival probability $\{S(NS)\}$ was common to the top 3 models based on $QAIC_c$, and these models collectively embraced approximately 88% of the total support among the candidate models we considered (Table 7). Point estimates obtained under the $QAIC_c$-selected model indicated that snow geese from the northern stratum

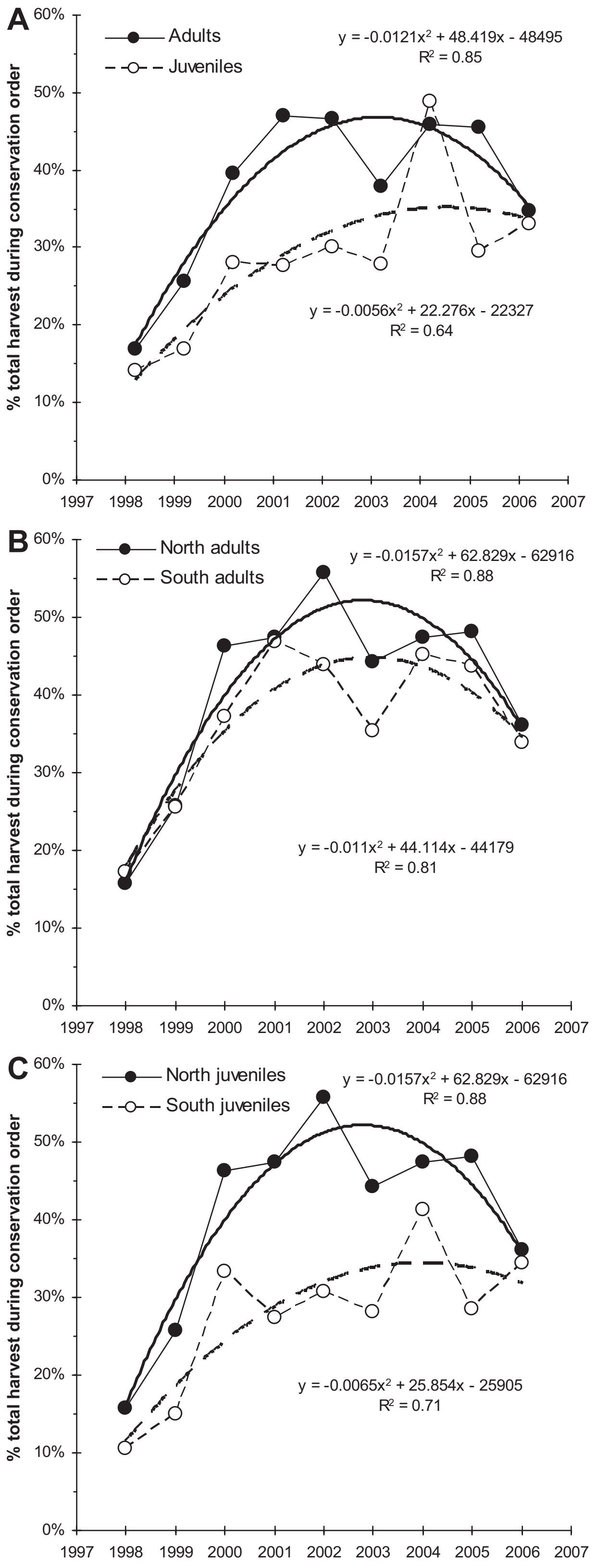

Figure 8. Percentage of total harvest of midcontinent snow geese taken during the conservation order (in the U.S.) or during spring harvest (in Canada) each year (1998–2006) for (A) north and south breeding strata combined, (B) adults by breeding stratum origin, and (C) juveniles by breeding stratum origin.

(composed of those from QMG, BAF, and SOU) survived at a higher annual rate (0.962; 95% CI = 0.765–0.995) than did snow geese from more southerly regions (0.828; 95% CI = 0.750–0.885). Overall, results of this analysis support the suggestion that survival-rate estimates from QMG were generally representative of snow geese from northern nesting areas, whereas those from LPB more likely reflected survival rates of snow geese nesting along south Hudson Bay. Thus, we proceeded with model selection and estimation of survival and recovery probabilities for snow geese stratified by northern and southern nesting areas from 1989 to 2006.

Breeding strata north and south of 60°N latitude, 1989–2006.—Our estimate of the variance inflation factor for this analysis was $\hat{c} = 1.058$. We considered 52 models in the candidate set (Appendix D), of which 39 were a priori and 13 a posteriori. We considered a posteriori models, denoted as survival stratified by NOR(.) or SOU(.), after it was clear that the best a priori models all suggested an interaction between effects of conservation order, total harvest, or time trend on survival and breeding stratum. There appeared to be changes in survival of snow geese marked south of 60°N latitude, but no changes among those marked north of that latitude. Confidence was high for an effect of breeding stratum on survival change found in all models with weight >0; the top 4 models with $\Delta\text{QAIC}_c < 2$ had 0.79 cumulative QAIC_c weight (Table 8). In general, these models reflected differences in both survival (Fig. 9) and recovery probabilities between snow geese marked north and south of 60°N latitude.

The best model, model 1 ($\{S[\text{NOR}(.)\ \text{SOU}(H)], f(g+t)\}$ with $w = 0.32$; Table 8), suggested constant survival among northern snow geese from 1989 to 2005 but a negative relationship with total annual harvest in southern snow geese (95% $\text{CI}(\hat{\beta}_{\text{H}}) = -1.15 \pm 0.40$ on the logic scale). A competing model, model 2 ($\{S[\text{NOR}(.)\ \text{SOU}(\text{CO})], f(g+t)\}$; Table 8), suggested constant survival among northern snow geese from 1989 to 2005 but an effect of the conservation order on southern snow geese. For southern geese, with pre-conservation-order seasons (i.e., <1998) coded as 0 in the design matrix of Program MARK and conservation-order (i.e., >1997) coded as 1, the parameter estimate indicated an inverse relation between existence of the conservation-order and survival of 95% $\text{CL}(\hat{\beta}_{\text{CO}}) = -0.44 \pm 0.15$ on a logit scale. Model 3 ($\{S[\text{NOR}(.)\ \text{SOU}(R+C)], f[g+t]\}$; Table 8) was similar to model 1 in function, except that model 3 partitioned effects of total annual harvest, H_i, on southern geese into regular-season harvest, R_i, and conservation-order harvest, C_i. The slope estimated between survival in southern geese and regular-season harvest, 95% $\text{CL}(\hat{\beta}_{\text{R}}) = -1.58 \pm 1.18$, was approximately 1.5 times steeper than the slope of survival and conservation-order harvest 95% $\text{CL}(\hat{\beta}_{\text{C}}) = -1.00 \pm 0.57$, although there was broad overlap in confidence between them. The last model with $\Delta\text{QAIC}_c < 2.0$ was $\{S[g * H], f[g+t]\}$ (Table 8). All other models had little empirical support.

Overall, the weight of evidence suggested that adult survival of southern snow geese declined concurrently with increased adult harvest but that survival of northern snow geese had not changed from 1989 to 2006. However, model-selection uncertainty, noted above, motivated us to calculate model-averaged estimates of survival and recovery probabilities for each year and for both

Table 7. Best of 31 models (Appendix C) for estimation of survival probability ($\hat{S}$, 2003–2005) and recovery probability ($\hat{f}$, 2003–2006) of midcontinent lesser snow geese captured and marked as adults (AHY, after-hatch year, i.e., >1 year old) in 6 regions of Canada's central and eastern arctic and subarctic. Models ranked by quasi-Akaike's Information Criterion with adjustments for overdispersion ($\hat{c} = 1.3674$) and small-sample bias (Burnham and Anderson 2002), QAICc. Only shown are models with weight ≥0.01. Regions include Queen Maud Gulf (QMG), Baffin Island (BAF), Southampton Island (SOU), La Pérouse Bay (LPB), Cape Henrietta Maria (CHM), and Akimiski Island (AKI). Model notation follows Lebreton et al. (1992): *t* denotes time-dependence (i.e., annual variation), *T* denotes linear time trend, *g* denotes group differences (i.e., differences among regions), (.) denotes constancy over time and regions. NS represents survival or recovery probability stratified according to northern (QMG, BAF, and SOU) and southern (LPB, CHM, and AKI) strata of the nesting distribution (see text and Appendix C for details).

Model	ΔQAIC$_c$[a]	QAIC$_c$ weight[b]	K[c]	Quasi deviance
$\{S(\text{NS}), f(g + t)\}$	0.0	0.41	11	43.2
$\{S(\text{NS}), f(\text{NS} + t)\}$	0.2	0.37	7	51.4
$\{S(\text{NS} * t), f(\text{NS} + t)\}$	2.8	0.10	9	49.9
$\{S(g), f(g + t)\}$	3.8	0.06	15	38.9
$\{S(.), f(g + t)\}$	5.9	0.02	10	51.1
$\{S(\text{NS}), f(\text{NS} + T)\}$	7.1	0.01	5	62.3
$\{S(g + t), f(g + t)\}$	7.4	0.01	17	38.5

[a] Difference between QAIC$_c$ of the current model and the lowest observed value.

[b] Normalized Akaike (QAIC$_c$) weight (Burnham and Anderson 2002).

[c] K = number of parameters estimated.

Table 8. Best 10 of 52 models considered (Appendix D) for estimation of survival probability ($\hat{S}$, 1989–2005) and recovery probability ($\hat{f}$, 1989–2006) for midcontinent snow geese marked, 1989–2006, as adults (AHY, after-hatch year, i.e., >1 year old). Data were structured according to stratum where marked (*g*) in Canada's central and eastern arctic and subarctic, year (*t*), 1989–2006, or unstructured (.). Strata were either northern (NOR includes QMG, BAF, SOU in Table 7 and West Hudson Bay, WHB) and southern (SOU includes LPB, CHM, and AKI in Table 7) regions of the nesting distribution (see text and Fig. 1 for details). Annual covariates include existence of the conservation order (CO = 0 for 1989–1997 [pre], and CO = 1 for 1998–2006), annual harvest (total [*H*], regular season [*R*], and conservation order [*C*], Table 5), and time trend (linear [*T*] or quadratic [T^2]), with 1989 = 1). (See text and Appendix D for details.) Models ranked by quasi-Akaike's Information Criterion with adjustments for overdispersion ($\hat{c} = 1.058$) and small-sample bias (Burnham and Anderson 2002), QAICc.

Model	ΔQAIC$_c$[a]	QAIC$_c$ weight[b]	K[c]	Quasi deviance
$\{S(\text{NOR}(.)\ \text{SOU}(H)), f(g + t)\}$	0.00	0.32	22	362.22
$\{S(\text{NOR}(.)\ \text{SOU}(\text{CO}), f(g + t)\}$	1.13	0.18	22	363.35
$\{S(\text{NOR}(.)\ \text{SOU}(R + C), f(g + t)\}$	1.45	0.16	23	361.66
$\{S(g * H), f(g + t)\}$	1.85	0.13	23	362.07
$\{S(g * \text{CO}), f(g + t)\}$	3.13	0.07	23	363.35
$\{S(g * R + C), f(g + t)\}$	4.07	0.04	25	360.28
$\{S(g * T^2), f(g + t)\}$	4.36	0.04	25	360.58
$\{S(\text{NOR}(.), \text{SOU}(T)), f(g + t)\}$	4.38	0.04	22	366.59
$\{S(\text{NOR}(.), \text{SOU}(C)), f(g + t)\}$	5.91	0.02	22	368.13
$\{S(g * T), f(g + t)\}$	6.34	0.01	23	366.56

[a] Difference between QAIC$_c$ of the current model and the lowest observed value (83092.17).

[b] Normalized Akaike (QAIC$_c$) weight (Burnham and Anderson 2002).

[c] K = number of parameters estimated.

northern and southern origins (Fig. 9). Model-averaged estimates supported the general inference of a response by southern snow goose adults but not by those from the northern breeding stratum. The lowest survival probability estimated was 0.87 for northern geese and 0.82 for southern geese. We suspect that differences in survival response between northern and southern nesting snow geese was due to an interplay between 1) differences in timing of migration (Figs. 5 and 6) and location of harvest (Fig. 3) and 2) large differences in contribution from the larger stratum of snow geese that nested north of 60°N latitude compared to the smaller stratum nesting south of this latitude (Fig. 2). Weighting survival estimates by relative contributions of the northern (90%) and southern (10%) strata, we obtained $\hat{S}^{w}_{2005} = 0.87$ as a composite-weighted estimate for the midcontinent population in the most recent year of the time series.

Estimates of survival probability for southern geese during 2003–2005 appeared to be consistent whether estimated using models from the 6-region analyses using 2003–2006 data ($\hat{S}^{\text{south}}_{2003-2005} = 0.83$; Table 7) or estimated for 2003–2005 from the north–south analysis based on the full 1989 to 2006 data ($\hat{S}^{\text{south}}_{2003-2005} = 0.83$; Table 8). However, there was a large apparent discrepancy between respective estimates for northern geese of $\hat{S}^{\text{north}}_{2003-2005} = 0.96$ from the 6-region analysis and $\hat{S}^{\text{north}}_{2003-2005} = 0.87$ from the north–south analysis.

Probability of recovery in the top models was structured with annual variation additive to an effect of origin (Table 8). Recovery was unequivocally greater for snow geese from the southern breeding stratum than from the north. For example, when we restructured the top a priori model $\{S(g * H), f(g + t)\}$ as $\{S(g * H), f(g * t)\}$ for an interaction effect between origin and year on recovery probability, QAIC$_c$ increased from 1.85 to 14.43 (Appendix D). Likewise, when we similarly restructured the top a

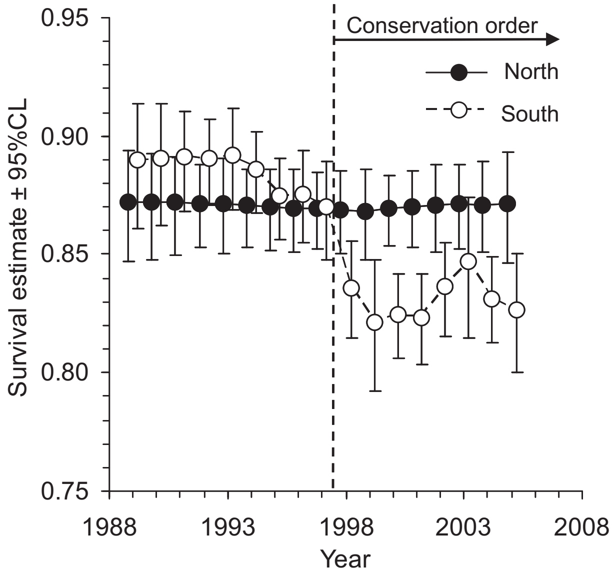

Figure 9. Model-averaged estimates (±95% confidence limits) of survival probability, 1989–2005, of midcontinent snow geese marked as adults (AHY, after-hatch year) in the northern (north of 60°N latitude, filled circles) or southern (south of 60°N latitude, solid circles) nesting stratum in Canada's central and eastern arctic and subarctic. Heavy vertical dashes show start of the conservation order. We offset symbols by 0.2 years to reduce overlap between northern and southern strata.

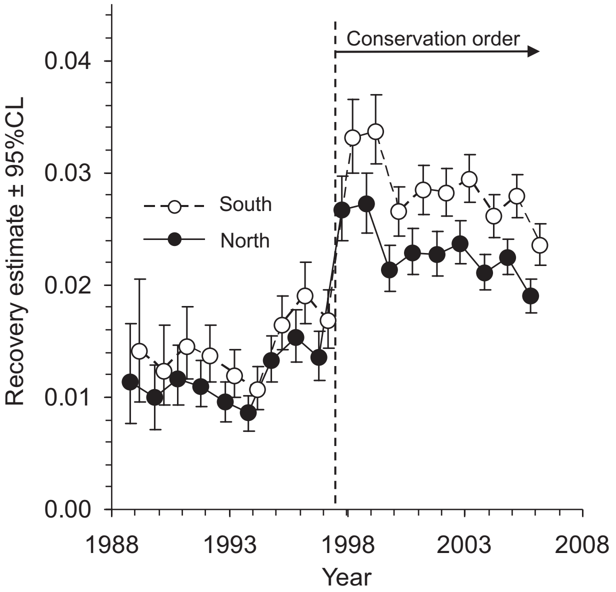

Figure 10. Model-averaged estimates (±95% confidence limits) of recovery probabilities, 1989–2006, for midcontinent snow geese marked as adults (AHY, after-hatch year) in the northern (north of 60°N latitude, filled circles) or southern (south of 60°N latitude, solid circles) nesting stratum, in Canada's central and eastern arctic and subarctic. Note declining trend over time since start of the conservation order during 1998–1999 harvest period (heavy vertical dashed lines). We offset symbols by 0.2 years to reduce overlap between confidence intervals of northern and southern strata.

posteriori model $\{S[\mathrm{NOR}(.)\ \mathrm{SOU}(H)], f(g+t)\}$, $\mathrm{QAIC_c}$ increased by 12.43. From the best-supported model, the stratum effect on recovery probability was 95% $\mathrm{CL}(\hat{\beta}_g) = -0.22 \pm 0.06$ on the logit scale, with the northern stratum coded as 1 and southern as 0 in the Program MARK design matrix.

Model-averaged estimates of recovery probability were only approximately 0.01 before increasing in 1995 (Fig. 10), the first year of progressive introduction of legbands with a toll-free telephone number engraved on them so that hunters could more easily report bands. The highest recovery probabilities estimated for the time series in our study were only 0.034 among southern snow geese and 0.027 among northern snow geese in the 2 years following start of special-harvest measures to complement the 1998 season. Even so, recovery probabilities declined thereafter to approximately 0.03 and 0.02 for respective breeding strata; by 2004–2006, upper 95% CL of recovery probabilities had declined to below the lower confidence limits of respective estimates for 1998 and 1999. Note that reward bands were applied to snow geese from 2003 to 2005 and were included in our survival analysis. Thus, higher reporting rates for those bands should have increased recovery rates.

When we plotted annual-survival estimates as a function of annual harvest, intercepts provided an estimate of survival probability in the absence of harvest (Alisauskas et al. 2006*a*). In the absence of harvest, predicted survival of snow goose adults marked near southern breeding areas was 0.923 compared to 0.872 for northern geese (Fig. 11A). Clearly, some form of additive mortality was evident for southern geese, but harvest appeared to have been below a threshold where such additivity of harvest mortality to natural mortality might occur among northern geese. In accordance with the most recent survival probabilities for each breeding stratum, and direct estimates of harvest from reward bands (Table 5), recovery and thus harvest rates of southern snow geese were consistently higher than those for northern geese (Figs. 10 and 11B).

Long-Term Recovery and Harvest Rates

It can be instructive to consider current harvest rates in the context of historical trends. Based solely on direct recoveries of 1) birds with tarsal bands, 2) birds with control bands in reward band studies (but not birds with reward bands), and 3) birds with normal metal legbands, recovery rate declined substantially from 1971 until 1994, when the lowest rates occurred in both adult and juvenile geese (Fig. 12A). This period was before the beginning of the use of 1–800 legbands in 1995, which were designed to enhance band-reporting rates.

Adjusting recovery probabilities for band-reporting probability provided estimates of harvest rate (Fig. 12B), which declined from approximately 0.15 for adults in 1971 to a minimum of approximately 0.01 for both age groups in 1994, after which there was a moderate increase. However, harvest probability of adults, pooled between northern and southern geese, did not exceed approximately 0.04 after 1988, despite 2- to 3-fold increases in annual harvest of adults (Fig. 13). Mean harvest rates increased from 0.024 during 1989–1997 for northern geese to 0.027 during 1998–2006 and from 0.031 to 0.037, respectively, for southern geese (Fig. 14).

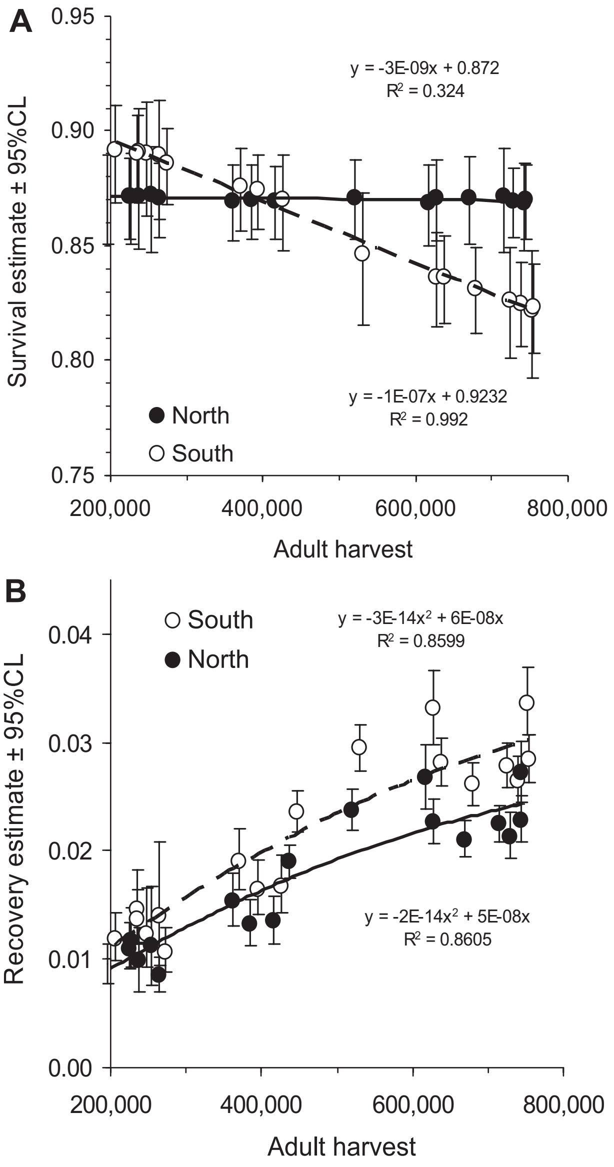

Figure 11. Probabilities (±95% confidence limits) of (A) survival, 1989–2005, and (B) recovery, 1989–2006, for midcontinent snow geese marked as adults (AHY, after-hatch year, i.e., >1 year old) scaled against total annual harvest of adults. We stratified data according to whether geese were captured in the northern (north of 60°N latitude, filled circles) or southern (south of 60°N latitude, solid circles) nesting stratum in Canada's central and eastern arctic or subarctic. Linear regression equations and coefficients of determination are for point estimates only. Note that *y*-axis does not cross the origin, so estimates of intercepts should be read from respective linear-regression equations. We offset symbols by harvest of 5,000 to reduce overlap between confidence intervals of northern and southern strata.

Estimation of Population Size and Growth Rate

Application of Lincoln's method to harvest and harvest rate for each age group provided age-specific estimates of population size for midcontinent snow geese at the time of marking in August (Fig. 15); we did not calculate population estimates in years with <20 direct recoveries. Regardless, low harvest probabilities in some years occasionally resulted in poor population estimates for both adults and young (e.g., 95% CL($\hat{N}^{\mathrm{AHY}}_{1994}$) = 21 ± 12 million). Otherwise, annual estimates of population size, and especially the increasing trend in population size over time, appeared credible (Fig. 15).

Bias adjustment to weighted harvest rates from northern and southern strata according to stratum-specific contributions to the metapopulation (equation 8) did not result in estimates of $\hat{\lambda}$ that were consistently different from unadjusted estimates (Table 9). So, we based inference on unadjusted estimates since those were derived from times series with fewer years of missing data. In general, growth rate in number of young alive in August was positive but lower than for adults in all time periods we considered (Table 9).

Long-term trajectory of August estimates of adults (1971–2006) unadjusted for bias was best fit by a logistic-growth model (Table 10). No other models in the candidate set had any support in relation to the logistic model, suggesting continued population increase of adult snow geese, although at a reduced rate. This conclusion was supported by the results from our structural-change analysis. Using the longest possible time series for AHY data, the most parsimonious model had strong support for 2 breakpoints: 1988–1989 and 1993–1994. If we combined AHY data with HY data, the most parsimonious models had strong support for only one breakpoint: 1993–1994. Presence of a breakpoint in 1993–1994 was also indicated in our subsequent analysis of the midwinter count data. When we restricted AHY data to 1990–2006, a model with one breakpoint at 2001–2002 was best supported in the data, although the difference in the slopes between the 2 segments was marginal (before 2001–2002: $\hat{\beta} = 0.121$; after 2001–2002: $\hat{\beta} = 0.043$; $0.05 < P < 0.10$). Inclusion of HY data in the analysis did not change the overall results. The lack of a second breakpoint in 1993–1994 for this subset of our data reflects the smaller sample size (length of time series) used in this analysis. Estimated slopes for each segment were positive and did not suggest population decline over this interval. This result is consistent with our simple log-linear regression analysis of HY and AHY data from this period (Table 9).

We considered 9 models from which to choose the best description of the full-time series available from 1955 to 2008 to assesses changes in the trajectory of annual midwinter counts, W_i ($n = 54$ counts, Table 11). Note that we could not compare the 2 most recent W_i to contemporaneous $\hat{N}_i$, which were unavailable for years after 2006. The best model seemed unequivocally to be a cubic fit of W_i to year with 1955 coded as year $i = 1$ (Table 11, Fig. 16) with model weight $w = 0.92$. The next-best model was a logistic growth form with $\Delta\mathrm{AIC_c} = 5.15$ and $w = 0.07$. Logistic and exponential growth models had little support from this full time series of midwinter count data. Thus, based on the full set of midwinter count data, the cubic model suggested that counts had leveled off in the last 10 years.

We inferred a similar leveling-off of counts for the time series of W_i from 1971 onwards ($n = 38$ counts with 1971 coded as year $i = 1$) except that the best models were equivocal among logistic ($w = 0.26$), cubic ($w = 0.24$), and linear ($w = 0.24$) forms. There was little or no support for exponential growth for either the 1955–2008 ($w = 0.00$) or 1971–2008 ($w = 0.02$) time series, requiring that its use be restricted to shorter time series.

These results were generally consistent with our structural-change analysis. Among a candidate model set of segmented models with 0–4 breakpoints (i.e., 0–4 separate time series in the regression model), only models with one breakpoint had any significant support in the data, using normalized AIC weights.

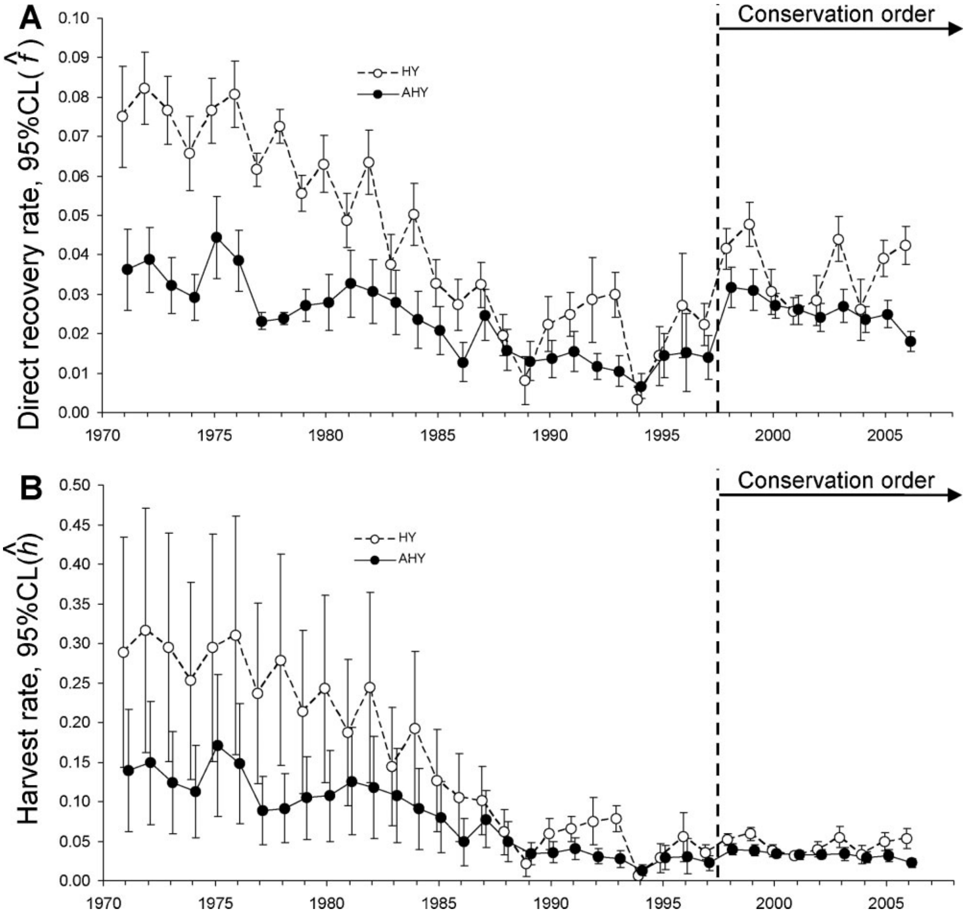

Figure 12. Estimates (±95% confidence limits) of (A) direct recovery rate and (B) harvest rate of adult (AHY, after-hatch year, i.e., >1 year old) and juvenile (HY, hatch year, i.e., <1 year old) midcontinent snow geese marked, 1971–2006, in Canada's central and eastern arctic and subarctic. We estimated direct-recovery rate using only snow geese without neckbands and reward bands, and we did not stratify our estimate by northern (those marked north of 60°N latitude) and southern (south of 60°N latitude) origins in arctic Canada. Heavy vertical dashes show start of the conservation order. We offset symbols by 0.2 years to reduce overlap of confidence intervals between AHY and HY snow geese.

Both generalized fluctuation and F tests gave similar results for overall support. When the analysis was conducted using all available data, the most parsimonious breakpoint was in 1993–1994, before implementation of the conservation order.

The estimated slope before the breakpoint $\hat{\beta} = 0.028$ was consistent with an exponentially increasing population trajectory, whereas after the breakpoint, the population trajectory was actually negative, $\hat{\beta} = -0.017$, although the confidence interval of

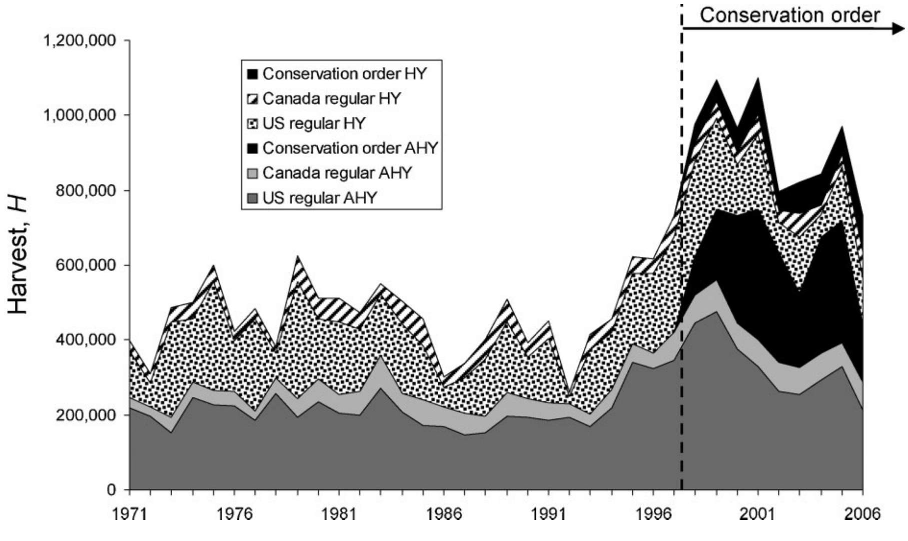

Figure 13. Historical annual harvest of midcontinent snow geese adults (AHY, after hatch year, i.e., >1 year old) and juveniles (HY, hatch year, i.e., <1 year old) in Canada and the United States during regular seasons (1971–2006) and the conservation order (1998–2006).

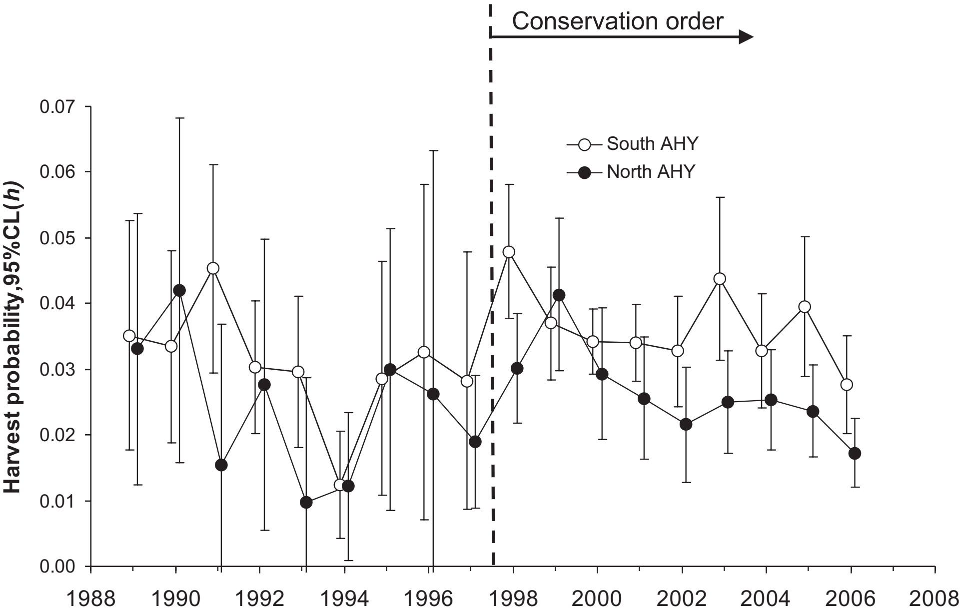

Figure 14. Comparison of harvest probability for midcontinent snow goose adults marked in northern and southern nesting strata before (1989–1997) and during the conservation order (1998–2006), in Canada's central and eastern arctic and subarctic. Harvest rates were estimates of direct-recovery rates adjusted for band-reporting rate. Heavy vertical dashes show start of the conservation order. We offset symbols by 0.1 years to reduce overlap of confidence intervals between northern and southern strata.

the estimate bounded zero. When we restricted the analysis to 1990–2008, the results were essentially identical, with support for a breakpoint in 1993–1994. This result, combined with a similar result from the analysis of Lincoln estimates, suggested that the identification of a breakpoint at 1993–1994 was not likely to be an artifact of the range of years used in the analysis.

Percent annual increase in midwinter counts during 1990–1998, a 9-year span of seasons leading up to and including the first year of special harvest incentives, was 7.0 ± 3.1%, but declined to −1.8 ± 1.7% during 1998–2006, when special harvest incentives were in place (Table 12, Fig. 16). However, use of all available midwinter counts since start of special harvest incentive (1998–2008) yielded an annual growth rate of 0.1 ± 2.0% because of a substantial increase in counts in 2007 and 2008 compared to trajectory of counts from the preceding 9 winters. By comparison, the percent annual increase in Lincoln estimates, based on pooled harvest rates, of adult snow geese was 14.4 ± 4.0% for 1990–1998 and 5.0 ± 5.5% for 1998–2006 (Table 9). Thus, midwinter counts produced consistently lower estimates of annual population growth (Table 12).

We made direct comparisons between midwinter counts, W_i, and Lincoln estimates, $\hat{N}_i$, for 1971–2006, which were correlated ($r = 0.17$, $n = 35$, $P < 0.001$, Fig. 17A) but better described by a quadratic rather than linear model. During the 1970s, when Lincoln estimates were generally <3 million and midwinter counts were <2 million, Lincoln estimates were only about 2 times greater than winter counts. There has since been a large divergence in values, and the magnitude of this difference, expressed as a ratio, has been increasing exponentially over time. Currently, Lincoln estimates of midcontinent adult snow geese are about 10 times the number of light geese counted during winter (Fig. 17B).

DISCUSSION

Our results suggest that changes in harvest management of midcontinent snow geese designed to reduce adult survival, with the ultimate goal being population reduction for alleviation of damage to arctic vegetation, have fallen short. Although there was some uncertainty between the conclusions of reduced growth versus stationarity during the conservation order, there was no strong evidence that the midcontinent population of snow geese had declined as a result of increased harvest. Liberalization of harvest regulations during regular hunting seasons and implementation of special conservation measures increased total harvest but not sufficiently to reduce adult survival to levels that were previously advocated (i.e., <0.80; Rockwell et al. 1997, Cooke et al. 2000, Rockwell and Ankney 2000) to reduce the size of the midcontinent population. Despite unprecedented opportunities to hunt midcontinent snow geese in Canada and the United States, total harvest apparently has not increased sufficiently to outpace concurrent population growth and result in harvest rates > 0.05. Instead harvest rates remain very low and appear to have declined since the first harvest period (1998–1999) that included spring harvest in either Canada or the United States. Apparently, this population, whose adult members enjoy a 0.87 probability of surviving for another year, cannot be reduced solely by harvesting only 1 out of every 40 adults each year.

Is the Midcontinent Population Declining?

Two available metrics assumed to reflect changes in annual population size of midcontinent snow geese are winter counts, W_i (Eggeman and Johnson 1989), and August population size, $\hat{N}_i$, estimated using Lincoln's (1930) method of dividing total annual harvest by contemporaneous harvest rate (Boyd 1976, Boyd et al. 1982, Alisauskas et al. 2009). Winter counts were

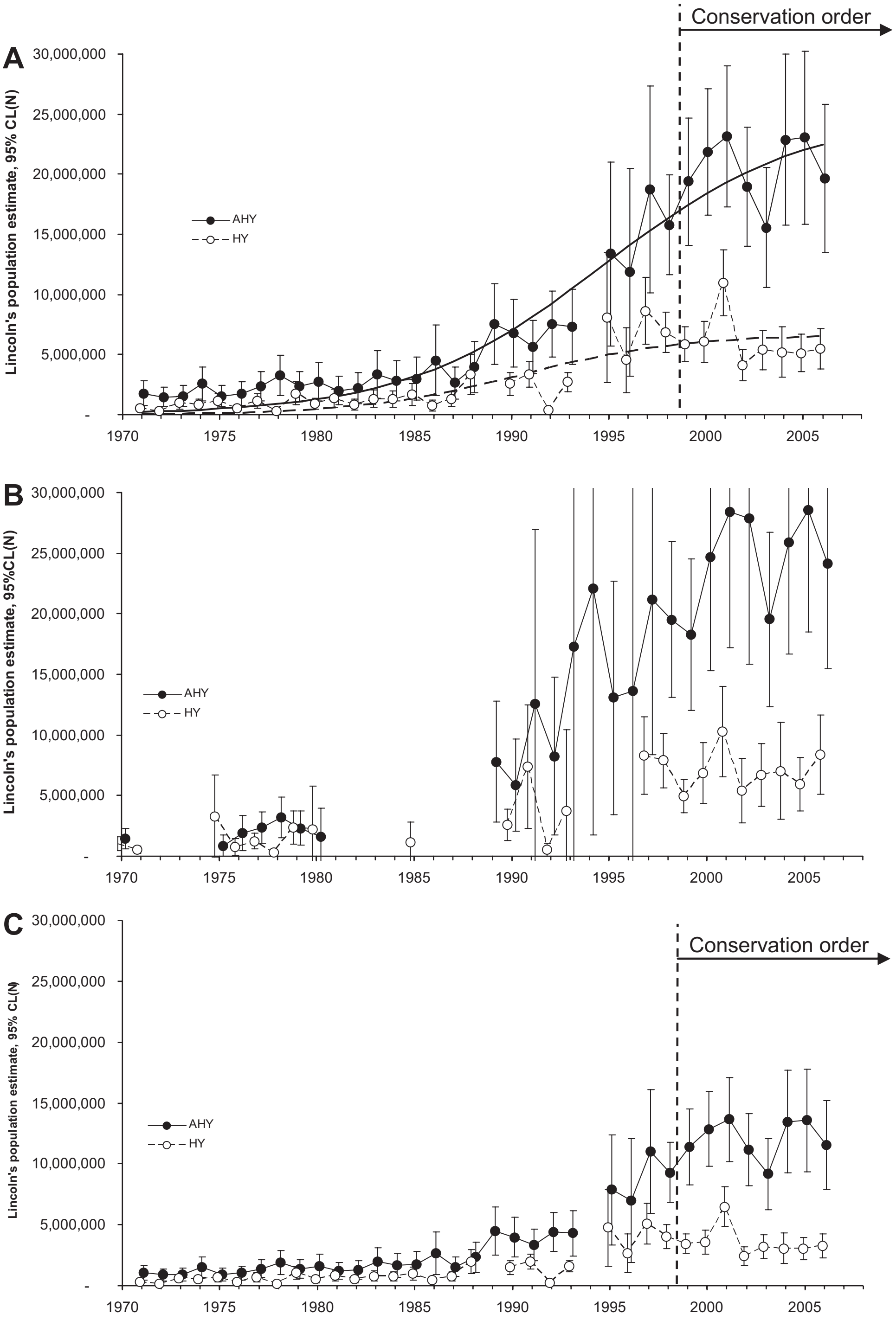

Figure 15. Abundance of midcontinent lesser snow goose adults (AHY, after hatch year, i.e., >1 year old) and juveniles (HY, hatch year, i.e., <1 year old) in August, 1971–2006, in Canada's central and eastern arctic and subarctic, estimated using Lincoln's (1930) method. Shown are population sizes (±95% confidence limits) estimated (equation 6) using (A) unweighted harvest rates (equation 7) and total harvest (Fig. 7A,B), (B) harvest rate weighted by number of geese in northern and southern strata (equation 8) and total harvest (Fig. 7A,B), and (C) unweighted harvest rate (equation 7) and total harvest after bias correction of 0.589 (P. Padding, U.S. Fish and Wildlife Service, personal communication; cf. Johnson et al., in press). Not shown are estimates calculated from <20 direct recoveries. Heavy vertical dashes show start of the conservation order.

intended to provide total counts, or represent a constant fraction of total numbers, of waterfowl from specific areas each year. However, Eggeman and Johnson (1989) documented in the Atlantic Flyway that the intended consistency of coverage was not met by various states over time. Additional problems with winter counts include absence of a geographic sampling frame, lack of knowledge about what constitutes a sample unit, lack of a clear sampling design, and variation in sampling effort, coverage, personnel and methodology (aircraft, boat, and vehicle). Also, attempts to count free-ranging geese by eye in large aggregations are known to result in underestimates of true numbers and this bias increases with flock size (Spinner 1949, Ely et al. 1993, Boyd

Table 9. Annual rates of population change ($\hat{\lambda}$) ±95% confidence limits of midcontinent lesser snow geese from 1970 to 2006 estimated from annual population estimates using Lincoln's (1930) method for adult and young geese separately. Estimates are for juveniles (HY, hatch year, i.e., <1 year old), adults (AHY, after-hatch year, i.e., >1 year old), or sum of age groups (HY + AHY). Two sets of Lincoln estimates for $\hat{\lambda}$ ±95% confidence level involved (A) harvest rate calculated from direct recoveries pooled between northern and southern breeding origins, and (B) harvest rate weighted by the presumed contribution of northern and southern breeding geese to the midcontinent population, following equation 8.

	(A) Unadjusted for heterogeneous $\hat{h}$									**(B) Adjusted for heterogeneous $\hat{h}$**								
	HY			**AHY**			**HY + AHY**			**HY**			**AHY**			**HY + AHY**		
Time period	***n*[a]**	**$\hat{\lambda}$**	**95% CL**	***n***	**$\hat{\lambda}$**	**95% CL**	***n***	**$\hat{\lambda}$**	**95% CL**	***n***	**$\hat{\lambda}$**	**95% CL**	***n***	**$\hat{\lambda}$**	**95% CL**	***n***	**$\hat{\lambda}$**	**95% CL**
1970–1994	25	1.069	0.038[b,c]	25	1.076	0.015[b]	25	1.071	0.012[b]	12	1.083	0.075[b]	12	1.114	0.031[b]	12	1.084	0.027[b]
1971–2006	36	1.085	0.019[b]	36	1.095	0.008[b]	36	1.091	0.010[b]	22	1.081	0.024[b]	24	1.096	0.012[b]	20	1.087	0.012[b]
1971–1998	28	1.099	0.029[b]	28	1.094	0.013[b]	28	1.094	0.013[b]	14	1.106	0.038[b]	16	1.113	0.016[b]	12	1.103	0.015[b]
1990–1998	9	1.199	0.187[b]	9	1.144	0.040[b]	9	1.153	0.051[b]	6	1.146	0.155	9	1.140	0.060[b]	6	1.146	0.069[b]
1998–2006	9	0.962	0.089	9	1.050	0.055	9	0.988	0.051	9	1.034	0.075	9	1.029	0.051	9	1.028	0.049

[a] Sample size in years.
[b] Confidence limits exclude 1.
[c] Lincoln estimates span 1970–1994 because harvest estimates ($\hat{H}_i$) were not available from Canada before 1970.

2000). Thus, a large drawback associated with winter counts is the requirement for individuals to visually estimate numbers of geese in large aggregations, often in the tens or hundreds of thousands in each flock, comprised of both snow and Ross's geese in unknown proportions.

Other issues also limit inferences about population change in snow geese from year to year or over longer periods using winter counts. There is no knowledge about the detectability of snow goose flocks in any year, even if survey coverage was documented, or about spatial variation in detection of geese and in ability to count them and how this may change from year to year and among observers. Changes in winter distribution, such as midcontinent snow geese shifting northward, may not be completely captured by the counting effort (McLandress 1979, Abraham et al. 2005, Brook et al., 2009). Eggeman and Johnson (1989) suggested that substantial unmeasured error associated with coverage and counts has limited the utility of the winter count as a sensitive index to population change and concluded by urging caution when making comparisons of winter counts between years or states in the Atlantic Flyway. Similar issues probably exist in other flyways. For instance, McLandress (1979) documented how growth and winter expansion of Ross's geese in California was undetected by the usual winter counts.

Estimates of breeding snow geese based on aerial photography are available for specific known colonies in the Canadian arctic (e.g., Kerbes et al. 2006), but these are not done annually, nor are all known colonies surveyed in the same year (Appendix F). Use of these estimates as a metric of metapopulation size also is compromised by incomplete detection of all colonies, a focus only on nesting birds of which there may be very few in years of late snow melt, and untested assumptions about detection of geese during photo interpretation (Boyd et al. 1982). Despite apparent increases in some breeding regions and declines in others (Appendix F), the metapopulation of known breeders appears to have continued to increase an average of 3.0% each year during the conservation order, compared to 5.0% for adult snow geese derived using Lincoln's estimates of abundance in August (Table 9). In contrast, winter counts of light geese during the conservation order changed annually by −1.8% from 1998 to 2006, or 0.1% from 1998 to 2008 (Table 12).

The abundance of nonbreeding birds relative to nesters may have changed substantially as populations have grown (Alisauskas et al. 2009). Boyd et al. (1982) noted that both midwinter counts of snow geese, W, and photo estimates in the arctic, $\hat{P}$, underrepresented the population size of geese alive in August, $\hat{N}$. The ratio of $\hat{N}/W$ from estimates of Boyd et al. (1982) ranged

Table 10. Candidate set of models fit to unadjusted Lincoln estimates, $\hat{N}_i$, of midcontinent snow goose adults (AHY, after-hatch year, i.e., >1 year old) in August, 1971–2008, in Canada's central and eastern arctic and subarctic (see Fig. 15A), where $t = \text{year}_i - 1970$.

Model	**ΔAIC$_c$[a]**	**AIC$_c$ weight[b]**	***K*[c]**
$N_i = \frac{K}{1+(K-N_0)N_0^{-1}e^{(-rt)}}$	0.00	0.95	4
$N_i = \beta_0 + \beta_1 t + \beta_2 t^2 + \beta_3 t^3$	7.22	0.03	5
$N_i = \beta_0 + \beta_1 t + \beta_2 t^2$	8.78	0.01	4
$N_i = \beta_1 t + \beta_2 t^2$	9.17	0.01	3
$N_i = \beta_1 t + \beta_2 t^2 + \beta_3 t^3$	11.48	0.00	4
$N_i = N_0 e^{rt}$	15.81	0.00	3
$N_i = \beta_0 + \beta_1 t$	32.67	0.00	3
$N_i = \beta_1 t$	37.48	0.00	2

[a] Difference between Akaike's Information Criterion with adjustments for small-sample bias (QAIC$_c$; Burnham and Anderson 2002) of the current model and the lowest observed value.
[b] Normalized Akaike (AIC$_c$) weight (Burnham and Anderson 2002).
[c] K = number of parameters estimated.

Table 11. Candidate set of models fit to winter counts, W_i, 1955–2008, of midcontinent light geese (snow and Ross's goose adults [AHY, after-hatch year, i.e., >1 year old], and juveniles [HY, hatch year, i.e., <1 year old]), in the Central and Mississippi Flyways including the West Central Flyway, where $t = \text{year}_i - 1954$.

Model	**ΔAIC$_c$[a]**	**AIC$_c$ weight[b]**	***K*[c]**
$W_i = \beta_0 + \beta_1 t + \beta_2 t^2 + \beta_3 t^3$	0.00	0.9211	5
$W_i = \frac{K}{1+(K-N_0)N_0^{-1}e^{(-rt)}}$	5.15	0.0700	4
$W_i = \beta_0 + \beta_1 t$	10.06	0.0060	3
$W_i = \beta_0 + \beta_1 t + \beta_2 t^2$	11.58	0.0028	4
$W_i = \beta_1 t + \beta_2 t^2$	21.28	0.0000	3
$W_i = N_0 e^{rt}$	19.96	0.0000	3
$W_i = \beta_1 t + \beta_2 t^2 + \beta_3 t^3$	23.62	0.0000	4

[a] Difference between Akaike's Information Criterion with adjustments for small-sample bias (QAIC$_c$; Burnham and Anderson 2002) of the current model and the lowest observed value.
[b] Normalized Akaike (AIC$_c$) weight (Burnham and Anderson 2002).
[c] K = number of parameters estimated.

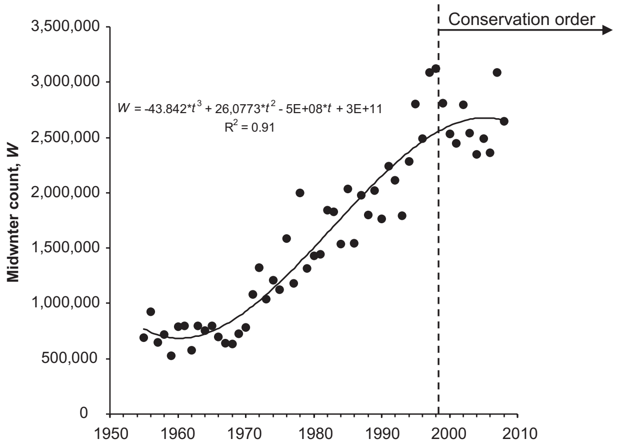

Figure 16. Midwinter counts of light geese (snow and Ross's geese) with adults (AHY, after hatch year, i.e., >1 year old) and juveniles (HY, hatch year, i.e., <1 year old) combined in the Central and Mississippi Flyways 1955–2008. Included are counts done in the west Central Flyway in addition to midcontinent counts from both flyways (K. Kruse and D. Fronczak, United State Fish and Wildlife Service, unpublished data). Fitted line is a third-order polynomial where $t = \text{year} - 1954$. Heavy vertical dashes show start of the conservation order.

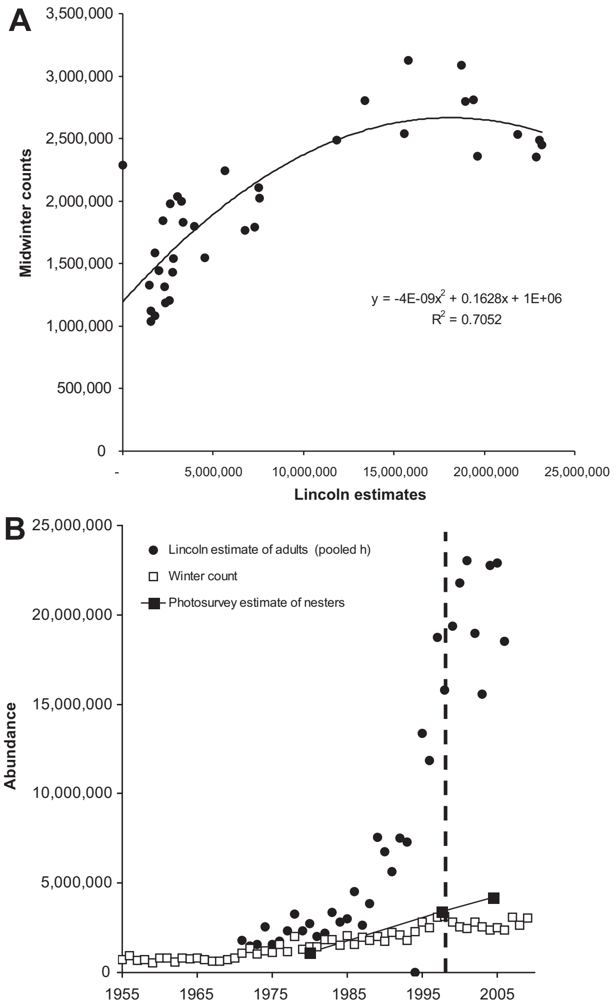

Figure 17. (A) Quadratic relationships between winter counts of midcontinent snow geese including counts from the west Central Flyway (Kruse 2009) and Lincoln's estimates of abundance in August, 1971–2006, in Canada's central and eastern arctic and subarctic. (B) Time series of winter counts of light geese, 1955–2009, and Lincoln's estimates of August population size; also shown are nesting light geese estimated in June by aerial photography at known colonies in Canada's central and eastern arctic and subarctic (Kerbes et al. 2006; preliminary estimates from 2003 to 2006 were supplied by K. Meeres, Canadian Wildlife Service); only nesting geese from regions north of 60°N latitude shown, and nonbreeding geese are not sampled (Appendix F). Heavy vertical dashes show start of the conservation order.

Table 12. Annual rates of population change ($\hat{\lambda}$) ±95% confidence limits, 1969–2006 estimated from the midwinter index, which is a count of snow geese and Ross's geese combined, including adults (AHY, after-hatch year, i.e., >1 year old) and juveniles (HY, hatch year, i.e., <1 year old). Midwinter count data (K. Kruse and D. Fronczak, United States Fish and Wildlife Service, unpublished data) covers the midcontinent area of the Mississippi and Central Flyways, including the west Central Flyway.

Time period	n[a]	$\hat{\lambda}$	95% CL
1969–1994	26	1.029	0.008[b]
1971–2006	36	1.027	0.005[b]
1971–1998	28	1.034	0.007[b]
1990–1998	9	1.070	0.031[b]
1998–2006	9	0.982	0.017
1998–2008	11	1.001	0.020

[a] Sample size in years.

[b] Confidence limits exclude 1.

between 1.2 and 3.7 from 1970 to 1979, which was remarkably consistent with the range of between 1.1 and 2.4 from our Lincoln estimates obtained for the same years using a pooled harvest rate (Fig. 18). This ratio has increased markedly since, and was ≥9 by 2004, because growth in August numbers apparently increased far more rapidly than did the ability to count all midcontinent geese during winter.

We believe that, of the metrics considered, Lincoln's method allows superior inference about annual abundance and rates of growth of the midcontinent population of snow geese. The method relies on a number of assumptions, but these appear to be reasonably satisfied and the method has produced credible estimates of annual rates of population change and of population size for other species of arctic-nesting geese (Alisauskas et al. 2009). Lincoln's method uses annual estimates of harvest and harvest rate that are both based on sound statistical methodology and inference. Instead of a count done over a few days intended to represent all geese over their entire range, Lincoln's method has advantages in that once a marked sample of geese is released, the second sample by hunters occurs over a wide geographic area and over a longer time period. Unlike winter counts and arctic photosurveys of nesting geese, the sampling coverage provided by hunters ensures that the scope of inference from Lincoln's method is range-wide in the case of midcontinent snow geese (Boyd et al. 1982, Alisauskas et al. 2009). Lincoln's estimator is currently the only tractable method for obtaining annual estimates of total population size for midcontinent snow geese. Other indices, such as midwinter surveys or photographic surveys of nesting adults, account for an unknown proportion of the overall population in a given year and probably have provided inferences about population size that are biased low. For example, $\hat{\lambda}_{1971-1994} = 1.114$ for adults estimated with bias-corrected harvest rates, which was similar to the estimate of $\hat{\lambda}_{1969-1994} = 1.107$ projected by Rockwell et al. (1997) for approximately the same period using vital rates measured at the

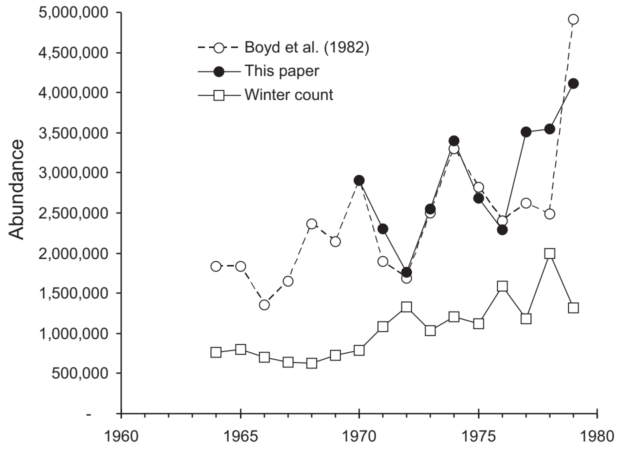

Figure 18. Lincoln's estimates of August population size (sum of adults [AHY, after hatch year, i.e., >1 year old] and juveniles [HY, hatch year, i.e., <1 year old]): open circles, 1964–1979, are estimated from Boyd et al. (1982), and closed circles, 1970–1979, are estimates using a pooled harvest rate from our study (see Fig. 15A); open squares are winter counts in the Central and Mississippi Flyways, 1964–1979.

LPB colony. However, both of these were considerably higher than $\hat{\lambda}_{1969-1994} = 1.029$ estimated from midwinter counts for the same period (see below).

Despite differences in assumptions and methodology among all 3 metrics of abundance, there has been broad agreement in support of the inferred population increase before the start of the conservation order (Kerbes et al. 2006, Kruse et al. 2009, Alisauskas et al. 2009). This agreement was also recognized by Boyd et al. (1982) for the 1960s and 1970s. However, different methods led to different conclusions about population change during the conservation order; Lincoln's estimates for 1998–2006 suggested either unimpeded growth or continued growth at a reduced rate (Table 9), whereas winter counts suggested a decline in population size from 1998 to 2006 or population stability from 1998 to 2008 (Table 12).

Overall, we conclude that the midcontinent population of snow geese not only has not declined, but also has continued to grow during the conservation order, although at a reduced rate. We noted a response in survival probability only in a small proportion of its members that nested along the southern periphery of its breeding range during early phases of the conservation order. Similarly, Ross's geese also appear to have continued to increase in abundance despite their inclusion in the United States conservation order (Alisauskas et al. 2009).

Special conservation measures to arrest population growth of greater snow geese, by comparison, appeared to have been successful initially (Reed and Calvert 2008). Survival was reduced from 0.83 during the 8 years before the measures to 0.73 for the first 5 years of the program, although there was considerable annual variation in survival during both periods (Calvert and Gauthier 2005). However, population growth has resumed in recent years such that the population size is now back to pre-conservation measures level (Calvert et al. 2007; J. Lefebvre, CWS, unpublished data). It appears that, in the case of greater snow geese, harvest rates (adults: 0.134 [95% CI: 0.115–0.153], juveniles: 0.433 [95% CI: 0.206–0.660]) were sufficiently high in the first few years of implementation of special measures to result in a negative growth rate, but these harvest levels could not be maintained over time (Calvert et al. 2007). This reduction in total harvest is likely due to a steady decline in the number of hunters participating in spring harvests (9,643 active hunters in 1999 vs. 3,063 in 2008; B. Collins and M. Gendron, CWS, unpublished data) and behavioral adaptations of geese in response to increased hunting pressure (Béchet et al. 2003). Implementation of a special conservation order in the United States states of the Atlantic Flyway in 2008–2009 could have an impact on population growth of greater snow geese if increases in realized harvest are sufficiently high (Gauthier and Reed 2007).

Implications of Harvest Estimation

Unbiased harvest estimation is central not only to understanding removals of geese from the population, but also for estimation of August population size. Boyd (1976) justified his seminal application of Lincoln's method to snow-goose-population estimation with the assumption that total harvest was estimated with sufficient accuracy. Although procedures for harvest estimation in both Canada and the United States were standardized in the 1970s (Padding et al. 2006), there have been notable changes to methodology in the United States since 1999 (Fig. 4). Beyond the switch from the mail-in questionnaire sampling to the HIP program for sampling hunter harvest, Johnson et al. (in press) suggested that regular-season harvest estimates in the United States are biased high by 1.7 times. It remains undetermined if such an apparent bias might apply to Canadian harvest estimates. Use of estimates adjusted for this apparent bias would influence not only notions about regular-season United States harvest, but also our estimates of conservation-order harvest (Table 6) and our Lincoln estimates of August population size (Fig. 15A,B). Estimated conservation-order harvest would decline to 58.9% of values based on traditionally estimated regular-season harvest, as would our estimates of August population size, if bias-adjusted estimates of regular-season harvest (Johnson et al., in press) were used.

There was a wide discrepancy between our estimates of conservation-order harvest and those from individual states, which were an average of 2.2 (range = 1.5–3.4) times greater than our estimates based on band recoveries, after confirming homogeneity in band-reporting rates between regular-reason and conservation-order harvest (Table 4). Part of this difference resulted from state estimates not distinguishing between snow geese and Ross's geese during the conservation order. The discrepancy between harvest estimates for light geese would increase further with the downward adjustment in regular-season harvest proposed by Johnson et al. (in press; Fig. 4), from which we derived our estimates of conservation-order harvests (equation 4); state estimates of light-goose harvest would increase from being 2.2 times higher than our estimates (Table 6) to 3.7 times higher. It is not clear whether similar issues (e.g., prestige bias) thought to account for at least part of the apparent bias in regular-season United States harvest might also apply to Canadian harvest estimation.

Estimates of August population size (Fig. 15A) would decline proportionally with any downward adjustment to harvest estimates because total harvest is simply the numerator in Lincoln's estimator (equation 6). For example, where August abundance of adults was estimated to have been about 19.6 million AHY birds and 5.5 million HY birds in 2006, use of harvest estimates after adjustment for bias (Johnson et al., in press) produces Lincoln's estimates of 11.6 million and 3.2 million, respectively. Such numbers may appeal to some readers because they are considerably lower than estimates based on harvest unadjusted for apparent bias and are closer to both winter counts and photoestimates. However, investigators should not allow preconceived notions about abundance to dominate thinking, because past indices were not designed to provide population-level abundance estimates, as shown above, but instead were intended only to provide indices to population change. Nevertheless, knowledge about abundance is key to formulating prescriptions for harvest goals. The hypothesized bias in United States harvest estimation (Johnson et al., in press) has large implications not only for our analyses, but also for all analyses of waterfowl harvest done historically in the United States, and we trust that the issue will be resolved.

Whichever harvest numbers are used, the empirical evidence suggests that there were far more geese than implied by either midwinter counts or arctic photosurveys when recommendations about harvest goals were being made. If August abundance was 18.9 million adults and about 6.9 million juveniles during 1997–2000 (Fig. 15A), then a tripling of harvest to 2.2 million annually as recommended by Batt (1997) would have resulted in a combined harvest rate of 0.09. A harvest of 1.4 million recommended by Rockwell and Ankney (2000) would have resulted in a combined harvest rate of 0.05. Without compensation in associated mortality or recruitment with this substantially higher harvest rate (higher than has been achieved recently), these levels of harvest mortality subtracted from a population growth rate of 1.14 during 1990–1998 (Table 9) would still result in an expected population growth rate of 1.09. An appreciation for the true abundance of this population may have led to more ambitious harvest goals than were advocated, which may have shown greater effectiveness had they been achieved. Regardless, realized increases in harvest have failed to result in a measurable survival response for most of the midcontinent population.

Finally, although there is uncertainty about population size stemming from potential bias in harvest estimates, inference about rates of population change (Table 9) should not be affected if the hypothesized biases in United States harvest estimates (Fig. 4) were constant over time. In addition to advantages of using Lincoln estimates of population size mentioned above, another advantage is that it helps to directly relate changes in harvest rates and harvest to changes in population size, which might otherwise be measured on different scales. For example, winter counts in 2006 were about 2.5 million light geese (juveniles and adults of both Ross's and snow geese) in the midcontinent region, whereas total harvest of adult snow geese alone was about 555,000, and adult harvest rates were estimated to be about 0.025. In this case, the harvest rate estimate suggested that adult snow geese in the population should outnumber adults in the harvest by about 40 to 1, but winter counts could not account for even a 5:1 ratio of all light geese combined to adult snow geese in the harvest. In contrast, our Lincoln estimate in 2006 (using the unweighted harvest rate in Fig. 15A) suggested a population of about 19.2 million adult snow geese, estimated from a harvest of 442,000 adult snow geese, and a harvest rate of about 0.023.

Any bias in our estimates of either harvest or harvest rate would be offset by a similar bias in our estimate of population size; that is, the relationship between the 3 variables remains consistent, as long as any bias in harvest estimates was consistent over time. In addition, it may be more tractable to correct bias in harvest surveys or harvest-rate estimates than to develop and implement annual surveys for such a large, remote, and widespread population as midcontinent snow geese. Until more is known about causes for the hypothesized bias in harvest estimates, as well as its pervasiveness, we assume that inferred rates of population growth from Lincoln estimates are sound, especially with independent support from other sources (see below).

Changes in Geographical Patterns of Harvest

Harvest of snow geese had started to increase considerably from approximately 202,000 adults in 1993 to approximately 422,000 by 1997 before implementation of spring harvest in February 1999. The shift in proportionately greater Canadian harvest of snow geese in 1998–2006 compared to 1989–1997 likely was largely related to a large-scale shift in number of nonresident hunters that started to hunt geese on the Canadian Prairies (Boyd et al. 2002, Alisauskas et al. 2006*a*).

In addition to the elevated harvest pressure resulting from this increase in nonresident goose hunters in Canada, the duration of opportunities to hunt snow geese on the Canadian prairies may have increased because of apparently later fall migration (Table 3). Delays in fall migration through the United States were documented by Dzubin (1974) and Dzubin et al. (1975), but the longer stay by snow geese on the Canadian prairies may be related to later dates of freezing of roost areas or to the attraction of geese to larger acreages of pulse crops now grown there.

Why Has Increased Harvest Not Reduced Survival?

Empirical evidence is very strong that midcontinent snow geese currently have a very high potential for eluding death, a situation that has not changed since about 1988.

Cooke et al. (2000) estimated that snow geese marked at QMG from 1989 to 1995 survived with probability of approximately 0.93 and those from LPB with probability of approximately 0.94. Similarly, Alisauskas and Malecki (2003) estimated that snow geese marked in QMG between 1988 and 1998 survived with probability of 0.92. Although such high estimates were considered by Rockwell and Ankney (2000) to be biologically unrealistic, Rockwell et al. (1997) predicted survival probability without harvest mortality as 0.96, assuming complete additivity. Finally, our estimates of survival for northern geese marked from 2003 to 2006 averaged approximately 0.96 (Table 7). These meta-estimates for survival since 1989 are higher than most estimates made by Francis et al. (1992) and Cooch et al. (2001) for the period 1969–1990, during which survival increased from approximately 0.78 to approximately 0.88 for snow geese banded at La Pérouse Bay. As noted by Cooke et al. (2000), this period was also a time of increasing midwinter counts and increasing continental population size (Fig. 15).

Hunting mortality in geese generally is considered to be additive to natural mortality (Owen 1980) because mortality is low without harvest, thereby providing little potential for compensation (e.g., Rexstad 1992). Additive harvest mortality was inferred for southern-nesting snow geese in our study (Fig. 11A), for Ross's geese (Alisauskas et al. 2006*a*), and for greater snow geese (Gauthier et al. 2001). However, there was no effect of total harvest on survival of snow geese marked in the northern stratum (Fig. 11A) where most of this population is known to nest. We suspect that harvest was too low to reach the harvest threshold where additivity may have begun to operate, and so we could not anticipate the amount of harvest required to achieve a target survival rate of <0.80. However, assuming a population size of 20 million adults and an estimated invariant mortality probability of 1–0.87, we estimate that 2.6 million adults die annually, regardless of cause. Assuming further that any harvest in addition to current average annual harvest of 0.7 million adults (1998–2006, Table 5) would induce additive mortality, then for survival to decline from 0.87 to 0.80 would require an additional kill, K, of 1.4 million adults. Because harvest is defined as cK, where c represents a retrieval rate (Brownie et al. 1985), required harvest would be some unknown level <1.4 million because current retrieval rates are unknown. If a commonly assumed retrieval rate of 0.80 (Rockwell et al. 1997) is currently true, then required harvest additional to current levels would be 1.12 million adults.

Harvest rates of southern geese averaged 0.037 from 1998 to 2006, compared to 0.031 from 1989 to 1997 (Fig. 14). The increase in harvest rate between the 2 periods was associated with a corresponding decline in average survival from 0.89 to 0.83 for southern adults (Fig. 9). The decline in survival of 0.06 could not be accounted for solely by the increased harvest rate, which amounts to only about 12% of the decline in survival among southern snow geese. Even if increased harvest resulted in reduced efficiency by hunters at retrieving their kill, the discrepancy in differences between the 2 periods in either harvest rates, h, or kill rates, k, and the difference in survival was too great to explain this decline in survival. Given that $k = h/c$, then for kill rate, k, to have been the sole source of the observed survival decline (i.e., $k = 0.05$), then retrieval rate, c, would have had to have been only about 0.12. It seems highly unlikely that hunters retrieved only 12% of the southern stratum adult snow geese that they killed. An alternative explanation may be an underestimated harvest rate for this stratum because of an erroneously assumed homogeneity in band-reporting rate. Proportionately far more southern nesters were recovered north of the Canadian prairies (Fig. 3D,E) than were northern nesters (Fig. 3A,B), and the continental band-reporting rate estimated as 0.80 may not have been representative of that for hunters in northern Canada. Thus, the proportion of southern geese harvested in northern Canada, mostly along the south coast of Hudson Bay, may have been underestimated.

The collective effects of differences in migration phenology, harvest distribution, relative population sizes, and per capita food availability probably account for the fact that annual harvest rate of southern snow geese was about 30% greater than that of northern snow geese (Table 5, Fig. 14) and may explain why there appeared to be a survival response to harvest in southern geese but not northern geese (Fig. 9). We note that southern snow geese have received much more attention from banders, at least in the last 2 decades (Table 1), possibly because efforts to mark them were associated with tests of hypotheses specific to local populations (e.g., Cooke et al. 1995). Consequently, southern snow geese represented an average of 65% of snow geese banded (Table 1), although they represented only about 10% of the midcontinent population (Kerbes et al. 2006). Such use of marked subpopulations that do not represent the continental population should be avoided or at least treated with caution. The convenience of using the large sample of marked southern birds could easily have led to the incorrect inference that survival had declined in association with the conservation order. Failure to stratify geographically likely would have led to the erroneous conclusion that survival of midcontinent snow geese had declined.

The differential response in survival between arctic-nesting snow geese and those that nested in subarctic regions along south Hudson Bay likely was related to different migration phenologies (Fig. 6) stemming from large latitudinal differences in nesting range (Fig. 1), large differences in the contribution of each stratum to the population (Fig. 2), and slightly different geographical distributions of harvest (Fig. 3). Midcontinent snow geese that nested along south Hudson Bay faced shorter migration distances from staging areas in Prairie Canada that function as important sources of nutrients required for breeding (Alisauskas 2002) and where significant harvest of northern nesters first occurs during fall (Fig. 3). Thus, southern nesters likely could nest and hatch young well ahead of those nesting at more typical latitudes for the midcontinent population. The recession of melting snow certainly occurs sooner in most years at lower latitudes of approximately 60°N than it does approximately 778 km north at approximately 67°N (Fig. 1). For example, mean date of nest initiation by snow geese nesting from 1991 to 2007 at Karrak Lake south of Queen Maud Gulf was 10 June, whereas that of snow geese nesting at LPB from 1973 to 1992 was 27 May (Cooke et al. 1995). Such earlier nesting at southern latitudes apparently permitted goslings hatched there to grow, fledge, and migrate south with their parents 2 weeks earlier than those from northern latitudes (assuming that they survived nutrient limitation) and also allowed them to be harvested 2 weeks earlier each autumn in Canada (Fig. 5A) and 8 days earlier in the northern United States (Fig. 5B).

The smaller southern subpopulation tends to migrate to significant harvest areas before the much larger northern subpopulation and so encounters a higher ratio of hunters to geese. When the northern subpopulation subsequently migrates to harvest areas already occupied by the southern subpopulation, northern geese likely swell the ratio of geese to hunters, thereby lowering probability of harvest for any individual bird. Midcontinent snow geese marked south of 60°N latitude also had a much greater probability of harvest along southern Hudson Bay (Fig. 3E) than did northern nesters. This differential vulnerability resulted in large differences in the percentage of recoveries from Manitoba and Ontario of northern geese (5% and trace, respectively) compared to southern geese (19% and 2%, respectively).

Differences in relative vulnerability of northern and southern subpopulations to hunting also could be linked to differences in habitat quality and availability between regions. Snow geese nesting along south Hudson Bay occupy some of the most severely degraded coastal habitats that have been surveyed to date, and much of this degradation is related to the foraging activities of both the local nesting population and the larger numbers of spring and fall staging geese that nest further north

(Jefferies et al. 2003, Jefferies et al. 2006). Declines in availability of high-quality salt marsh foraging habitats have forced geese to make use of lower-quality freshwater foraging habitats (but see Slattery and Alisauskas 2007), which conceivably could influence fall body condition, which could increase vulnerability to hunters or may directly increase nonhunting mortality of adult birds.

An alternative hypothesis for the decline in survival of southern nesters is therefore related to density dependence and nutritional stress among adults. Previous work was consistent with density dependence through ecosystem degradation on fecundity and gosling survival in the southern stratum, specifically at La Pérouse Bay (Cooch et al. 1989, 1991, 1993; Francis et al. 1992). Possibly, continued environmental degradation by both resident snow geese and migrant northern snow geese that stage and feed in coastal marshes along southern Hudson and James Bays may have further increased density-dependent effects that now extend beyond effects on reduced survival by goslings to effects of reduced adult survival among southern geese (Francis et al. 1992). Continued growth in numbers of northern geese would have compounded plant removal if the same proportion continued to use these subarctic coastal marshes along James and Hudson Bays. Inability of resident adults to store sufficient reserves for southern migration after attempting to nest may have increased mortality of southern adults. Thus, an apparent relationship between increased harvest and reduced adult survival among southern nesters (Fig. 11A) may have been spurious and not due to cause and effect. The possibility that severe nutrient deficits contributed to reduced survival in the small population of southern nesters, combined with a lack of survival response by the bulk of the population that nests in the north (Fig. 11A) could lend more support to the conclusion that efforts to control midcontinent snow geese through harvest have been ineffective.

Habitat quality and availability have been less well studied in most areas of the Canadian arctic (but see Alisauskas et al. 2006*b*), but continued growth and expansion of nesting colonies farther north suggests that carrying capacity has not yet been reached, at least at some of these colonies (Alisauskas and Boyd 1994, Kerbes et al. 2006). Until recently (e.g., Alisauskas et al. 2006*b*), most habitat assessments occurred in the southern breeding range of midcontinent snow geese, with researchers focusing on the interplay between foraging activity of geese and long-term impacts on vegetation (Jefferies et al. 2003, 2004; Abraham et al. 2005). This focus also was influenced by the logistic convenience of doing research at colonies nearer to the closest communities, resulting in lower costs (Alisauskas and Malecki 2003). Other than for Queen Maud Gulf, there remains a lack of information about the state of arctic vegetation at important northern areas such as Southampton Island and Baffin Island used for nesting by midcontinent snow geese (Didiuk et al. 2001).

Nevertheless, the impacts of light geese on arctic vegetation may be greater in the southern portion of snow goose nesting range than at latitudes more commonly used by midcontinent snow geese for nesting because a large portion of the midcontinent population uses the southern portion for staging and foraging in both spring and fall. For example, although there appeared to be clear effects on local vegetation at a large northern colony near Karrak Lake (Alisauskas et al. 2006*b*) and on nearby brood-rearing areas (Slattery 2000) in the sanctuary south of Queen Maud Gulf, there still remain abundant and large areas of apparently suitable habitat that remain unused by light geese in that region (Didiuk and Ferguson 2005; R. T. Alisauskas and J. O. Leafloor, Environment Canada, personal observation).

Carrying capacity in Canada's central and eastern arctic regions may still exceed current population size because the midcontinent population continues to grow, albeit at a reduced rate (Fig. 15). This growth continues to be fueled by high survival thought to be largely subsidized by agricultural production on wintering grounds and along migration routes (Jefferies et al. 2003, 2004; Abraham et al. 2005). If agricultural policy favors greater production of corn, a food important to midcontinent snow geese (Alisauskas and Ankney 1992), and cereals for biofuels, then additional nutritional subsidy may improve carrying capacity on the United States wintering grounds and possibly further increase already high survival probability. Such policies seem likely and would accelerate the rate at which midcontinent snow geese alter tundra ecosystems in arctic Canada.

We think that the apparent discrepancy between survival rate estimates of approximately 0.96 for northern geese marked from 2003 to 2006 and approximately 0.87 for northern geese marked from 1989 to 2006 was an outcome of the different age structures of adult birds between these 2 samples. We propose a higher likelihood of senescence in the larger sample of birds marked from 1989 to 2006, which on average had to be older than the smaller, more recent sample marked from 2003 to 2006. For example, recoveries of northern snow goose adults marked in 1989 continued until at least 2006 (Appendix B), which means that such birds were $\geq$18 years old, given that they were marked 17 years earlier as adults. Although senescence appeared not to influence survival in LPB snow geese until 10 years of age (Cooke et al. 1995), our north–south analysis had a much higher likelihood for inclusion of individuals that could have been $\geq$18 years of age, if they were marked as adults in 1989. We propose a senescence hypothesis with the prediction that survival probability declines with number of years since marking and that onset of senescence varies between northern and southern strata.

Why Has Total Harvest Not Increased Sufficiently?

The 2.5- to 3.5-fold increase in harvest (above 1993–1994 levels) that we estimated failed to reduce the composite probability of annual survival below 0.87; this increased harvest was within the range initially proposed by Rockwell et al. (1997), but below the amended estimate proposed by Rockwell and Ankney (2000), to be sufficient to reduce survival probability to a level that would result in population decline. Specifically, the maximum annual harvest achieved during this study never exceeded 0.75 million adult snow geese in both 1999 and 2001. Thus, despite liberalization of hunting opportunities for midcontinent snow geese since 1998 with the objective of meeting harvest goals set by Rockwell et al. (1997) or Rockwell and Ankney (2000), hunters were unable to harvest sufficient numbers of adults to reduce survival to the prescribed level.

Many of the harvest goals initially recommended for achieving a desired reduction in population size were based on incomplete or outdated knowledge about estimates of vital rates, harvest, and population size. Although Rockwell et al. (1997) projected that

$\overline{\lambda}_i \cong 1.107$ from a Lefkovitch matrix constructed of vital-rate estimates from La Pérouse Bay, they instead assumed an annual rate of population change of $\overline{\lambda}_i \cong 1.049$ based on midwinter counts, which they estimated using linear regression. Further assuming adult survival probability $\overline{S}_i = 0.88$, they proposed that annual harvest needed to be tripled from $\hat{H}_{1994} = 0.3$ million snow geese to $\overline{H'}_i = 915,000$ snow geese to achieve $\overline{S}'_i = 0.72$ and a desired annual growth rate of $\overline{\lambda'}_i \cong 0.85$; optionally, a doubling of annual harvest to 610,000 was predicted to produce $\overline{S}'_i = 0.79$, in turn expected to result in $\overline{\lambda}'_i \cong 0.95$.

Cooke et al. (2000) disputed these predictions, suggesting that projections made by Rockwell et al. (1997) were based on outdated estimates. Specifically, Cooke et al. (2000) estimated that $\hat{\overline{S}}_{1989-1995} \cong 0.94$ for both QMG and LPB but noted that precision of this estimate, which was based on a model that allowed survival to vary among years, was very poor due to low numbers of snow geese banded. Cooke et al. (2000) suggested using a range of then-current survival probabilities between 0.89 and 0.94 for modeling population response but noted that these were still higher than values used by Rockwell et al. (1997). These apparently small differences in survival probability used by each set of authors resulted in large differences in the estimate of harvest required to achieve the same reductions in survival probability to 0.72 and 0.79. Cooke et al. (2000) estimated that to achieve the same survival probabilities proposed by Rockwell et al. (1997) to result in annual rates of population change of 0.85 and 0.95, respectively, would require approximately 4- and 6-fold increases in harvest of snow geese above those estimated for 1994 (269,000 adults and 188,000 juveniles, Table 5).

Rockwell and Ankney (2000) updated initial harvest estimates to 1.4 million adults and young as leading to sufficient reductions in survival to result in population decline. The USFWS (2007) accepted this level of harvest as sufficient to reduce the midcontinent light goose population. Using the sum of regular-season and conservation-order harvest (including snow and Ross's geese in aggregate) estimated by individual states (Table 6), the USFWS (2007) stated that annual harvest estimates of between 1.2 million and 1.5 million from what is referred to as the Central and Mississippi Flyway (CMF) light goose population at times have exceeded the required harvest of 1.4 million prescribed by Rockwell and Ankney (2000). However, the conservation-order harvest of light geese (snow and Ross's geese in aggregate) estimated by individual states was 1.5–3.0 times greater than harvest during conservation-order harvest of snow geese estimated using the band-recovery method that we used (Table 6). Reasons for this discrepancy are unknown because methodologies used by different states are not documented, but part of the reason is likely related to inclusion of Ross's geese in the state estimates. We suggest that harvest is far lower than suggested by these state estimates and that neither the level assumed nor the one we demonstrated are sufficient to affect survival or population growth rate by midcontinent snow geese. Part of the reason that past and current projections may have been unrealistically optimistic is that the sheer abundance of snow geese has been assumed to be far lower than apparently was the case.

Clearly, additional or alternative approaches (Johnson and Ankney 2003) to achieving increased adult mortality or reduction in recruitment are required if previously stated objectives of population reduction through management action are to be realized. Lack of sufficient incentives, or the presence of disincentives, has impeded increases in numbers of snow goose hunters in Prairie Canada each spring. One such disincentive may be the closure of spring harvest of Ross's geese in Prairie Canada because of a judicial decision following a court challenge to initial proposals by Canadian Wildlife Service for spring harvest of light geese in Prairie Canada. Alisauskas et al. (2006*a*) suggested that this restriction could be removed, justifying it from the perspective of conserving traditional populations of Ross's geese, while encouraging harvest of snow geese in places that had no Ross's geese until recently. Concerns about threats to Ross's geese seem unfounded given that continental estimates of size of the August population of Ross's geese have continued to grow and have recently exceeded 2 million (Alisauskas et al. 2009), a number far in excess of the stated North American Waterfowl Management Plan population goal of 0.1 million.

Rockwell et al. (1997) used elasticity analyses to determine the relative impact of equal proportionate changes in vital rates on the population growth rate of snow geese. Results indicated that reducing adult survival would be the most efficient means of reducing population growth. They noted, however, that changing the highest elasticity variable might not always be the most politically or economically feasible action. Since that time, several lines of research have revealed other potential limitations on the use of elasticity in reaching management decisions. Although elasticities provide a conceptual starting point, they fail to address efficacy of management actions to control vital rates and ignore the reality of decisions based on costs of alternative management strategies. For this reason, Nichols and Hines (2002) cautioned against a focus solely on vital rates with the highest elasticities and proposed a metric that, in essence, is an elasticity weighted by the efficiency with which a management action influences a vital rate and by the cost of that management action (e.g., x geese removed/dollar). Recent management efforts to reduce survival of midcontinent snow geese through increased opportunities to harvest them, although of little cost, appear to have suffered from 2 inefficiencies.

The first inefficiency was the inability to increase harvest sufficiently. Reasons for this failure are not clear but likely relate to the sheer abundance of geese at the time of implementation of the conservation order. Second, although both harvest and harvest rate increased initially in response to liberalization, they have since been declining (Figs. 7, 12B, 13, and 14). Thus, although total harvest increased in response to liberalization and is still higher than it was before start of conservation measures (Figs. 7 and 13), the rate of increase in harvest was not sufficient to offset the rate of increase in the population (Fig. 15), resulting in the observed recent decline in harvest rate. It remains unclear whether this second inefficiency is simply a matter of goose population size or was compounded by 1) a functional response by geese becoming more wary and thus less vulnerable or 2) some aspect of hunter behavior, such as an attenuation in effort/hunter or general willingness to pursue snow geese after an initial interest for doing so during the beginning of the conservation order. Both a functional behavioral response by geese and changes in hunter behavior were observed following implementation of liberalizations in greater snow geese harvest regulations (Béchet et al. 2003, Calvert et al. 2007). Additional focus on understanding these aspects of partial controllability and hunter behavior would be useful.

Management actions focused on alteration of vital rates to reduce the growth of overabundant populations may change abundance in unanticipated directions (Koons et al. 2006, Zipkin et al. 2009). Sudden changes in adult survival or reproductive success will necessarily alter the age structure of the population and could force the system into a period of transient dynamics (Koons et al. 2005). This shift in dynamics, in turn, can translate into a momentum effect where final population size is substantially higher or lower than anticipated (Hauser et al. 2006, Koons et al. 2006). Positive momentum does not appear to be the reason that the population has continued to increase beyond levels anticipated by Rockwell and Ankney (2000) because increased harvest should have impacted both adult and juvenile survival, which are demographic characters whose reductions have opposite momentum effects (Rockwell et al., in press).

Research Implications

Midcontinent snow geese appear to have escaped the ability of harvest management to reduce adult survival or control population growth. The removal of past limits to carrying capacity through exploitation by geese of agricultural landscapes in the midcontinent (Abraham et al. 2005) induced rapid growth in this population over the past 35 years (Fig. 15). Present agricultural policies for biofuel production likely will be favorable to snow goose survival and possibly population increase. However, carrying capacity in northern Canada may limit growth eventually. Predictions about this limitation remain elusive without additional research on 1) the distribution of suitable habitat, both occupied and as yet unoccupied, and 2) the primary productivity of foods relevant to snow geese within such arctic landscapes. A key research need is estimation of carrying capacity on a broad scale within the breeding range of midcontinent snow geese and would involve additional efforts to catalogue arctic habitats through remote sensing (e.g., Didiuk and Ferguson 2005), as well as direct measurements of standing crop among habitat strata within those landscapes. In addition, there is need for a more complete understanding of habitat use by snow geese, particularly with respect to staging habitats north of agricultural regions of prairie Canada. Presently, we know little about the distribution of snow geese in spring from the time they leave agricultural regions in early to mid-May until they arrive on northern nesting areas in early to mid-June. Therefore, ongoing impacts to staging habitats are only partly known (e.g., along the James Bay and Hudson Bay coasts).

Continued and expanded banding of geese in an effort consistent with their breeding distribution in Canada's central and eastern arctic is a critical research priority. The population apparently continues to grow, although at an attenuated rate. Evidence is weak that harvest management has played a direct role in this attenuation. If population growth rate has reached a point of inflection, it will require more years of monitoring to detect this because of the unavoidable time required to summarize and distribute recovery information and to conduct national harvest surveys to estimate and report harvest. Expansion of arctic banding effort in 2000 and 2003 to improve coverage of major areas used by this population in the northern nesting stratum was an important development (Table 1), and this research activity is the highest priority to maintain.

In conjunction with reports of recoveries by hunters, and existing programs in Canada and the United States to estimate regular-season harvest, banding is critical to our state of knowledge about the population dynamics of snow geese at the broadest range-wide scale. Beyond the benefits of the expansion in representative marking effort specifically for 1) inferences about survival and harvest rates from band-recovery models (Brownie et al. 1985) and 2) Lincoln's estimates of abundance each August, better coordinated coverage of the summer range lends itself to examine midcontinent snow geese from a breeding metapopulation perspective. Uninterrupted banding operations in arctic regions that support large numbers of highly clumped distributions of snow geese would allow researchers to address population parameters that are estimable from mark-recapture of individual geese (Cooch and White 2009). Such an approach would allow a focus on facets of metapopulation biology, such as local dynamics in abundance, survival, and recruitment, as well as the exchange of geese among breeding subpopulations (Alisauskas et al., in press) while continuing to allow an assessment of the role that exploitation by hunters may play in population dynamics.

Further, we believe the Lincoln method has high potential for monitoring midcontinent snow geese and other widely dispersed, remotely nesting populations. Lincoln's method resulted in wide confidence intervals, yet we believe corresponding inferences about abundance are less biased than those resulting from photo-inventory or midwinter surveys because Lincoln's method relies on effectively sampling the entire population with hunter harvest. Improving Lincoln estimates through bolstering precision of harvest and harvest-rate estimation via banding samples, periodic work on goose reporting rates, and better harvest survey during the regular season and spring harvest may provide a cost-effective monitoring program able to supplement or supplant other surveys for these geese.

Greater attention needs to be devoted to the role that annual variation in recruitment plays in population change. Age ratios in midcontinent snow geese have shown a long-term decline even before the conservation order, but the reasons remain unclear, although density-dependence may have played a role (Alisauskas 2002). A full treatment of age-ratio data from harvest surveys adjusted for variation in relative vulnerability of young, and modeling of juvenile survival, are the next important steps. The most informative approach to understanding the influence of local recruitment on local and metapopulation dynamics may rest with the mark-recapture approach mentioned above used in conjunction with reverse-time multi-state models (e.g., Nichols et al. 2000), with an integration of band-recovery information.

Factors that motivate behavioral change in hunters also may influence continental harvest. A detailed evaluation of changes in numbers of snow goose hunters, and harvest/hunter could be accompanied by questionnaire surveys designed to understand social and economic factors (e.g., age, equipment ownership, income, satiation) that may modify patterns in hunter behavior (e.g., number of days hunting, miles traveled) that are pertinent to hunter success. Developments in shotgun design and associated ammunition, such as 8.89-cm (3.5-in.) shells and nontoxic shot that are now used by more hunters, warrant an attempt to gain updated estimates of retrieval rate so that kill rate could be estimated properly from harvest rate.

Finally, increased harvest efforts may have been compensated by changes in snow goose behavior such that increased wariness of birds may partially explain declining harvest and kill rates. One approach toward examining this possibility might be to estimate vulnerability of snow and Ross's geese in relation to a goose species that is largely sympatric with light geese during migration and winter, such as midcontinent white-fronted geese (*Anser albifrons*). Associated with a test of the declining vulnerability hypothesis is the prediction that recovery rates of light geese, relative to those of midcontinent white-fronted geese, have declined in the last decade in response to the conservation order.

MANAGEMENT IMPLICATIONS

We provide 5 major recommendations to goose managers. First, unprecedented harvest provisions implemented to date in both Canada and the United States for midcontinent light geese could be viewed not as a short-term solution, but as a core of stabilized regulations to which additional population reduction efforts could be applied. Second, spring harvest of closely related Ross's geese could be legalized in Canada, as in the United States; even though the abundance and range of Ross's geese continues to increase at a rate more rapid than that of snow geese, the spring closure on Ross's geese in Canada impedes some spring harvest of snow geese (Alisauskas et al. 2006*a*, 2009). Third, restrictions on light goose hunting that have been removed in the United States (e.g., daily bag and possession limits during the conservation order) could be removed in Canadian provinces and territories where they still exist. Fourth, although harvest opportunities for midcontinent snow geese are virtually unlimited in the United States, either during regular seasons or the conservation-order, the harvest per hunter may have hit a limiting threshold. If the objective of reduction in damage to arctic ecosystems is to be achieved through population reduction, then additional harvest measures will need to be implemented. These measures include active management such as direct control of geese and their eggs (Alisauskas and Malecki 2003, Johnson and Ankney 2003), which is not currently exercised.

Finally, efforts to increase harvest of snow geese might be considered a form of passive management through the removal of many traditional constraints associated with waterfowl hunting. Management could include active efforts that would encourage increased numbers of snow goose hunters, such as the legalization of commerce in harvested light geese or through subsidized hunting licenses. For example, if such incentives are effective to the point where a doubling of hunter numbers results, then increase in total harvest of both snow and Ross's geese might be sufficiently large to push harvest rate past the threshold where hunting mortality becomes additive to natural mortality. An effective means of increasing recruitment of snow goose hunters remains unknown, but whatever attempts are made should be accompanied by a proper evaluation that integrates cost and effectiveness of each option (Nichols and Hines 2002). Given the challenges to arctic ecosystems from the continued increase in number of light geese, managers are strongly encouraged to consider the options we outlined above for further action.

The ineffectiveness of recent harvest to affect survival and abundance of midcontinent snow geese warrants a review and possibly revision of original objectives (Batt 1997). This review may include acceptance that large-scale alteration of arctic ecosystems will continue to the point where light geese begin to regulate not only themselves but other sympatric wildlife as well. Lack of further management action would imply tacit acceptance of this likely outcome. Regardless, research attention on the interplay of geese, arctic vegetation and other sympatric wildlife should be expanded beyond past focus on the coastal marshes of Hudson and James Bay in the southern nesting stratum (see Abraham et al. 2005). The much larger northern stratum supports most of the midcontinent population of snow geese and virtually all Ross's geese, and comparatively little is known about their ecological impacts there. Such an endeavor will either inform us that the impacts are not as intense or widespread as previously assumed from work farther south or leave us armed with knowledge of what has been lost and what more we stand to lose. In the event that all management attempts to reverse or even arrest population growth remain ineffective, perhaps the only consolation is that harvest of midcontinent light geese remains an example of an exploited population capable of great persistence, regardless of the maximum level of exploitation realized. From the perspective of sustainable resource exploitation, this observation could be viewed as a benefit.

SUMMARY

- We used a model-based approach to test the hypothesis that survival probability of adult snow geese from the Midcontinent Population declined concurrently with start of special measures designed to increase kill.
- Migration and harvest chronology of snow geese from a northern stratum (north of 60°N latitude) was 15 days later, on average, if recovered in Canada, and 8 days later if recovered in the United States than that of snow geese marked from a southern stratum (south of 60°N latitude) with implications for differences in harvest and survival probabilities. About 90% of the midcontinent population nests in the northern stratum and 10% in the southern stratum.
- Ninety-seven percent of snow geese harvested outside the regular season were taken in the U.S. The states with the greatest conservation-order harvest were South Dakota (19–21% of conservation-order harvest), Missouri (13–18%), Arkansas (13–15%), and Nebraska (11–12%).
- We estimated that band-reporting probability was 0.83 ± 0.17 (95% CL) if we made no adjustment for band loss and 0.80 ± 0.16 after adjustment.
- Harvest of midcontinent snow geese during the regular season (including special provisions in 1998 and 1999) increased from approximately 201,000 in 1993 to approximately 561,000 adults in 1999 (Table 6, Fig. 6).
- Regular-season harvest declined from 1999 each year in sequence until 2003 to reach approximately 327,000, after which any trend to 2006 was unclear.

- We used band recoveries during the regular- and conservation-order seasons in conjunction with regular-season harvest to estimate conservation-order take.
- Estimates of total adult harvest never approached a million geese and exceeded 700,000 adults during only 4 harvest periods since 1998 (1999–2001, and 2005).
- Conservation-order harvest accounted for an average of about 37% of total annual harvest of adults and 28% of juveniles from 1998 to 2006.
- The weight of evidence suggested that adult survival of southern snow geese, representing about 10% of the midcontinent population, was inversely related to increased adult harvest and declined from approximately 0.89 in 1989 to approximately 0.83 by 2006.
- Survival of northern snow geese (0.872), representing about 90% of the midcontinent population, was unrelated to harvest and had not changed from 1989 to 2006.
- Harvest probability of adults, pooled between northern and southern geese, never exceeded approximately 0.04 after 1988, despite 2- to 3-fold increases in annual harvest of adults.
- Harvest probability was higher for southern geese than northern geese but harvest probability of both has been declining since the start of the conservation order.
- Lincoln's estimator suggests that August populations of midcontinent snow geese have exceeded approximately 20 million adults and approximately 5 million goslings since the start of the conservation order.
- A period of rapid annual growth rate of the adult population before the conservation order (95% CL($\hat{\lambda}$) $= 1.144 \pm 0.040$) was followed by an attenuated rate (1.050 ± 0.055).
- The decline in growth rate was not accompanied by declines in survival and may have been a density-dependent response in recruitment unrelated to harvest.
- Further analyses are warranted to examine potential effects of harvest on recruitment by midcontinent snow geese either through reduced survival of young or the role that disruption of spring fattening may play in reducing breeding propensity of adults.

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Appendix A. Recovery matrices for midcontinent lesser snow geese captured as adults (AHY, after hatch year, i.e., >1 year old) near 6 regions of Canada's central and eastern arctic and marked with standard or reward legbands or plastic tarsal bands (i.e., no neckbands) during July or August, 2003–2006. Recoveries of dead birds considered were only those shot as normal wild birds in North America either by hunters or others under permit from 1 August to 30 June.

		Number of bands recovered or number of birds banded by year in region											
		Queen Maud Gulf				Southampton Island				Baffin Island			
Stratum	**Year that recoveries were banded**	**2003**	**2004**	**2005**	**2006**	**2003**	**2004**	**2005**	**2006**	**2003**	**2004**	**2005**	**2006**
Northern	2003	77	54	51	41	32	27	35	28	24	26	22	18
	2004		75	57	42		35	45	35		21	14	9
	2005			69	48			36	37			52	23
	2006				29				29				17
	No. banded	2,897	3,356	3,168	1,994	1,604	1,799	1,998	2,056	1,095	791	1,816	1,098

		Number of bands recovered or number of birds banded by year in region											
		La Pérouse Bay				Cape Henrietta Maria				Akimiski Island			
Stratum	**Year that recoveries were banded**	**2003**	**2004**	**2005**	**2006**	**2003**	**2004**	**2005**	**2006**	**2003**	**2004**	**2005**	**2006**
Southern	2003	90	46	51	37	60	19	40	20	5	5	0	5
	2004		109	87	65		50	36	26		15	8	11
	2005			93	58			64	32			11	6
	2006				54				44				13
	No. banded	2,364	3,667	2,798	2,195	1,597	2,003	2,021	2,172	213	579	482	652

Appendix B. Recovery matrices for midcontinent lesser snow geese captured as adults (AHY, after hatch year, i.e., >1 year old) in Canada's central or eastern arctic and subarctic either north of 60°N latitude (above) or south (below) and marked with standard or reward legbands or plastic tarsal bands (i.e., no neckbands) during July or August, 1989–2006. Recoveries of dead birds considered were only those shot as normal wild birds in North America either by hunters or others under permit from 1 August to 30 June.

		Number of bands recovered or number of birds banded by year																	
Stratum	**Year banded**	**1989**	**1990**	**1991**	**1992**	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Northern	1989	10	6	2	3	7	6	9	4	6	5	5	4	4	3	2	1	0	1
	1990		10	7	3	2	3	7	1	4	4	6	6	2	3	2	1	2	1
	1991			2	4	1	1	7	7	1	6	4	2	3	2	0	0	1	2
	1992				7	2	5	3	7	1	7	6	6	5	2	3	2	0	0
	1993					1	2	2	3	0	5	1	3	2	1	1	3	1	1
	1994						7	11	10	7	11	14	8	3	5	6	4	0	2
	1995							11	11	6	16	11	5	5	8	3	4	3	1
	1996								2	0	3	5	5	5	0	1	0	2	1
	1997									15	21	23	20	26	17	10	9	8	6
	1998										55	52	27	32	26	25	20	25	15
	1999											52	29	25	24	17	18	15	8
	2000												36	26	33	17	20	22	12
	2001													31	23	27	21	13	16
	2002														31	31	33	21	22
	2003															133	107	108	87
	2004																131	116	86
	2005																	162	112
	2006																		72
	Banded	801	626	341	585	272	801	671	155	1,191	2,228	1,531	1,441	1,457	1,738	5,596	5,946	7,182	5,148
Southern	1989	16	10	18	17	13	7	7	5	4	6	18	7	7	5	3	5	1	0
	1990		21	18	17	18	13	15	15	18	16	15	11	9	7	4	5	1	2
	1991			34	28	19	12	26	25	16	38	32	19	19	13	6	4	3	2
	1992				40	33	36	36	36	34	55	53	34	26	20	11	19	5	6
	1993					27	21	29	28	25	52	37	21	25	13	19	6	8	6
	1994						11	17	27	20	20	26	16	20	20	6	7	4	9
	1995							15	20	14	26	18	10	7	15	10	5	5	3
	1996								7	4	5	4	4	3	8	4	4	2	0
	1997									9	10	11	8	5	5	1	7	6	2
	1998										96	53	41	39	28	34	33	22	21
	1999											78	42	56	43	34	25	21	19
	2000												255	208	185	148	112	105	89
	2001													165	138	135	80	78	63
	2002														142	129	98	86	62
	2003															155	70	91	62
	2004																174	131	102
	2005																	168	96
	2006																		111
	Banded	1,199	1,651	1,981	3,298	2,397	1,728	1,055	438	457	2,482	2,619	9,242	5,992	5,426	4,174	6,249	5,301	5,019

Appendix C. Full results of model selection for models estimating survival probability (S) and recovery probability (f) of adult lesser snow geese captured and marked in 6 regions of Canada's central and eastern arctic, 2003–2006. Regions include Queen Maud Gulf (QMG), Baffin Island (BAF), Southampton Island (SOU), La Pérouse Bay (LPB), Cape Henrietta Maria (CHM), and Akimiski Island (AKI). Model notation follows Lebreton et al. (1992): t denotes time-dependence (i.e., annual variation), T denotes linear time trend, g denotes group differences (i.e., differences among regions), (.) denotes constancy. NS represents survival or recovery probability stratified according to northern (QMG, BAF, and SOU) and southern (LPB, CHM, and AKI) regions of the nesting distribution (see text for details).

Model	ΔQAIC$_c$[a]	QAIC$_c$ weight[b]	K[c]	Quasi deviance
$\{S[\mathrm{NS}], f[g + t]\}$	0.0	0.41	11	43.2
$\{S[\mathrm{NS}], f[\mathrm{NS} + t]\}$	0.2	0.37	7	51.4
$\{S[\mathrm{NS} * t], f[\mathrm{NS} + t]\}$	2.7	0.10	9	49.9
$\{S[g], f[g + t]\}$	3.8	0.06	15	38.9
$\{S[.], f[g + t]\}$	5.9	0.02	10	51.1
$\{S[\mathrm{NS}], f[\mathrm{NS} + T]\}$	7.1	0.01	5	62.3
$\{S[g + t], f[g + t]\}$	7.4	0.01	17	38.5
$\{S[\mathrm{NS} + t], f[\mathrm{NS} + t]\}$	9.1	0.00	9	56.3
$\{S[t], f[g + t]\}$	11.8	0.00	12	53.0
$\{S[.], f[g * t]\}$	19.0	0.00	25	34.2
$\{S[g + t], f[g]\}$	19.5	0.00	13	58.7
$\{S[g], f[g * t]\}$	19.6	0.00	30	24.7
$\{S[.], f[t]\}$	20.9	0.00	5	76.1
$\{S[g * t], f[g * t]\}$	20.9	0.00	31	24.1
$\{S[g], f[t]\}$	22.2	0.00	9	69.4
$\{S[g], f[g]\}$	22.7	0.00	11	65.9
$\{S[g * t], f[g + t]\}$	22.8	0.00	27	34.0
$\{S[t], f[t]\}$	24.2	0.00	7	75.4
$\{S[\mathrm{NS}], f[\mathrm{NS}]\}$	24.5	0.00	4	81.7
$\{S[g + t], f[t]\}$	25.8	0.00	12	67.0
$\{S[t], f[g * t]\}$	26.7	0.00	27	37.9
$\{S[t], f[g]\}$	27.2	0.00	8	76.4
$\{S[g * t], f[t]\}$	27.3	0.00	15	62.5
$\{S[.], f[g]\}$	28.6	0.00	7	79.8
$\{S[g * t], f[g]\}$	28.7	0.00	20	53.8
$\{S[t], f[.]\}$	39.3	0.00	4	96.5
$\{S[g * t], f[g * t]\}$ GLOBAL	41.7	0.00	42	22.8
$\{S[.], f[.]\}$	43.5	0.00	2	104.7
$\{S[g + t], f[.]\}$	43.9	0.00	9	91.0
$\{S[g], f[.]\}$	45.3	0.00	7	96.5
$\{S[g * t], f[.]\}$	48.9	0.00	16	82.1

[a] Difference between Akaike's Information Criterion with adjustments for overdispersion ($\hat{c} = 1.3674$) and small-sample bias (QAIC$_c$; Burnham and Anderson 2002) of the current model and the lowest observed value.

[b] Normalized Akaike (QAIC$_c$) weight (Burnham and Anderson 2002).

[c] K = number of parameters estimated.

Appendix D. Full results of model selection for models estimating survival probability (S) and recovery probability (f) for adult snow geese structured according to stratum where marked (g) and year (t), 1989–2006; years pooled denoted as (.). Strata were either northern (NOR includes Queen Maud Gulf, Baffin Island and Southampton Island regions in Table 7 and West Hudson Bay, WHB) or southern (SOU includes La Pérouse Bay, Cape Henrietta Maria and Akimiski Island regions in Table 7) portions of the nesting distribution (see text and Fig. 1 for details). Annual covariates include existence of the conservation order ($\mathrm{CO} = 0$ for 1989–1997 [before], and $\mathrm{CO} = 1$ for 1998–2006 [during]), annual harvest (total, H, regular season, R, and conservation order, C, Table 5), harvest rate (h, from data in Fig. 12B) and time trend, either linear (T) or quadratic (T^2), with $1989 = 1$).

Model	$\Delta\mathrm{QAIC}_c$[a]	QAIC_c weight[b]	K[c]	Quasi deviance
$\{S(\mathrm{NOR}(.)\ \mathrm{SOU}(H)), f(g + t)\}$	0.00	0.32	22	362.22
$\{S(\mathrm{NOR}(.)\ \mathrm{SOU}(\mathrm{CO})), f(g + t)\}$	1.13	0.18	22	363.35
$\{S(\mathrm{NOR}(.)\ \mathrm{SOU}(R + C)), f(g + t)\}$	1.45	0.16	23	361.66
$\{S(g * H), f(g + t)\}$	1.85	0.13	23	362.07
$\{S(g * \mathrm{CO}), f(g + t)\}$	3.13	0.07	23	363.35
$\{S(g * R + C), f(g + t)\}$	4.07	0.04	25	360.28
$\{S(g * T^2), f(g + t)\}$	4.36	0.04	25	360.58
$\{S(\mathrm{NOR}(.)\ \mathrm{SOU}(T)), f(g + t)\}$	4.38	0.04	22	366.59
$\{S(\mathrm{NOR}(.)\ \mathrm{SOU}(C)), f(g + t)\}$	5.91	0.02	22	368.13
$\{S(g * T)\ f(g + t)\}$	6.34	0.01	23	366.56
$\{S(\mathrm{NOR}(.)\ \mathrm{SOU}(\mathrm{pre}(T)\ \mathrm{CO}(T)), f(g + t)\}$	10.44	0.00	23	370.66
$\{S(g + t), f(g + t)\}$	12.20	0.00	37	344.40
$\{S(\mathrm{NOR}(.)\ \mathrm{SOU}(H)), f(g * t)\}$	12.43	0.00	39	340.63
$\{S(g * h), f(g + t)\}$	13.38	0.00	23	373.60
$\{S(g * H), f(g * t)\}$	14.43	0.00	40	340.63
$\{S(t), f(g + t)\}$	14.88	0.00	36	349.08
$\{S(\mathrm{NOR}(.)\ \mathrm{SOU}(\mathrm{CO})), f(g * t)\}$	14.96	0.00	39	343.16
$\{S(g + T), f(g + t)\}$	15.12	0.00	22	377.33
$\{S(g * \mathrm{CO}), f(g * t)\}$	16.85	0.00	40	343.05
$\{S(\mathrm{NOR}(.), \mathrm{SOU}(t)), f(g + t)\}$	19.30	0.00	35	355.50
$\{S(g + t), f(g * t)\}$	21.32	0.00	54	319.49
$\{S(\mathrm{NOR}(T)\ \mathrm{SOU}(.)), f(g + t)\}$	28.51	0.00	22	390.73
$\{S(.), f(g + t)\}$	28.96	0.00	20	395.18
$\{S(g), f(g + t)\}$	29.16	0.00	21	393.37
$\{S(\mathrm{NOR}(H)\ \mathrm{SOU}\ (.)), f(g + t)\}$	30.38	0.00	22	392.59
$\{S(g * t), f(g * t)\}$ GLOBAL	36.35	0.00	70	302.48
$\{S(g * t), f(g + t)\}$	37.50	0.00	53	337.68
$\{S(.), f(g * t)\}$	39.53	0.00	37	371.72
$\{S(g), f(g * t)\}$	39.53	0.00	38	369.73
$\{S(g + t), f(t)\}$	39.77	0.00	32	381.98
$\{S(\mathrm{NOR}(t), \mathrm{SOU}(.)\ f(g + t)\}$	52.67	0.00	37	384.87
$\{S(t), f(g * t)\}$	57.61	0.00	53	357.78
$\{S(t), f(t)\}$	58.07	0.00	35	394.27
$\{S(g), f(t)\}$	59.53	0.00	20	425.75
$\{S(g * T), f(g * \mathrm{CO})\}$	66.58	0.00	8	456.80
$\{S(.), f(t)\}$	69.39	0.00	19	437.60
$\{S(g * t), f(t)\}$	73.89	0.00	52	376.06
$\{S(g * T), f(g * T)\}$	257.36	0.00	8	647.58
$\{S(g + T), f(g * T)\}$	274.36	0.00	7	666.57
$\{S(g + T), f(g + T)\}$	274.46	0.00	6	668.68
$\{S(g + t), f(g * T)\}$	307.98	0.00	22	670.19
$\{S(\mathrm{NOR}(.)\ \mathrm{SOU}(\mathrm{CO})), f(g * T)\}$	342.03	0.00	7	734.24
$\{S(g + t), f(g)\}$	397.84	0.00	20	764.04
$\{S(g * t), f(g)\}$	407.97	0.00	36	742.15
$\{S(g + t), f(.)\}$	416.06	0.00	19	784.26
$\{S(g * t), f(.)\}$	428.58	0.00	35	764.77
$\{S(t), f(g)\}$	429.67	0.00	19	797.87
$\{S(t), f(.)\}$	433.59	0.00	18	803.79
$\{S(.), f(g)\}$	462.69	0.00	3	862.90
$\{S(g), f(g)\}$	464.36	0.00	4	862.57
$\{S(g), f(.)\}$	480.65	0.00	3	880.86
$\{S(.), f(.)\}$	488.83	0.00	2	891.04

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[a] Difference between Akaike's Information Criterion with adjustments for overdispersion ($\hat{c} = 1.058$) and small-sample bias (QAIC_c; Burnham and Anderson 2002) of the current model and the lowest observed value.

[b] Normalized Akaike (QAIC_c) weight (Burnham and Anderson 2002).

[c] K = number of parameters estimated.

Appendix E. Do lesser snow geese marked in Canada's central and eastern arctic and subarctic winter in the midcontinent?

Before analysis of spatio-temporal patterns in recoveries of snow geese marked at locations with regard to major north and south breeding strata (Table 1), we made detailed summaries with respect to proportion of recoveries by state or province, flyway, and country. The motivations for these summaries were 1) to provide readers with information specific to jurisdictions of interest at a finer scale by colony and 2) to test whether the sample of birds marked in Canada's central and eastern arctic and that we used for other analysis well represented lesser snow geese that migrate and winter in the midcontinent of North America. This analysis is pertinent because the efforts to reduce snow goose survival and thus abundance are focused in Saskatchewan and Manitoba, which cover the main Canadian landmass through which snow geese migrate to the midcontinent, and in the Central and Mississippi Flyways, which also contain midcontinent winter areas. The spatial and temporal patterns described here can be compared with those compiled by Dzubin (1974).

Distribution of Recoveries During Regular Seasons for Snow Geese of Different Origin

Although there was broad overlap in density of recoveries for adult snow geese from different banding origins, proportional recoveries by state or provincial jurisdictions differed markedly (Tables S1 and S2, available online at www.onlinelibrary.wiley.com). We judged only 6 (Akimiski, Baffin, Cape Henrietta Maria, La Pérouse Bay, and Queen Maud Gulf now including Rasmussen Lowlands) of 8 banding locations to have sufficient (>30) recoveries to calculate proportional recoveries by state or provincial jurisdictions. The most important jurisdictions for recoveries during regular seasons were Arkansas (11–22%), Louisiana (9–16%), Manitoba (6–18%), North Dakota (3–21%), Saskatchewan (5–19%), and Texas (5–25%).

Proportional distribution of recoveries during regular seasons was clearer on a broader scale (i.e., by country or flyway; Tables S3–S6, available online at www.onlinelibrary.wiley.com). For example, Canada accounted for 27–40% of recoveries of adults marked in each of Akimiski Island, Baffin Island, and Cape Henrietta Maria (Table S3, available online at www.onlinelibrary.wiley.com) but only 17–32% of recoveries from La Pérouse Bay and 20% from Queen Maud Gulf (Table S4, available online at www.onlinelibrary.wiley.com). Adult geese from Akimiski Island (50–66%), Baffin Island (53%), and Cape Henrietta Maria (71%) had greater proportions recovered in the Mississippi Flyway than in the Central Flyway (33–50%, 46%, and 29%, respectively), thus reflecting a general concordance between eastern breeding, migration and wintering distributions (Table S5, available online at www.onlinelibrary.wiley.com). Adult geese from more western banding locations were recovered in higher proportions from the Central Flyway (La Pérouse Bay: 46–56%, Queen Maud Gulf: 57%) than in the Mississippi Flyway (La Pérouse Bay: 44–54%, Queen Maud Gulf 39–44%; Table S6). Although most snow geese from Queen Maud Gulf showed strong affinities to the midcontinent, this was the only banding location in Canada's central or eastern arctic and subarctic with nontrace proportions of adult geese recovered in the Pacific Flyway (2–4%) or Mexico (3–4%; Tables S4 and S6, available online at www.onlinelibrary.wiley.com). Most Mexican recoveries of snow geese from Queen Maud Gulf were in the western interior. Queen Maud Gulf snow geese also showed more western affinities than other regions even in Canada and the Central Flyway. For example, recoveries from Alberta, Colorado, New Mexico, and California represented 7% of those marked in Queen Maud Gulf but only $\leq$1% of recoveries from all other arctic banding locations considered (Tables S1 and S2, available online at www.onlinelibrary.wiley.com). Similarly in Canada, Queen Maud Gulf snow geese were recovered in higher proportions from Alberta and Saskatchewan (18%) than from Manitoba (1%) compared to those from more eastern banding locations (Alberta and Saskatchewan: 6–18%, Manitoba: 6–18%, Tables S1 and S2, available online at www.onlinelibrary.wiley.com).

Changes in harvest distribution have occurred during regular seasons before and after initiation of conservation-order or spring harvests in 1998. Other than geese from Queen Maud Gulf, only trace proportions from any area were recoveries from Mexico. Hence, a test of independence between regular-season recoveries before (Pre) and after (Post) start of conservation order or spring harvests, and country (Canada, U.S.) excluded Mexican recoveries of geese marked in areas other than near Queen Maud Gulf. Sufficient recoveries for such a test were available only from La Pérouse Bay and Queen Maud Gulf. Proportion of recoveries in Canada increased during regular seasons from 17% before 1998 to 34% after 1997 for adult birds marked near La Pérouse Bay ($\chi^2_2 = 82.3$, $P < 0.001$), but did not change for birds marked near Queen Maud Gulf ($\chi^2_2 \approx 0.26$, $P = 0.88$, Table S4, available online at www.onlinelibrary.wiley.com).

We next considered only banding locations east of Queen Maud Gulf (i.e., on Baffin Island and near Hudson and James Bays; Akimiski Island, Cape Henrietta Maria, and La Pérouse Bay), with stronger affinities to eastern than western migration and wintering areas. Snow geese from La Pérouse Bay showed more western recovery distributions by flyway (Atlantic: <1%, Mississippi: 44–55%, Central: 45–56%, Pacific: <1%, Table S6, available online at www.onlinelibrary.wiley.com) than the other 3 colonies considered (Atlantic: 0–1%, Mississippi: 50–71%, Central: 29–50%, Pacific: 0%, Table S5, available online at www.onlinelibrary.wiley.com). This longitudinal difference in distribution of adult geese from these colonies was not evident from Canadian recoveries (Table S2, available online at www.onlinelibrary.wiley.com).

Knowledge about differences in general distributions of recoveries is important for understanding the appropriateness of linking potential effects of harvest on survival. These patterns in recovery distributions suggest that band recovery data from the arctic and subarctic areas considered, including the major banding locations of La Pérouse Bay and Queen Maud Gulf, well represent survival of snow geese harvested from the midcontinent. Distribution of recoveries for geese marked on Baffin Island, Cape Henrietta Maria, and Akimiski Island showed greater affinities to the Mississippi Flyway and represent snow geese from the Central Flyway less well. Hence, stratified data from these breeding populations generally appear well-suited for estimation of survival within the migration and winter range of our focal population of midcontinent snow geese.

Appendix F. Population change inferred from photosurveys of midcontinent snow geese nesting in Canada's central and eastern arctic and subarctic, 1979–2006.

Photosurveys of colonies in regions north of 60°N used by nesting snow geese were done in 1979–1982, 1997–1998 (Kerbes et al. 2006) and were repeated from 2003 to 2006 (K. Meeres, Canadian Wildlife Service [CWS], unpublished data). The main nesting regions and the year that photos were taken at each were Baffin Island (1979, 1997, and 2005), Central Arctic (1982, 1988, 1998, and 2006), Southampton Island (1979, 1997, and 2004), and West Hudson Bay (1980, 1997, and 2003). Corresponding estimates from the 1997 or 1998 survey, N_0, and one done between 2003 and 2006, N_t, of nesting snow geese from images counted on photos were 1,733,500 and 1,618,560, respectively, on Baffin Island; 657,313 and 1,665,643, respectively, in the Central Arctic; 712,000 and 652,546, respectively, on Southampton Island; and 211,600 and 261,080, respectively, on West Hudson Bay (Kerbes et al. 2006; K. Meeres, CWS, unpublished data). Rearranging the model for exponential growth (see Table 10), $\hat{\lambda}$ for each colony can be estimated by exponentiating the intrinsic rate of growth, $r = \ln(N_t/N_0)/t$, since $\lambda = e^r$. Thus, $\hat{\lambda}$was 0.990 for nesting snow geese on Baffin Island, 1.123 for those in the Central Arctic, 0.986 on Southampton, and 1.036 on West Hudson Bay. These estimates of average annual growth rely on only 2 endpoint values in a time series separated by 6–9 years and are likely highly sensitive to endpoint abundance estimates. Endpoint estimates, in turn, are influenced by phenology of local snowmelt and the number of geese that attempt to nest within colonies and so can be counted on photos. Such estimates of growth rate should be used with caution. Nevertheless, taking the sum of snow geese estimated from photos taken during 1997–1998 ($N_0 = 3{,}406{,}890$) and 2003–2006 ($N_{t=7} = 4{,}197{,}829$) and estimating $\hat{\lambda}$, as above, using an average interval of 7 years yields an annual rate of increase of $\hat{\lambda} = 1.030$ in the number of nesting geese, compared to an average rate from 1980 ($N_0 = 1{,}110{,}900$) to 1997–1998 ($N_{t=17} = 3{,}406{,}890$) of $\hat{\lambda} = 1.068$.