Breeding dispersal by Ross's geese in the Queen Maud Gulf metapopulation

K. L. Drake & R. T. Alisauskas

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Abstract
Breeding dispersal by Ross's geese in the Queen Maud Gulf metapopulation.— We estimated rates of breeding philopatry and complementary dispersal within the Queen Maud Gulf metapopulation of Ross's Geese (*Chen rossii*) using multistate modeling of neckband observations at five breeding colonies, 1999–2003. Probability of philopatry was female–biased, but varied among colonies. Probabilies of annual movement among breeding colonies ranged 0.02 to 0.14 for females and 0.12 to 0.38 for males and was substantially higher than expected. These estimates (1) underscore the potential for dispersal to alter breeding distribution, (2) demonstrates that the influence of immigration on colony–specific rates of population growth is nontrivial, and (3) provides behavioral evidence for extensive gene flow among subpopulations. Sex differences in apparent survival estimated from multistate models likely resulted from a combination of higher rates of neckband loss by males compared to females, and higher rates of permanent emigration by males from our study area.

Key words: Dispersal, Multistate, Philopatry, Ross's Goose, *Chen rossi*.

Resumen
Dispersión de los reproductores del ansar de Ross en la metapoblación del golfo de la Reina Maud.— Estimamos las tasas de filopatría de reproducción y la dispersión complementaria del ansar de Ross (*Chen rossii*) en la metapoblación del golfo de la Reina Maud utilizando la modelación multiestado a partir de las observaciones de animales marcados en el cuello en cinco colonias de reproducción, 1999–2003. La probabilidad de filopatría presentaba un sesgo a favor de las hembras, pero variaba de una colonia a otra. Las probabilidades de movimiento anual entre las colonias de reproducción oscilaban entre el 0,02 y el 0,14 para las hembras, y entre el 0,12 y el 0,38 para los machos, siendo considerablemente superiores a lo previsto. Estas estimaciones 1) subrayan las posibilidades de que la dispersión modifique la distribución de reproducción, 2) demuestran que la influencia de la inmigración en las tasas de crecimiento poblacional de cada colonia no es irrelevante y 3) proporcionan evidencia conductual acerca de un amplio flujo genético entre subpoblaciones. Las diferencias por sexo en la supervivencia aparente estimadas a partir de modelos multiestado probablemente fueron debidas a una combinación de tasas más elevadas de pérdida de marcaje en el cuello por parte de los machos en comparación con las hembras, y a tasas más elevadas de emigración permanente por parte de los machos de nuestra área de estudio.

Palabras clave: Dispersión, Multiestado, Filopatría, Ansar de Ross, *Chen rossi*.

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Introduction

Species distributions often encompass broad geographic ranges that include great spatial variability in landscape characteristics. Corresponding variability in ecological conditions leads to uneven distributions of density throughout a species' range, because animals congregate in areas where habitats are suitable. Such subpopulations are often geographically separated from each other by areas of less suitable habitats (Weins, 1997). Nevertheless, almost all species have evolved mechanisms that allow dispersal across unsuitable or less optimal habitats. Consequently, disjunct conspecific populations are potentially interconnected through migration networks or dispersal to new breeding areas. Such potential for movement among subpopulations is key to the concept of metapopulations (Gilpin & Hanski, 1991; Hanski & Gilpin, 1997), where persistence is a function of not only survival and recruitment of individuals but also of immigration and emigration between component subpopulations (Pulliam, 1988).

In North America, breeding and wintering distributions of continental populations of the closely–related Ross's Goose (*Chen rossii*) and Lesser Snow Goose (*Chen caerulescens*, hereafter Snow Goose, collectively referred to as 'light geese') are such that they fall within the conceptual domain of a metapopulation. Both species breed at spatially discrete colonies in arctic and subarctic habitats and winter in allopatric subpopulations across a broad range in southern North America (Ryder & Alisauskas, 1995; Mowbray et al., 2000). Despite spatial segregation of breeding subpopulations, there is tremendous potential for exchange of light geese because of mixing during migration when long–term pair bonds begin to form during late winter and continue through spring migration (Ryder & Alisauskas, 1995; Mowbray et al., 2000).

Much attention in North America has focused on the exponential population increase of light geese and their potential to damage breeding habitats (Batt, 1997; Moser, 2001). Regardless of causes resulting in unchecked population growth, light goose populations are markedly larger and occur over much broader winter ranges than they did 50 years ago. Winter range expansion highlights the ability of Snow Geese and Ross's Geese to adapt to changing landscape conditions (Alisauskas et al., 1988; Alisauskas, 1998). Despite these species' apparently adaptive nature during the nonbreeding period, female Snow Geese were thought to be generally philopatric to breeding colonies (Cooke et al., 1995), even when the consequences of philopatry appeared to be maladaptive such as when population densities exceed carrying capacity (Cooch et al., 1989; Cooch et al., 1991; but see Cooch et al., 2001). No information about vagility of Ross's Geese was available.

We estimated rates of movement among breeding colonies by Ross's Geese to gain insight about the potential for breeding dispersal to influence species distribution and gene flow in light geese. We focused the current analysis on Ross's Geese because of uninterrupted marking within the Queen Maud Gulf Bird Sanctuary (QMGBS) since 1989 that resulted in a substantial marked population at the outset of this study. Efforts to neckband Snow Geese in the QMGBS, and their subsequent resightings, have recently increased (Drake & Alisauskas, unpubl. data), but there remains insufficient data to include them in the current analysis. Nonetheless, Ross's Geese and Snow Geese associate throughout their annual cycles (Alisauskas, 2002), and the extent of such associations during breeding likely has increased recently with the growth in number of Snow Geese in the QMGBS where > 95% of the continental population of Ross's Geese breeds (Kerbes, 1994).

Materials and methods

Study area

Data were collected annually at five breeding colonies within the QMGBS (fig. 1) during 1999–2003. Colony 3 (hereafter, Karrak Lake 67º 14' N, 100º 15' W) contains the Karrak Lake Research Station where investigations of Ross's Goose breeding ecology have occurred continuously since 1991. Surveys for neckbanded geese began in 1994 at Karrak Lake and were extended to other colonies (nine, 10, 46 and 81) within QMGBS starting 1999. We selected these colonies because they represent some of the largest known colonies within QMGBS. We suggest that these colonies collectively account for ~90% of the known continental breeding population of Ross's Geese (Ryder & Alisauskas, 1995; Alisauskas et al., 1998).

Marking efforts and surveys for neckbanded geese

Following methods used by Alisauskas & Lindberg (2002), we captured and neckbanded adult and gosling Ross's Geese within brood–rearing habitats (fig. 2) during August 1991–2003. Marking efforts during 1991–1998 focused on areas north of Karrak Lake along the Karrak and Simpson River drainages, because we reasoned that most of the geese using these areas were from Karrak Lake. During 1999–2003, we continued to mark most geese north of Karrak Lake, but also began to neckband geese near colony 10, and the mouth of the McNaughton River (fig. 2). Because we could not assign with certainty Ross's Geese captured on brood–rearing areas in August to colonies in which they nested the previous June, we included only those birds that were resighted at breeding colonies in June 1999–2003. Only 501 goslings were neckbanded during 1999–2002 so we excluded these from consideration; we further judged that their inclusion would have doubled the number of parameters to be estimated while increasing the sample size only by ~15%. Hence, our analysis included adult birds

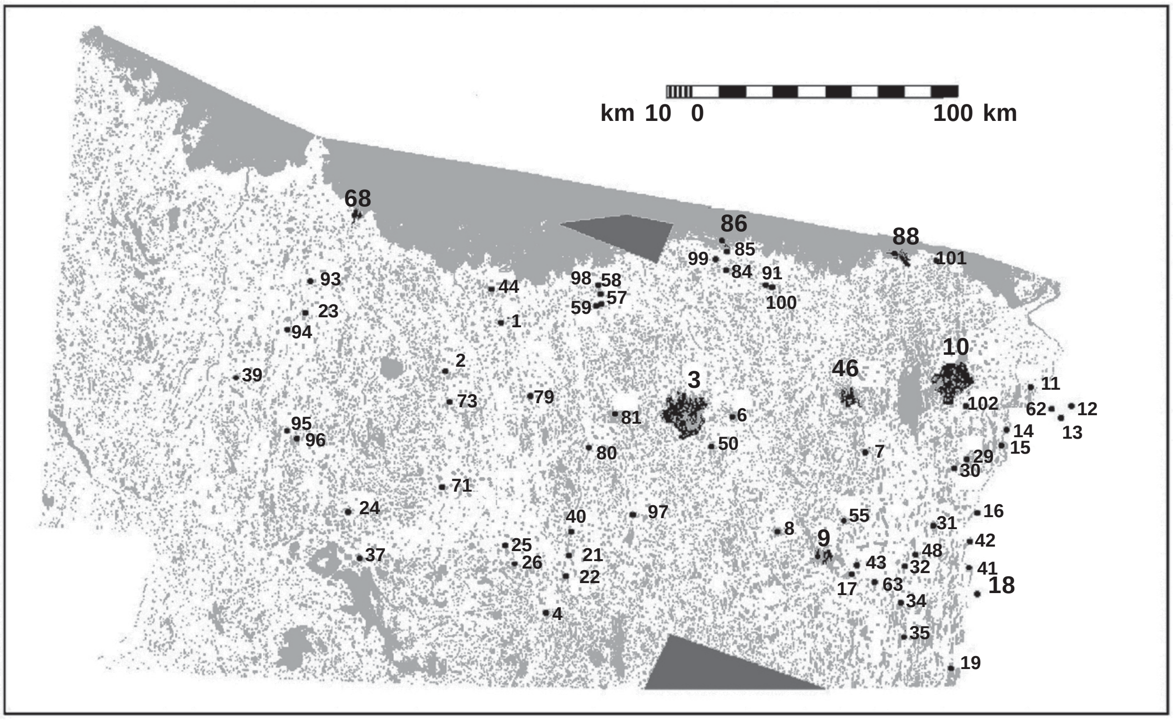

Fig. 1. Light goose colonies within the Queen Maud Gulf Bird Sanctuary, Nunavut, Canada. Numbers correspond to locations of goose colonies and black areas depict spatial extent of larger colonies. Surveys for neckbanded geese were conducted at colonies 3 (Karrak Lake), 9 (Simpson River), 10 (East McNaughton), 46 (West McNaughton), and 81 (Reference Lake) 1999–2003.

Fig. 1. Colonias de gansos menos pobladas de la Reserva Ornitológica del golfo de la Reina Maud, Nunavut, Canadá. Los números corresponden a emplazamientos de colonias de ánsares, mientras que las áreas en negro representan la extensión espacial de colonias más amplias. Los estudios correspondientes a los ánsares marcados en el cuello se llevaron a cabo en las colonias 3 (lago Karrak), 9 (río Simpson), 10 (McNaughton Este), 46 (McNaughton Oeste) y 81 (lago de referencia) 1999–2003.

(*n* = 3,233) sighted at least once at one of the sampled colonies during 1999–2003, regardless of year of marking.

We restricted observations for neckbanded geese to their 22–day incubation period (Ryder, 1972) because of our interest in estimating dispersal between breeding attempts. Observations strictly during incubation reduced potential for bias caused by sampling non–breeding adults, as territorial breeders displace most non–breeders from colonies by the onset of incubation (Ryder & Alisauskas, 1995). Extent of breeding distribution at each colony was mapped each year in June from a helicopter. Data were digitized and imported into SPANS GIS study area with Albers equal area projection. Layers showing colony extent were overlaid with a layer showing land and water (30 m resolution from LandSat imagery) to calculate the area of terrestrial habitat at each colony occupied by nesting geese. In 2002, for example, terrestrial habitat occupied by nesting geese was 164.9 km^2 at colony 3, 10.3 km^2 at colony 9, 151.2 km^2 at colony 10, 39.8 km^2 at colony 46, and 1.9 km^2 at colony 81. Due to this vast area in which neckbands could only be search for on foot, we were unable to survey all colonies entirely. Instead, we selected areas within each colony thought to have the highest nesting densities, generally in the center, to maximize efficiency at detecting neckbands. We maintained consistency among years by searching for neckbands in defined study areas in each colony. We assumed that the ratio of neckbanded to unmarked birds remained consistent regardless of variation in nesting density. Any broken neckbands found on the ground by observers in the course of travel through colonies during neckband surveys were noted.

Analysis

We used multistate modeling (Arnason, 1973; Hestbeck et al., 1991; Brownie et al., 1993; Schwarz et al., 1993) in Program MARK to analyze resight data of neckbanded Ross's Geese for estimation of dispersal and complementary philopatry probabilies. Multistate models allow estimation of probabilies for apparent survival, $\hat{\phi}$, detection, $\hat{p}$, and movement among states, $\hat{\psi}$. We considered variation by colony, sex, and year for each of these parameters, subscripted as $\{\phi_c, p_c, \psi_c\}$, $\{\phi_x, p_x, \psi_x\}$, or $\{\phi_t, p_t, \psi_t\}$, respectively. Thus, our fully parameterized global model $\{\phi_{c\cdot x\cdot t}, p_{c\cdot x\cdot t}, \psi_{c\cdot x\cdot t}\}$ had 240 potentially estimable parameters. The iterative routine used during the maximum likelihood function failed to converge numerically for this model, so we re–examined input data and found that movement was not detected in 99 of the 160 possible colony–, sex–, and time–specific movements. We obtained convergence after fixing these parameters to zero, but we were warned by Program MARK that convergence was suspect. Numerical estimation for a few models from the candidate set resulted in inconsistent deviances relative to the number of parameters being estimated (White, G. W., pers comm). Inconsistency in changes of deviance confirmed that the global model failed to converge properly even after fixing parameters. Consequently, we reduced the number of strata from five to three, thus reducing the number of parameters being estimated while maintaining biologically relevant models, as follows.

We constrained movement to occur among three strata only: Karrak Lake, Colony 10, and other colonies combined (nine, 46, and 81; hereafter, other colonies). Strata were redefined based on colony sizes (fig. 1) and sampling effort. Karrak Lake and colony 10 represent the two largest colonies within the QMGBS (~433,000 and ~386,000 breeding Ross's Geese in 1998, respectively), and colonies nine, 46, and 81 are substantially smaller (ranging between ~30,000 and ~95,000 in 1998; Alisauskas et al., 1998). Sampling effort varied somewhat among years at different colonies, from the interplay between spring phenology and availability of aircraft with which to visit study colonies. Sampling effort was highest at Karrak Lake, where unlike other colonies, it could be accessed entirely by foot or by boat from our permanent research facility. All other colonies were accessed by helicopter, and so neckband observations there ranged from one to four days. Relative effort among colonies was consistent such that sampling effort at Karrak Lake > colony 10 > other colonies, for all years of the study. Such reduction of structure of the global model resulted in numerical convergence.

Our reduced global model had 96 potential parameters, including all sources of variation and all possible interactions. Our modeling approach was to test fit of the global model to the data and then, based upon biological knowledge of the study organism and differences in sampling effort, compare a set of candidate models with reduced numbers of parameters to assess parsimony and fit of models to the data using AICc (Burnham & Anderson, 1998). Program MARK does not provide goodness–of–fit test specifically for multistate data sets, so we parameterized the data as a Cormack–Jolly–Seber (CJS) data set and tested for goodness–of–fit of $\{\phi_{x*t}, p_{x*t}\}$ (Lebreton & Pradel, 2002) using 1000 iterations of the parametric bootstrap available for such global models in Program MARK. Deviance of the global model was less than 85% of the simulated deviance indicating that the data were not overdispersed so a variance inflation factor ($\hat{c}$) was not used (Burnham & Anderson, 1998).

We considered 15 models in our candidate set. Movement probability was our primary parameter of interest, so our approach to hypothesis testing and parameter estimation was to sequentially reduce sources of variation in probabilities of resighting and then survival, while retaining full–structured variation in movement probabilities. First, we reduced sources of variation in $\hat{p}$. We retained effects of colony and time in all parameterizations of $\hat{p}$ because sampling effort varied among colonies, and because we suspected temporary emigration as the size of breeding populations at colonies varies annually (Alisauskas & Rockwell, 2001). We considered 4 additional parameterizations of $\hat{p}$ including (1) a multiplicative interaction between colony and additive effects of sex and time ($\hat{p}_{c\cdot[x+t]}$), (2) a completely additive model ($\hat{p}_{c+x+t}$), and (3) additive ($\hat{p}_{c+t}$) and (4) multiplicative ($\hat{p}_{c\cdot t}$) models without sex effects. We used the parameterization of $\hat{p}$ from the best of these models in all subsequent modeling of survival and movement probabilities.

Including the structure within the global model, we considered six parameterizations of $\hat{\phi}$. Breeding colonies represent subpopulations where the potential for colony–specific differences in $\hat{\phi}$ has implications for colony–specific growth rates as well as potential fitness costs to individuals. There is considerable clinal variation in winter and migration affinities of Ross's geese marked in the QMGBS over a narrow range of ~200 km of longitude (Alisauskas et al., 2005); thus it is likely that different segments of the QMGBS metapopulation are subject to geographically variable harvest pressure (Moser & Duncan, 2001), so we tested for colony specific rates of survival ($\hat{\phi}_{c\cdot x\cdot t}$) *vs*. ($\hat{\phi}_{x\cdot t}$). Most evidence suggests that true survival, $\hat{S}$, does not vary between sexes in most species of geese (Melinchuk & Ryder, 1980; Alisauskas & Lindberg, 2002; but see Francis & Cooke, 1992). However, sex differences in fidelity, F, to breeding colonies may still result in sex–specific ϕ, because $\phi = S * F$. So, we considered $\{\hat{\phi}_{c\cdot x\cdot t}\}$ *vs*. $\{\hat{\phi}_{c\cdot t}\}$. After testing for colony and sex effects, we considered models with additive effects of sex and time ($\hat{\phi}_{x+t}$), a linear time trend ($\hat{\phi}_{x+T}$), and a model that included only the effect of sex ($\hat{\phi}_x$).

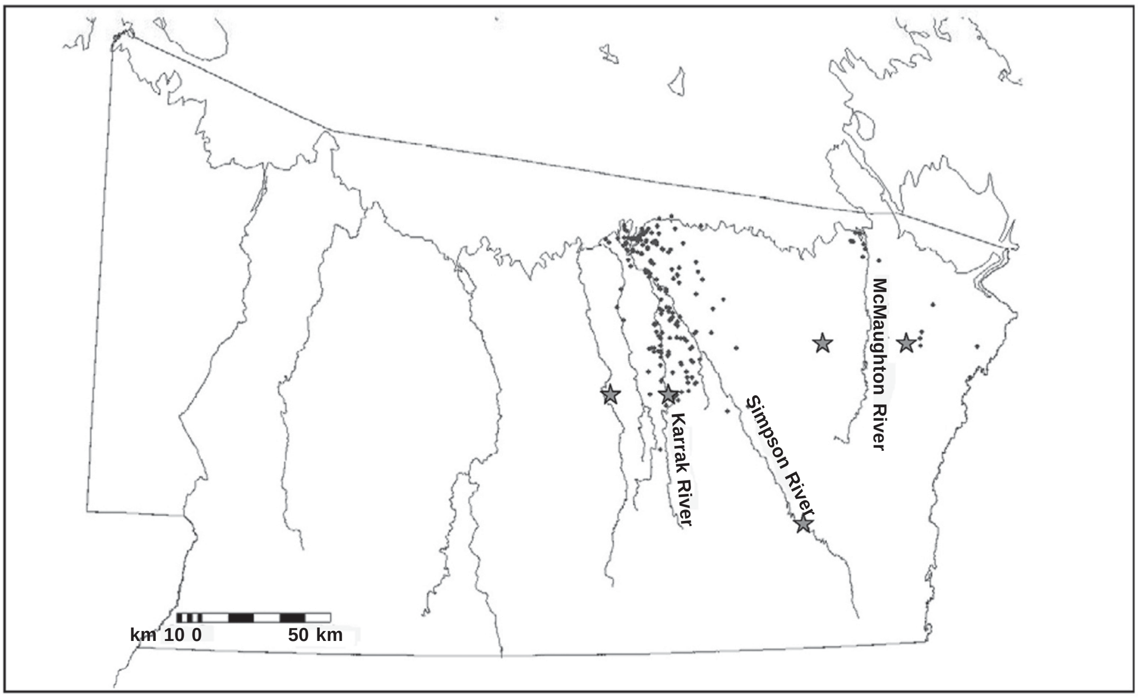

Fig. 2. Locations of Ross's Goose banding efforts within brood rearing areas in the Queen Maud Gulf Bird Sanctuary, Nunavut, Canada, 1999–2003. Banding drive locations are shown as dots, while stars delineate locations of breeding colonies that were surveyed for neckbanded geese.

Fig. 2. Emplazamientos de las campañas de marcaje en el cuello del ansar de Ross en áreas de crianza de la Reserva Ornitológica del golfo de la Reina Maud, Nunavut, Canadá, 1999–2003. Los emplazamientos de las campañas de marcaje en el cuello se indican como puntos, mientras que las estrellas definen los emplazamientos de las colonias de reproducción que se investigaron con respecto a los gansos marcados en el cuello.

We proceeded to estimate $\hat{\psi}$ starting with models optimally structured for $\hat{p}$ and $\hat{\phi}$. We retained colony structure in $\hat{\psi}$ in all models because of our interest in stratum–specific estimates. These included fully multiplicative effects of colony, sex and year $\{\hat{\psi}_{c \cdot x \cdot t}\}$, additive effects of sex and time specific to each colony $\{\hat{\psi}_{c \cdot [x+t]}\}$, complete additivity $\{\hat{\psi}_{c+x+t}\}$, a multiplicative model excluding the effect of sex $\{\hat{\psi}_{c \cdot t}\}$, and an additive model with colony and sex effects $\{\hat{\psi}_{c+x}\}$. All manipulations of model structure were done using the design matrix in Program MARK, and all models were fit using the logit link function (White & Burnham, 1999).

Results

Model $\{\hat{\phi}_{x+t}, \hat{p}_{c+t}, \hat{\psi}_{c+x}\}$ was clearly best supported by our data (w_{AICc} = 0.993, table 1); thus, all estimates were based on this model. This model showed that apparent survival varied over time in parallel between sexes, but that survival was equal among colonies. Predictably, recapture probabilities varied among colonies, but differences were consistent for all years of study. Movement probability was constant but varied among colonies in parallel between sexes. Estimates of apparent survival ranged between 0.631 ± 0.038 (SE) and 0.682 ± 0.033 for females, and between 0.489 ± 0.034 and 0.546 ± 0.044 for males (table 2). Recapture probabilities varied in an additive fashion among colonies and years, but were as low as 0.069 ± 0.025 for colonies nine, 46 and 81, and as high as 0.612 ± 0.037 at Karrak Lake (fig. 3). Colony– and sex–specific dispersal probabilities ranged from 0.023 ± 0.024 to 0.344 ± 0.085 for females and from 0.122 ± 0.063 to 0.376 ± 0.074 for males (fig. 4a).

We found 44 broken neckbands that had fallen off of male Ross's Geese but only 12 from females. Compared to 7,904 males and 7,718 females that had been marked with neckbands, this represents a strong male bias in apparent rates of neckband loss (likelihood ratio χ^2 = 8.76, df = 1, $P < 0.005$)

Table 1. Model structure, AIC_c, ΔAIC_c, model weight (w_{AICc}), number of parameters (K), and model deviance, for multistate modeling of apparent survival (ϕ), recapture (p), and dispersal (ψ) probabilities of neckbanded Ross's Geese within the Queen Maud Gulf metapopulation, 1999–2003. Dots indicate multiplicative interactions between colony (c), sex (x), time (t) and time–trend (T). Plus signs indicate an additive model.

Tabla 1. Estructura de los modelos, AIC_c, ΔAIC_c, peso de los modelos (w_{AICc}), número de parámetros (K), y desviación de los modelos, para la modelación multiestado de probabilidades de supervivencia (ϕ), recaptura (p) y dispersión (ψ) de ánsares de Ross marcados en el cuello en la metapoblación del golfo de la Reina Maud, 1999–2003. Los puntos indican interacciones multiplicativas entre la colonia (c), el sexo (x) el tiempo (t) y la tendencia temporal (T). Los signos más indican un modelo aditivo.

Model	AIC_c	ΔAIC_c	w_{AICc}	K	Model deviance
$\{\phi_{x+t}\ p_{x+t}\ \psi_{c+x}\}$	7045.07	0.00	0.99	22	471.50
$\{\phi_{x+t}\ p_{x+t}\ \psi_{c\cdot x}\}$	7055.23	10.16	0.01	15	495.81
$\{\phi_{x+t}\ p_{x+t}\ \psi_{c\cdot(x+t)}\}$	7059.02	13.95	0.00	39	450.85
$\{\phi_{x+t}\ p_{x+t}\ \psi_{c\cdot x\cdot t}\}$	7069.92	24.85	0.00	51	437.14
$\{\phi_{x+t}\ p_{x+t}\ \psi_{c+x+t}\}$	7071.52	26.45	0.00	17	508.06
$\{\phi_{x\cdot t}\ p_{c+t}\ \psi_{c\cdot x\cdot t}\}$	7072.85	27.78	0.00	54	433.88
$\{\phi_{c\cdot x\cdot t}\ p_{c+t}\ \psi_{c\cdot x\cdot t}\}$	7073.95	28.88	0.00	66	410.15
$\{\phi_{x}\ p_{c+t}\ \psi_{c\cdot x\cdot t}\}$	7075.55	30.48	0.00	50	444.82
$\{\phi_{x+T}\ p_{c+t}\ \psi_{c\cdot x\cdot t}\}$	7077.50	32.43	0.00	51	444.72
$\{\phi_{c\cdot x\cdot t}\ p_{c+x+t}\ \psi_{c\cdot x\cdot t}\}$	7078.21	33.14	0.00	70	406.10
$\{\phi_{c\cdot x\cdot t}\ p_{c\cdot(x+t)}\psi_{c\cdot x\cdot t}\}$	7078.46	33.39	0.00	74	398.02
$\{\phi_{c\cdot x\cdot t}\ p_{c\cdot t}\ \psi_{c\cdot x\cdot t}\}$	7081.36	36.29	0.00	72	405.08
$\{\phi_{c\cdot x\cdot t}\ p_{c\cdot x\cdot t}\ \psi_{c\cdot x\cdot t}\}$	7081.86	36.79	0.00	72	405.58
$\{\phi_{c\cdot t}\ p_{x+t}\ \psi_{c\cdot x\cdot t}\}$	7094.46	49.39	0.00	60	443.10
$\{\phi_{x+t}\ p_{x+t}\ \psi_{c\cdot t}\}$	7127.93	82.86	0.00	33	532.02

Discussion

Movement probability

Until development of methods for unbiased estimation of philopatry (and it's complement, dispersal) that account for detection probability, inferences were often based on return rates (Geramita & Cooke, 1982; Anderson et al., 1992: table 11–3). Although our conclusion about female–biased breeding philopatry in Ross's Geese qualitatively is consistent with general patterns for waterfowl, our results demonstrate that return rates offer only tentative inference about philopatry, similar to other investigations that have used mark–recapture methods (Lindberg et al., 1998; Doherty et al., 2002; Blums et al., 2003). Estimates of breeding philopatry for both male and female Ross's Geese were substantially higher than sex–specific return rates reported for many goose species (Anderson et al., 1992: table 11–3).

Our results were consistent with the general prediction for female–biased breeding philopatry based upon the mating–system hypothesis (Greenwood, 1980; Rohwer & Anderson, 1988). Nevertheless, female philopatry was highly variable among colonies, and was less than absolute in all cases. This underscores the importance of dispersal in colony–specific population dynamics of Ross's Geese in the QMGBS, and its potential to influence breeding distribution and gene flow.

We applied estimates of female dispersal probabilities to size of breeding subpopulations and found that they represent a large numbers of birds that switch colonies annually. We used breeding population estimates of light geese at Karrak Lake (~866,000) from Alisauskas et al. (1998) and assumed that about 50% are Ross's Geese, half of which are females (216,500). Assume that 216,500 females nest at Karrak Lake during year *i*, survive at a rate of 0.83 (Alisauskas et al., 2005), and breed during *i* + 1 at a hypothetical rate of 0.75. Thus, at *i* + 1 there are ~179,700 (216,500 x 0.83) surviving individuals of which 134,800 (179,700 x 0.75) will breed. Of those breeders, ~14,600 (134,800 x 0.108) will disperse from Karrak Lake and breed at another colony. Accordingly, assuming that average nesting density is equal among colonies, then based on colony area (km^2, Alisauskas et al., 1998), colony 10 had ~772,000 geese (~193,000 female Ross's Geese) and colonies 9, 46 and 81 combined represented ~339,000 geese (~84,800 female Ross's Geese). Assuming the same rates of survival and breeding probability, we applied stratum–specific estimates of dispersal from the other colonies to Karrak Lake and found that ~17,400 (193,000 x 0.83 x 0.75 x 0.145) females emigrate from colony 10, and ~18,200 (84,800 x 0.83 x 0.75 x 0.344) females emigrate from the other combined colonies to Karrak Lake. Such calculations suggest a net increase of ~21,000 (35,600–14,600) females to Karrak Lake within a given year due to breeding dispersal alone (fig. 4b).

Based upon limited information about movements of geese to and from La Pérouse Bay (LPB), and overwhelming female–bias in re–encounters at the colony, Cooke et al., (1995) argued that gene flow was male–mediated among breeding subpopulations of Snow Geese, while acknowledging that females showed some dispersal (Geramita & Cooke, 1982). More recently, Cooch et al. (2001) used a retrospective analysis to analyze life table response of the LPB colony and showed that emigration of adults had increased over time. Their results suggested that philopatry to brood rearing areas may be more flexible than fidelity to nesting areas. Our results suggest that breeding philopatry is also a flexible trait in closely–related Ross's Geese. Given similarities in life histories of these congeners and their sympatry throughout the annual cycle, we suspect that female dispersal in Snow Geese is more common that previously thought.

Although our analysis was focused on Ross's Goose movement between breeding colonies within the QMGBS metapopulation, 21% (680/3233) of the Ross's Geese used in our analysis were immigrants to the QMGBS that were banded along the West Coast of Hudson Bay (WHB), and 8.5% (58/680) of these were females. Movement of WHB geese represent breeding dispersal of distances ranging 500–800 km depending upon colony of settling, but because observations have not yet been done there, we could not estimate reverse movements.

Our estimates of annual dispersal among breeding colonies by Ross's Geese provide strong behavioral evidence for extensive gene flow among breeding subpopulations. These findings for Ross's Geese are consistent with genetic studies of Snow Geese which suggested little or no phylogeographic structure in frequency of mtDNA haplotypes detected in Snow Geese from different breeding areas across North America (Avise et al., 1992; Quinn, 1992). Additionally, based on recoveries from each of the Pacific, Central and Mississippi Flywyas (Alisauskas et al., in review), there is great overlap in winter range used by Ross's Geese marked in different brood–rearing areas used by the QMGBS metapopulation. Overall, Ross's Geese from QMGBS now have one of the most extensive winter ranges of any arctic–nesting goose species from a single arctic region. As well, high rates of movement by both sexes of Ross's Geese among colonies in QMGBS, hint at considerable movement by Ross's Geese to QMGBS from WHB. Shared winter areas of Ross's Geese with different breeding locations suggest that subpopulations of light geese are extensively interconnected by broadly overlapping migration networks which likely enhances likelihood of breeding dispersal. Such movement patterns are consistent with the "considerable population connectedness" inferred by Avise et al. (1992).

Table 2. Apparent survival estimates from multistate modeling of neckbanded adult Ross's Geese breeding within the Queen Maud Gulf metapopulation, 1999–2003. Survival was best modelled by including sex and time effects, but was equal among sampled colonies. Probabilities are given ± SE.

Tabla 2. Estimaciones de supervivencia aparente a partir de la modelación multiestado de la reproducción de ansar de Ross adultos marcados en el cuello en la metapoblación del golfo de la Reina Maud, 1999–2003. La mejor modelación de supervivencia se obtuvo incluyendo los efectos del sexo y del tiempo, pero fue similar entre las colonias muestreadas. Las probabilidades se indican ± SE.

	Survival probability	
Year	Female	Male
1999	0.682 ± 0.038	0.546 ± 0.044
2000	0.657 ± 0.035	0.516 ± 0.040
2001	0.653 ± 0.033	0.489 ± 0.035
2002	not estimated	not estimated

Studies of other colonial geese have shown that dispersal increases with increasing population density (Lindberg et al., 1998) and, that emigration can be an adaptive response to habitat degradation (Cooch et al., 1993; Cooch et al., 2001). We were unable to estimate population density at breeding colonies within the QMGBS, other than for Karrak Lake, and so were precluded from directly assessing breeding dispersal as a function of breeding density. Nevertheless, we found an asymmetry favouring movement toward Karrak Lake despite it being the most expansive colony of the ones studied. Slattery & Alisauskas (2002) detected density dependent effects on growth and survival of gos-

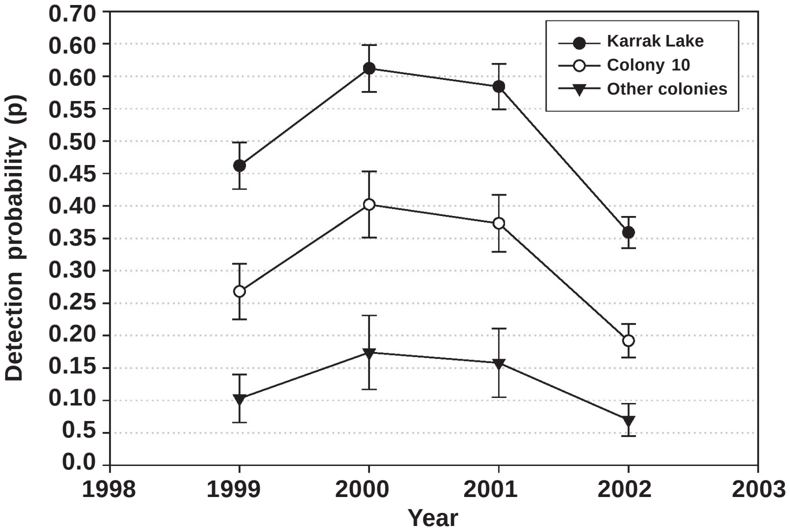

Fig. 3. Colony–specific detection probabilities from multistate modeling of neckbanded adult Ross's Geese resighted at breeding colonies within the Queen Maud Gulf metapopulation, 1999–2003. Bars represent standard error of the estimate.

Fig. 3. Probabilidades de detección para cada colonia a partir de la modelación multiestado de ánsares de Ross adultos marcados en el cuello que fueron reavistados en colonias de reproducción en la metapoblación del golfo de la Reina Maud, 1999–2003. Las barras representan el error estándar de la estimación.

lings marked on brood–rearing areas north of Karrak Lake, so other factors may override a connection to dispersal probabiltiy. For example, there is a strong cline in chronology of snowmelt with that in the west of QMGBS consistently far in advance (e.g., ~5% snow cover in 2003) compared to that 300 km to east (> 75% snow cover in 2003, Alisauskas, pers. obs.). Early nesting by arctic–breeding geese has strong fitness benefits (Cooke et al., 1984) because of the short time available for goslings to attain flight before freeze–up (Raveling, 1978). Hence, geese at Karrak Lake consistently may enjoy more favourable snow–free nesting conditions compared to most other colonies to the east. Consistent with this idea is that female emigration from colony 10, the most eastward colony examined, exceeds female immigration to colony 10 for both Karrak and other colonies.

The pattern of asymmetry in movement to Karrak Lake may also relate to east–west differences in likelihood of mate loss and subsequent repairing by widowed Ross's Geese. Alisauskas et al. (2005) found that Ross's Geese banded in the vicinity of colony 10 in eastern QMGBS were most likely to be recovered in the Central and Mississippi Flyway's; whereas, geese banded north of Karrak Lake were more likely to be recovered in the Pacific Flyway. Due to changes in management of light geese (Moser & Duncan, 2001), harvest in the Central and Mississippi Flyway has increased while it has remained relatively stable in the Pacific Flyway. Breeding geese mix non–homogenously among different wintering and migration locations such that breeding populations from eastern QMGBS show greater affinities to Central and Mississippi Flyway winter areas. These geese are subjected to higher hunting mortality and mate loss than populations toward the west of QMGBS, which have greater affinities to the Pacific Flyway winter areas. Thus, our suggestion for higher probability of mate loss by geese from Colony 10 may lead to repairing with maturing geese from Karrak Lake, and so partially account for asymmetry in movement from Colony 10 to Karrak Lake than vice versa.

Apparent survival rates

Sex differences in apparent survival provide insights to potential sources of bias when we interpret our results, given what is known about true survival estimates. Our estimates of apparent survival for neckbanded Ross's Goose females corresponded closely with estimates for true survival rates of neckbanded females from band recovery models (Alisauskas et al., 2005). Accordingly, we suggest that at least part of differences in apparent survival of males and females from multistate modeling resulted from violation of model assumptions rather from differences in true survival between sexes. Multistate models are constrained to $\Sigma\psi = 1$, which

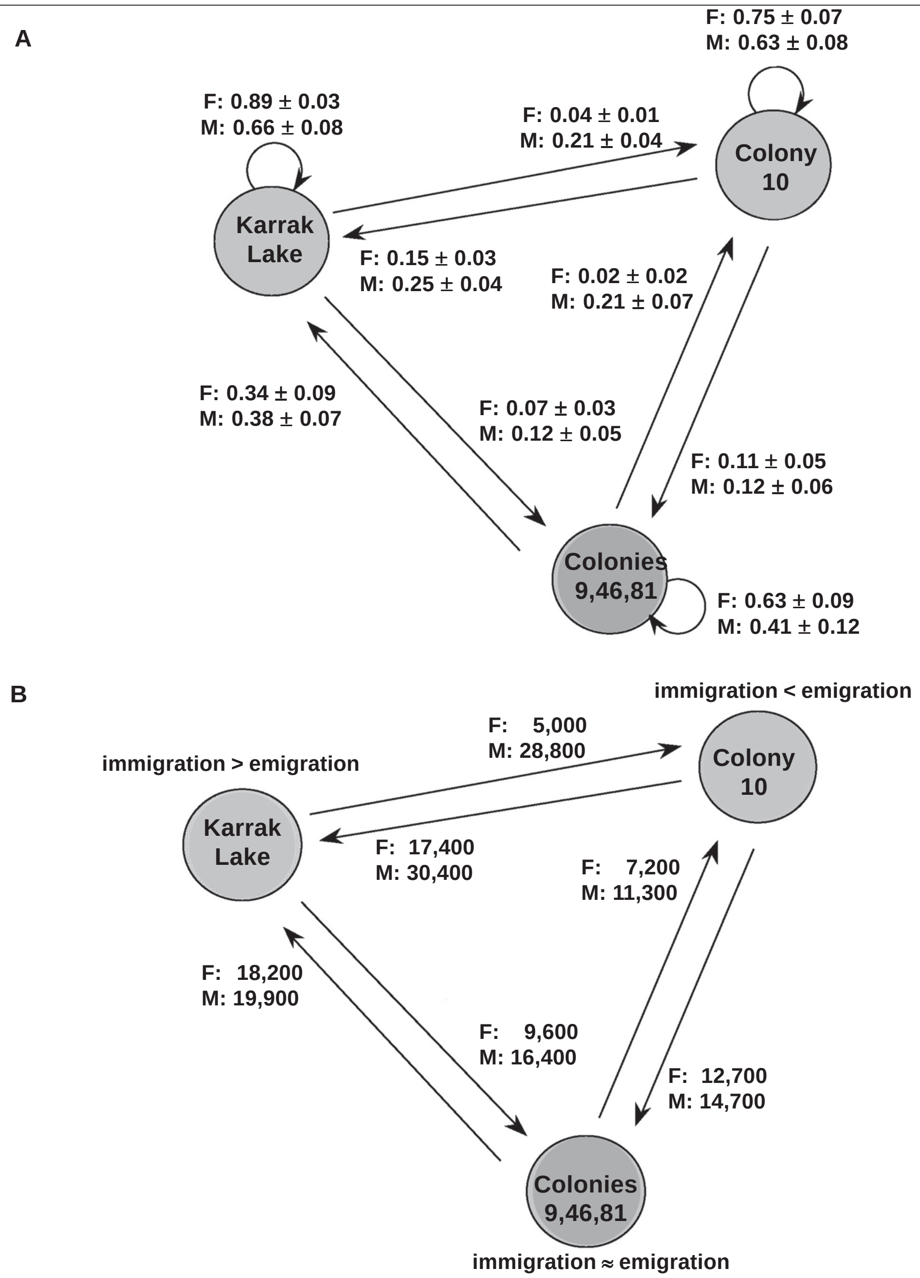

Fig 4. Breeding philopatry and dispersal of female (F) and male (M) Ross's Geese from multistate modeling of neckband resightings at breeding colonies within the Queen Maud Gulf metapopulation, 1999–2003: A. Dispersal probabilities ± SE; B. Calculated numbers combining movement probabilities with estimates of population size for each colony.

Fig. 4. Filatropía reproductora y dispersión de ansar de Ross hembras (F) y machos (M) a partir de la modelación multiestado de reavistajes de marcas en el cuello en colonias de reproducción en la metapoblación del golfo de la Reina Maud, 1999–2003: A. Probabilidades de dispersión ± SE; B. Números calculados que combinan probabilidades de movimiento con estimaciones del tamaño poblacional para cada colonia.

allows separate estimation of otherwise confounded probabilities of survival and movement. Under this necessary restriction, multistate models will produce survival estimates that are biased low if movement of individuals to an unobserved state occurs (i.e., permanent emigration from the sampled areas and/or marker loss). We suggest that the sex differences in estimates of apparent survival resulted from a combination of (1) higher rates of permanent emigration by males from surveyed areas than by females and (2) higher rates of neckband loss by males. Higher rates of permanent emigration by males from our study area is consistent with our finding of greater vagility within our study area by male than by females. Additionally, rates of neckband loss are generally higher for males in numerous other goose species (Alisauskas & Lindberg, 2002 and references therein). Low recapture probability of Ross's Geese during annual banding efforts precluded direct estimation of neckband loss as done by Alisauskas & Lindberg (2002). Nevertheless, our discovery of nearly 4 times as many broken neckbands from males than from females, despite similar numbers marked, is in agreement with the general pattern of higher neckband loss by males. Most of these neckbands were lost probably during aggressive behaviour by males on breeding territories. The close correspondence between estimates of survival for neckbanded females from multistate modeling to those for neckbanded females from band recovery models suggests that the probability of permanent emigration from QMGBS by females was close to zero during the course of this study.

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