

## Body size and age of recruitment in Snow Geese *Anser c. caerulescens*

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'At what age to start breeding?' is a question fundamental to analysis of life histories. While there has been considerable interest in the theoretical aspects of age of first breeding, comparatively little work has been done on the problems of estimating recruitment rates in wild populations. Most studies to date have relied on *ad hoc* methods that rely on one or more assumptions which may be generally untenable. Recently, it has been suggested that mark–recapture analysis can provide a robust, statistically formal approach for the analysis of recruitment, by using 'reverse capture-histories' to estimate the probability of entering the population over a given interval. We applied this approach to data from the arctic-breeding Lesser Snow Goose *Anser c. caerulescens*, using data from a long-term study in subarctic Canada. We tested the hypothesis that recruitment rate in this species was influenced by structural size. Since arctic-nesting geese rely heavily on endogenous nutrient reserves for reproduction, structurally smaller birds may be less able to recruit at a young age than larger birds. However, despite significant long-term changes in body size, and significant annual variation in recruitment rate, we found no evidence of correspondence between the two.

In some species of birds, the energy and nutrient requirements for reproduction are met by stored reserves usually acquired well before breeding (capital breeders). Proximate constraints on the amount of nutrient that can be stored prior to breeding are thought to be important determinants of variation of reproductive performance.<sup>1,2</sup> For example, in the case of arctic-nesting geese, it has been suggested that variation in structural size may impose such a constraint; structurally larger birds should be able to breed more frequently (i.e. under a greater range of conditions) and lay more or larger eggs, since they have more nutrient reserves in the absolute sense than do smaller birds (*sensu* Alisauskas & Ankney,<sup>3</sup> and references therein).

We examine the effects of body size variation on age of first breeding (recruitment) in a classic capital breeder, the Lesser Snow Goose *Anser c. caerulescens*, using data from the long-term study of the breeding colony at La Pérouse Bay, located in northern Manitoba, Canada. The age at which individuals breed for the first time is an important life history trait.<sup>4</sup> If smaller birds have less reserves available for breeding, they may be more susceptible to annual variation in condition (i.e. the amount of reserves available for reproduction) and may be less able to start breeding at as early an age as larger birds. Recent evidence in support of this hypothesis has been presented for a colony of Black Brant *Branta bernicla* nesting in Alaska.<sup>5</sup>

However, most previous field studies of recruitment have relied on *ad hoc* estimation methods, which may suffer significant bias.<sup>5,6</sup> For example, the use of return rate (stratified by age-class) to assess recruitment implicitly assumes that individuals of all ages have the

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same encounter rate (recapture or resight rate). An individual observed breeding at age  $x$  could have bred previously at an earlier age, and simply not have been observed. Mark-recapture methods provide a tractable means for assessing variation in recruitment rate, while simultaneously controlling for variation in encounter rate. In this paper, we apply mark-recapture methods to the analysis of variation in recruitment in Snow Geese, focusing on the degree to which variation may reflect differences in body size.

## METHODS

### Collection of recruitment data

Data on the breeding biology of the Snow Goose have been collected annually from the colony at La Pérouse Bay from 1968 to the present. General field methods are described elsewhere.<sup>7</sup> Procedures particularly relevant to this study are described briefly below.

The colony, presently numbering 15 000–20 000 breeding pairs, is on the southern edge of the species' breeding range. Each year, about 2000 nests are monitored at hatching, and each hatchling is weighed and marked with an individually numbered web-tag. Approximately five weeks after hatch, before the goslings are fully fledged, the adults moult their primary flight feathers and are temporarily flightless. By this time, non-breeders have left the colony for distant moulting sites (i.e. adults present at this time have at least attempted to breed).<sup>7</sup> While the adults are flightless, about 1500 families (about 4000–5500 adults and goslings) are rounded up, aged, sexed and ringed. A proportion of goslings and adults captured each year are also measured and weighed. Our analyses were restricted to adult females of known age (in years). We used only females in the analysis because only females are philopatric to the natal colony.

We maximized our sample size by using several sources of resighting information. An adult female was classified as 'having bred' in a given year if it was observed either (a) at ringing, (b) during brood rearing (with or without goslings) or (c) during incubation. Because only the ringing sample comprises true 'recaptures' (i.e. birds which are physically handled), we use the term 're-encounter rate' throughout.

As our primary interest was in determining whether or not recruitment rate varied as a function of body size, and because adult body size in geese is significantly influenced by early growth conditions,<sup>8–11</sup> we partitioned our data into birth-cohort groups. Preliminary analyses showed that a minimum of eight sampling occasions was required within a cohort for adequate testing of model fit (see below). Data were available for 12 birth-cohorts (1971–81).

### Body size measurements

We compared recruitment rates between large and small adults using total tarsus-length (measured to the nearest 0.1 mm)<sup>12</sup> as an index of structural size. Although multivariate measures of structural size are preferred,<sup>13</sup> we used tarsus-length because it was measured for the largest number of birds. We used the mean of measurements made for each individual in the sample in different years to minimize the effects of measurement error. This is valid because Snow Geese do not grow significantly after the first year.<sup>14</sup> Although adult body size is a continuous character, current software limitations required us to classify birds (within cohorts) as either large or small (large:  $\geq \bar{x} + 0.2\sigma$ ; small:  $\geq \bar{x} - 0.2\sigma$ ). For most cohorts, this comprised 70–75% of the available data.

### Analysis methods

Early attempts to use mark-recapture approaches to assess recruitment made a number of assumptions (equivalency of survival rates among breeders and non-breeders, constancy of survival through time, no age-specificity of 'true' recapture rates) that are likely to be violated in most cases.<sup>15–17</sup>

Recently, however, Pradel<sup>18</sup> suggested that analysis of encounter histories of individually marked individuals, written 'backwards' (temporally), can be used to analyse recruitment without limiting assumptions. The approach is based on a simple duality; if the encounter history written going *forward* through time allows us to estimate the probability that an individual *leaves* the population permanently between two sampling occasions (i.e. the mortality rate), then the same encounter history, written *backwards*, provides estimates of the probability that an individual

enters the population permanently (i.e. recruitment rate). The estimated parameter ( $\gamma_i$  following Pradel<sup>18</sup>) is the 'probability that an animal alive and in the population at time  $i$  (time = age within cohort) was also alive and in the population at time  $i - 1$ '.

In all analyses, we refer to a bird as a *non-breeder* until it has been *recruited*, at which point it is a *breeder* and remains so as long as it remains alive. This does not mean that it breeds every year (*breeding propensity*), merely that, as a breeder, it makes an annual decision to breed or not in that year. While recruitment and breeding propensity are both important to life history analysis, only the former is accessible using the methods described by Pradel. Breeding propensity is analogous to the problem of temporary emigration, which can be accommodated using other approaches.<sup>19</sup>

### Model notation and selection

General model notation followed Lebreton *et al.*<sup>20</sup> The factorial structure of the model is represented by subscripting the primary parameters ( $\phi$ ,  $p$  and  $\gamma$ ), using 'a' for age effects, 't' for time effects, and 's' for size effects. Relationships among factors were indicated using standard linear model notation.<sup>20,21</sup>

Our primary interest was in determining whether or not recruitment rate varied as a function of body size. We approached this question in two ways. First, we tested for covariation of annual differences in age-specific recruitment rates with patterns of body size variation over time. As the size of the La Pérouse Bay colony has increased, there has been a corresponding decline in the amount of food available for growing goslings, which has led in turn to a long-term decline in cohort-specific size of surviving adults.<sup>9</sup> Thus, we would predict a significant long-term decline in age-specific recruitment rate if body size significantly influences recruitment. We tested for long-term trends in recruitment using *a priori* linear contrasts among cohorts.<sup>22</sup>

Second, for a subset of cohorts, sufficient data were available to compare recruitment rate directly among large and small birds. Within cohorts, age and time are synonymous, and it is not possible to differentiate temporal differences from true age differences. However, it is not entirely necessary that we are able to do

so, as we are interested simply in whether or not the pattern of recruitment differs among large and small birds; whether this reflects age or temporal differences is less important.

The first step of our analyses involved goodness-of-fit (GOF) testing of our starting models. In mark-recapture studies, robust GOF tests are available only for a fairly small set of models. However, one such model for which GOF tests are available is the time-dependent Cormack-Jolly-Seber (CJS) model ( $\phi, p, \gamma$ ). As age and time are synonymous within cohort (cohort = year-age), the pooled within-cohort GOF test of the time-dependent CJS model is equivalent to an overall test for age-differences across cohorts.<sup>23</sup> We used a modification of program RELEASE for all GOF testing.<sup>23-25</sup>

Subsequent model selection was based on Akaike's information criterion (AIC) and likelihood-ratio tests (LRT).<sup>26</sup> AIC values, test statistics and estimated standard errors for individual parameters were modified as needed for extrabinomial variation.<sup>20,27</sup> All models were fitted using program SURGE (v. 4.2). Comparisons among pairs or groups of estimates were made using a modified version of program CONTRAST.<sup>28</sup>

## RESULTS

### Intra-cohort model selection

Within-cohorts, the most general starting model available was the fully time-dependent CJS model. Goodness-of-fit (GOF) testing showed that the CJS model was rejected for five of 12 cohorts ( $\alpha = 0.10$ ), as well as overall ( $\gamma_{s \times c \times a} p_{s \times c \times a}$ ) (Table 1). For all cohorts where the CJS model was rejected, the ratio of the model  $\chi^2$  to the degrees of freedom  $c$  was  $< 2$ , suggesting extrabinomial variation rather than structural deficiencies in the model. However, partitioning the GOF statistics generated by RELEASE into the four component tests (2.Ct, 2.Cm, 3.SR, 3.Sm) showed differences in which tests were significant (Table 1). In theory, extrabinomial variation should affect each of the four component tests approximately equally. There was a greater tendency for test 2.Cm to be significant (seven of 12 cohorts) than for the other three tests; of the five cohorts where the overall GOF test was significant (test 2 + test 3; Table 1), test 2.Cm was significant in all cases.

**Table 1.** Within-cohort GOF test results for Snow Goose data to the time-dependent Cormack–Jolly–Seber model ( $\phi, p$ ). Capture histories for all cohorts truncated at 10 occasions.

Cohort	df	$\chi^2$	2.Ct	2.Cm	3.SR	3.Sm	P	c
1970	31	49.81	0.275	0.004	0.292	0.391	0.018	1.61
1971	25	22.55	0.534	0.317	0.551	0.608	0.604	0.90
1972	33	38.41	0.401	0.041	0.524	0.793	0.238	1.16
1973	34	47.76	0.064	0.029	0.190	0.966	0.059	1.40
1974	26	29.37	0.197	0.777	0.296	0.252	0.295	1.13
1975	33	58.78	0.239	0.026	0.655	0.004	0.004	1.78
1976	34	67.35	0.230	0.025	0.001	0.370	<0.001	1.98
1977	39	39.42	0.792	0.051	0.769	0.690	0.451	1.01
1978	28	27.68	0.262	0.852	0.590	0.164	0.481	0.99
1979	39	59.65	0.304	0.068	0.050	0.198	0.018	1.53
1980	39	48.85	0.041	0.855	0.040	0.447	0.143	1.24
1981	30	29.69	0.214	0.759	0.460	0.368	0.481	0.99
Total	391	518.92	2/12*	7/12*	3/12*	1/12*	<0.001	1.33

$\chi^2$  shows the overall goodness-of-fit of the data to the model, from program RELEASE. The overall  $\chi^2$  is the sum of four component tests (tests 2.Ct, 2.Cm, 3.SR and 3.Sm). Test 2 (2.Ct and 2.Cm) generally tests for violations of assumptions of equality of catchability among marked and unmarked individuals, whereas test 3 (3.Sr and 3.Sm) tests for violations of assumptions of equality of survival among marked and unmarked individuals.<sup>23</sup>  $c = \chi^2/df$  (used to adjust statistics for extrabinomial variation, see text).

\*Significant at  $\alpha = 0.10$ .

Test 2.Cm assesses when individuals seen at  $i$  were next seen again, conditioned on whether or not they were seen at  $i + 1$ . Rejection of hypothesis 2.Cm can be diagnostic of temporary emigration. However, examination of the individual contingency tables comprising test 2.Cm for these five cohorts showed no systematic departure from expectations (i.e. when seen again was not systematically different as a function of seen at  $i + 1$  or not). Thus, we accepted the structure of the starting model for each cohort, and used the cohort-specific correction factors (Table 1) to adjust test statistics and standard errors accordingly.

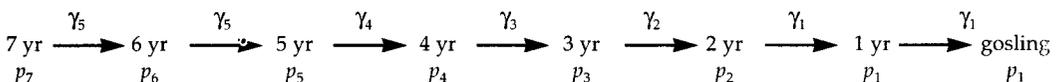
There was significant temporal variation in both recruitment rate ( $\gamma$ ) and re-encounter rate ( $p$ ) in all cohorts. In general, the most parsimonious group of time-dependent models for all cohorts for recruitment had three age-classes ( $\gamma_{ns}$ ; age = 2, 3, 4+ years) (Diagram 1).

The initial record in the original capture history (corresponding to the gosling marking event), is set as zero in the reversed capture

history. Since Snow Geese do not breed as yearlings,  $\gamma_1$  was fixed at 0. Similarly,  $p_1$  was also fixed at zero. Subsequent modelling of recruitment was based on this starting model structure.

In eight of 12 cohorts, recruitment rate increased linearly over time (i.e. with age). In the remaining cohorts, recruitment rate for the oldest age-class in the model (greater than four years) was always significantly greater than for the youngest age-class (two years) ( $P < 0.01$  for all cohorts). Thus, recruitment rate appears to increase with age, although not always in a linear fashion.

In contrast, there was no consistent pattern to variation in re-encounter rate. Five of 12 cohorts showed temporal variation in re-encounter rate, while seven of 12 did not (Table 2). Further, of those cohorts that did show significant temporal variation, the most parsimonious model for four of five cohorts had re-encounter rate constrained to be a linear function of time. Among these cohorts, the



**Diagram 1.**

**Table 2.** QAIC values for within-cohort model tests for Snow Goose data. These are AIC values corrected for lack of fit to time-dependent Cormack–Jolly–Seber model (see Table 1). Model syntax and structure outlined in the text. Boxes indicate the most parsimonious model (lowest corrected AIC).

Cohort	n	Models				
		$\gamma_t P_t$	$\gamma_t P_{lim}$	$\gamma_{lim} P_{lim}$	$\gamma_{lim} P_t$	$\gamma_{lim} P$
1970	184	617.82	600.66	598.66	619.82	597.47
1971	80	442.63	431.96	435.22	444.63	435.02
1972	164	792.55	782.72	780.93	794.54	780.25
1973	279	946.58	935.60	937.09	944.62	942.16
1974	111	462.77	453.24	452.96	462.91	454.93
1975	305	826.22	812.33	815.87	824.48	813.89
1976	249	614.69	603.74	601.89	614.69	600.22
1977	249	1032.33	1023.96	1022.54	1034.33	1020.54
1978	112	470.68	459.81	456.36	470.79	454.49
1979	361	881.36	886.20	884.21	883.36	882.27
1980	404	1255.14	1253.46	1251.91	1257.14	1250.73
1981	121	588.88	579.98	582.65	590.68	580.77

slope of the re-encounter rate function with time was decreasing for all four cohorts (i.e. lower re-encounter rate at younger ages), although the magnitude of the decline from first to last occasion was generally <10%.

### Variation among cohorts

As there was heterogeneity among cohorts in the magnitude of the lack of fit to the time-dependent model (Table 1), we were unable to correct test statistics simultaneously in our inter-cohort analyses, and report only the uncorrected values. There was significant heterogeneity over cohorts in both  $\gamma_2$  (the probability that a bird breeding as a three-year-old started breeding at age two) ( $\chi^2_{11} = 20.3$ ,  $P = 0.042$ ), and  $\gamma_3$  ( $\chi^2_{11} = 21.9$ ,  $P = 0.026$ ; Fig. 1). Variation across cohorts in  $\gamma_4$  was not significant.

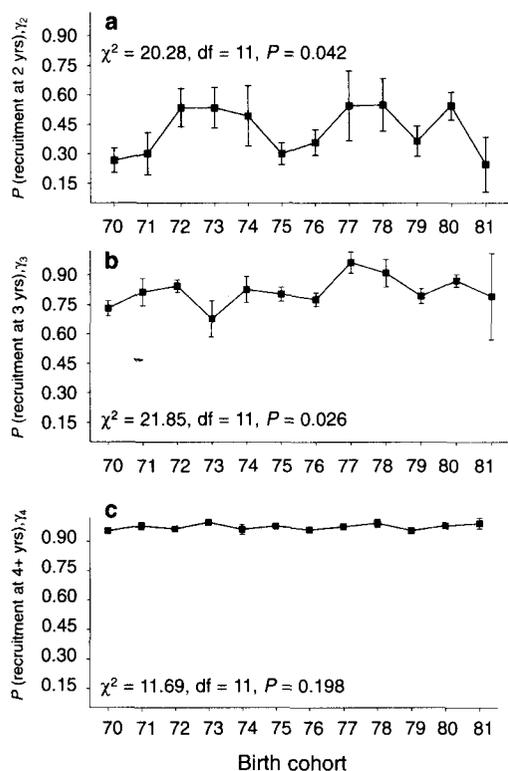
There was no evidence for a systematic change in the proportion of breeders recruited at age two years (test for linear trend in  $\gamma_2$ ;  $\chi^2_1 = 0.165$ ,  $P > 0.5$ ), despite the fact that cohort-specific body size has declined significantly over the course of the study.<sup>9</sup> There was also no detectable trend in  $\gamma_3$  ( $\chi^2_1 = 0.769$ ,  $P > 0.35$ ). Further analyses of covariation of cohort-specific estimates of both  $\gamma_2$  and  $\gamma_3$  with several variables which reflected aspects of the

'quality' of a given year – including: (a) residuals from a regression of both adult and gosling cohort-specific body size on cohort (following Cooch *et al.*<sup>8,9</sup>); (b) annual mean date of nest initiation; and (c) both (a) and (b) lagged by two years (since birds born in year  $i$  can only start to breed in year  $i + 2$ ) – were all non-significant.

### Variation within cohorts: large versus small

For a subset of cohorts for which sufficient data were available (1975, 1976 and 1979), we were able to compare recruitment rate directly between large and small females. We first tested the fit of the CJS model (as described above) to both size classes separately; in all three cohorts, the CJS was accepted (however, since the overall GOF  $\chi^2$  for the 1975 cohort was near-significant ( $P = 0.063$ ), we adopted the conservative approach and applied a variance inflation adjustment as described previously for both size classes for this cohort;  $c = 1.28$ ).

Based on the preceding analysis, we used an equivalent three-age-class ( $\gamma_{a3}$ ; age = 2, 3, 4+ years) model as our starting model for  $\gamma$  and a fully time-dependent model for re-encounter rate. For all three cohorts, a model where recruitment rate was constrained to be a linear



**Figure 1.** Inter-cohort variation in recruitment rate by age-class: (a) recruitment at 2 years; (b) recruitment at 3 years; (c) recruitment at 4+ years. Bars show  $\pm 1$  se of the estimates adjusted for extrabinomial variation using variance inflation factor (c, Table 1). Test statistics are for a test of the null hypothesis of no heterogeneity in  $\gamma$  over cohorts.

function of age (time) fitted significantly better than the time-dependent model. The most parsimonious model for re-encounter rate was a constant model, with no differences between large and small birds (i.e. no group term).

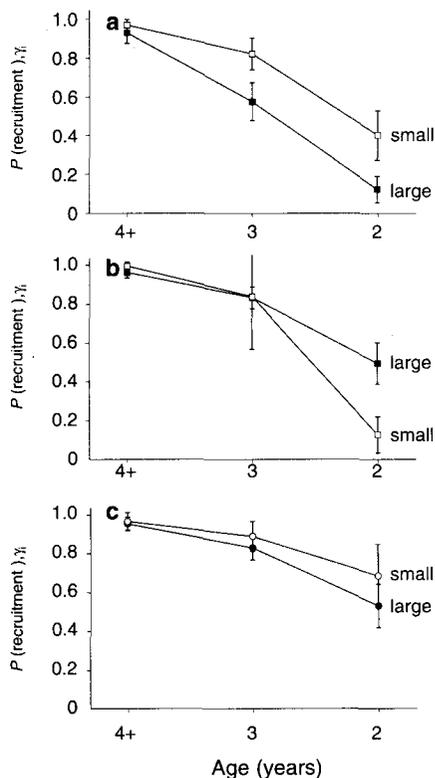
The results of our model testing differed among the three cohorts (Fig. 2). In 1979, there was no detectable difference in recruitment rate between large and small birds ( $n = 174$ ; AIC for model  $\gamma_{s+a} = 752.21$ ; AIC for model  $\gamma_a = 750.87$ ;  $\chi^2 = 0.669$ ,  $P > 0.4$ ). In contrast, for the 1976 cohort, recruitment rate was significantly higher for large birds ( $n = 159$ ; AIC for model  $\gamma_{s+a} = 798.93$ ; AIC for model  $\gamma_a = 800.56$ ;  $\chi^2 = 3.63$ ,  $P = 0.057$ ), while for the 1975 cohort the reverse was true; recruitment rate was significantly higher for small birds ( $n = 159$ ; AIC for model  $\gamma_{s+a} = 732.07$ ; AIC for model  $\gamma_a = 735.26$ ;  $F_{1,29} = \{LRT$

$$\chi^2/df/c = \{5.19/1\}/1.28 = 4.05, P = 0.054).$$

## DISCUSSION

Using the statistical formalism available in mark-recapture analyses, we can test various hypotheses about variation in recruitment in a more robust fashion, and with fewer limiting assumptions, than is possible using *ad hoc* methods. While the use of 'backwards capture histories' to estimate recruitment represents a considerable advance, an analysis which examines both age of first breeding and breeding propensity simultaneously is ultimately needed.<sup>19</sup>

Our data showed significant heterogeneity in recruitment rate among cohorts, but we failed to detect any evidence that this variation corresponded to differences in structural size of the birds. There are several possible reasons for this. There may not be a causal relationship



**Figure 2.** Inter-cohort comparison of recruitment rate between large and small birds: (a) 1975 cohort; (b) 1976 cohort; (c) 1979 cohort. Standard errors of the estimates for the 1975 cohort were adjusted for extrabinomial variation.

between body size and recruitment in the Snow Geese breeding at La Pérouse Bay. Previous analyses of this population have generally found little evidence for any significant fitness consequences resulting from variation in adult body size, which is consistent with the relatively high heritability of body size characters in birds in general.<sup>7,14,29</sup>

However, there are several other possibilities. Firstly, we may have committed a type II error – accepting the null hypothesis (no trend) when in fact the null hypothesis is incorrect. Our most direct tests (comparisons of large and small birds within cohorts) may have suffered by being too few in number (only three cohorts had adequate data) and having perhaps too few birds (about 150 birds per cohort). However, our samples were relatively large for the inter-cohort analyses, and we feel that we had acceptable statistical power.

Second, for the intra-cohort analyses, we were forced to use an arbitrary partitioning of birds into two size-classes, when body size should ideally be incorporated as a continuous individual covariate. Although partitioning the distribution into a large number of groups typically yields equivalent results, we did not have sufficient data to create more than two size-classes.

Finally, previous analysis of this population has shown that there is considerable heterogeneity in subsequent breeding propensity among birds that breed for the first time at either two or three years of age.<sup>30</sup> Recapture rate should therefore, ideally, be conditioned on whether or not birds bred for the first time at two years. In our present analyses we were unable to do this and thus the estimated recapture rate confounds birds which have recruited at different ages. This in turn introduces a bias in the estimates. The magnitude of this bias, and the impact on model selection, is not known.

However, we were unable to detect age (or time) specificity in re-encounter rates in many cohorts (Table 2). In an analysis which pooled cohorts (ignoring inter-cohort differences), strong age-specificity of recapture rates was detected, and yet temporal variation in recapture rate was detected in only five of the 12 cohorts for which data were available. This is perhaps further evidence of reduced power in our within-cohort analyses. However, tem-

poral variation in recruitment was strongly detected in all cohorts, with most showing a significant increase in recruitment rate with age (Table 2).

While it is generally accepted that slow gosling growth leads to reduced first-year survival in most species of geese, the ultimate consequences of variation in body size among birds surviving to adulthood remains contentious. Recently, Sedinger *et al.*<sup>5</sup> showed that adult size variation resulting from differences in early growth was an important factor contributing to fitness variation in Black Brant; in particular, they noted lower incidences of breeding among smaller birds. In contrast, an earlier analysis of this population of Snow Geese found no differences in the age-specific changes in recapture rate between large and small birds. As observed recapture rate also reflects breeding propensity, this was interpreted as evidence that large and small birds were equally likely to breed in a given year.<sup>7</sup> In this study, using a robust mark–recapture approach, we also found no evidence for size-specific differences in age of recruitment and we tentatively suggest that body size may not be a particularly important determinant of breeding decisions in this species, at least at La Pérouse Bay. As suggested previously,<sup>5,29</sup> many of the apparent differences in results may reflect differences in both the average size of the birds in question (for example, Brant are considerably smaller than Snow Geese), and breeding latitude (Brant typically nest in the high arctic, whereas La Pérouse Bay is at the southern end of the range).

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