

Transient animals in a resident population of snow geese: local emigration or heterogeneity?

ROGER PRADEL, EVAN COOCH & FRED COOKE, *Department of Biological Sciences, Simon Fraser University, Canada*

SUMMARY *The estimation of survival rates from analysis of recapture of individually marked animals assumes that all individuals are equally likely to be re-encountered. This assumption is frequently violated in natural populations due to movements to and from the sampling area. We evaluated potential sources of heterogeneity using data from recaptures of 36000 individually marked female lesser snow geese, *Anser c. caerulescens*, from an expanding population in northern Manitoba, Canada. By stratifying individuals according to marking age and origin (hatched at the colony or not), we assessed the degree to which variation in apparent survival reflected permanent or temporary differences in emigration and effects of handling. In general, for birds ringed as adults, estimated apparent survival rates were significantly lower during the first year after ringing than in subsequent years. By comparing birds ringed as adults (classified by origin) with those ringed as goslings, we were able to demonstrate that these differences are not due to permanent emigration from the colony by transient individuals or heterogeneity of individual capture probability, but more likely reflect differences among individuals in their response to initial marking. Approximately 25% of birds permanently emigrate from the sampling area following marking.*

1 Introduction

In general, estimation of survival probabilities from an analysis of capture–recapture data makes several assumptions. First, every marked animal has the same probability of capture. Second, every marked animal has the same probability of survival between any two occasions. Third, all samples are virtually instantaneous, and all animals are immediately released following marking. And, fourth, marks are not lost or overlooked. However, in many capture–recapture studies, the

sampling area is logistically constrained (either spatially or temporally). Since animals are generally mobile during the sampling period, it is often very difficult to define a sampling area that will ensure that every animal in the population has an equal chance of being marked while at the same time preventing the capture of animals from other populations. In an attempt to circumvent this difficulty, live recaptures will often take place on sites to which individuals tend to exhibit a high degree of philopatry. But even so, there is always the risk of capturing transient individuals from other populations and, unless the site is uniformly sampled (which is rarely feasible), some individuals in the population are more likely to be captured than others.

Francis and Cooke (1993), analyzing the live recaptures of adult female lesser snow geese (hereafter snow geese) from a colony at La Pérouse Bay, Manitoba, Canada ($58^{\circ}44'N$, $94^{\circ}28'W$), demonstrated that apparent survival probabilities for the period immediately after ringing were significantly lower than the survival probabilities of previously captured individuals. Based on recovery analysis, they were able to show that these differences did not reflect differences in 'true' survival, and suggested that the observed difference in apparent survival (from the recapture analysis) was due to 'heterogeneity in site fidelity or capture probabilities'. What sources of heterogeneity might be expected in snow geese? Does heterogeneity represent real differences in behaviour among birds from the La Pérouse Bay population, or is it an artefact of sampling bias?

In general, female snow geese exhibit strong philopatry to their natal colony, and are traditional in their use of the same feeding and nesting areas where they were reared as goslings (Cooke *et al.*, 1975; Cooke & Abraham, 1980; Healey *et al.*, 1980). Colonial breeding and foraging, and philopatry to specific nesting and brood-rearing areas, may reflect evolutionary adaptations to minimize mortality due to predation (Findlay & Cooke, 1982), and a strong synergistic relationship between geese and their principal salt-marsh food plants (Jefferies, 1988). However, as the size of the La Pérouse Bay colony has increased, the synergistic relationship between the geese and their food plants has broken down, and geese are increasingly likely to disperse from the traditional nesting and feeding areas at La Pérouse Bay to newer areas extending from Cape Churchill, Manitoba (approximately 15 km east of La Pérouse Bay) south along the coast for approximately 50 km (Cooch *et al.*, 1993, Fig. 1). These changes in dispersal behaviour may have effected a heterogeneity in capture of the type that Francis and Cooke (1993) demonstrated can result in an apparent reduction in initial survival. The effects of handling is another possible cause of reduced initial survival. Recently, Williams *et al.* (1993) demonstrated that, as feeding conditions on the colony have systematically deteriorated, post-ringing gosling mortality and family integrity may also be negatively affected. Finally, Geramita and Cooke (1982) demonstrated that philopatry to the natal colony is not absolute in this species. Periodically, significant numbers of birds from another colony may immigrate to La Pérouse Bay (or, alternatively, on occasion, La Pérouse Bay birds may emigrate to another colony). Pradel *et al.* (in revision) have demonstrated that the presence of such transient birds in a population, if they permanently emigrate from the colony after a year, always results in an apparent reduction in initial survival. The magnitude of this reduction (as contrasted to the true survival of resident individuals) is equal to the proportion of transients among unmarked individuals.

Based on these results, and making use of different marking schemes, we

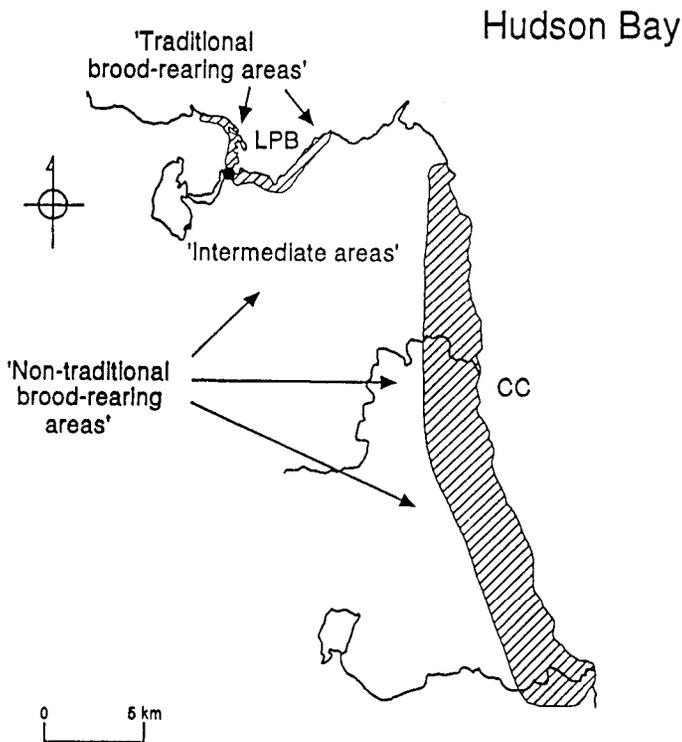


FIG. 1. Geographic regions from which birds were ringed during annual ringing drives: LPB—La Pérouse Bay, CC—Cape Churchill.

attempt here to discriminate between the different explanations of the heterogeneous survival rates found by Francis and Cooke (1993):

- (1) true heterogeneity of capture;
- (2) presence of transient animals from other colonies;
- (3) local emigration to new nesting and feeding areas; or
- (4) effect of handling.

In addition, Viallefont *et al.* (1995) have recently shown that in the year after their first observation as an adult at the colony, young geese tend to stay away from the colony resulting in a lower than usual capture probability at this time. This phenomenon must be taken into account in any analysis as a source of temporary heterogeneity in capture.

2 Material and methods

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 in Finney and Cooke (1978) and Cooke *et al.* (1985). Each year, approximately 2000 nests are monitored at hatching, and each hatching gosling is weighed and marked with an individually numbered web-tag. Approximately 5 weeks after hatch, before goslings are fully fledged, the adults moult their primary flight feathers and are temporarily flightless. By this time, non-breeders have left the colony to distant moulting sites. It is during this period that approximately

1500 families are rounded up, aged, sexed and ringed. A random sample of both goslings and adults captured have web-tags (web-tags can last several years on an individual). The presence or absence of a web-tag and the age (gosling or adult) when a bird was ringed were used to categorize individuals in some of our analyses (see below).

2.1 Sampling regions

From 1968 to 1989, virtually all goslings and adults in the sample were captured, marked and released in the 'traditional' brood-rearing areas at La Pérouse Bay (Fig. 1). However, from 1985 to present, birds have also been marked and released in 'non-traditional' areas along the coast. Some of the goslings and adults marked and released in these non-traditional areas had web-tags, indicating that they hatched at La Pérouse Bay, and were reared elsewhere. Although we do not have any data at present to estimate precisely the proportion of time goslings captured in the non-traditional areas had previously spent at La Pérouse Bay, the large distance between the two areas (Fig. 1) suggests that birds captured in the non-traditional areas probably spent a significant proportion of their time foraging away from La Pérouse Bay. To avoid this complication, most of our analyses were restricted to birds marked and recaptured in the traditional La Pérouse Bay sampling region.

2.2 Data sets

In our analyses, we were concerned with variation in apparent survival of adult individuals. Thus, the capture history of birds ringed as goslings up to their first re-observation as an adult was not relevant to the present study, and the first adult capture event was used as the starting point of each capture history. A total of 13 185 female snow geese were observed at least once as adults during ringing drives at La Pérouse Bay between 1969 and 1991. Of this sample, 2726 (20%) had been previously ringed as goslings (hereafter referred to as 'adults ringed as goslings') and retained their ring when observed for the first time as adults. The remaining 10 459 birds were ringed as adults (minimum age at time of ringing = 2 years). Of these birds ringed as adults, 632 (5% of the total sample) also retained web-tags from the time they were goslings. Hereafter, we refer to these birds as 'web-tagged adults'. The remaining 9827 birds ringed as adults, constituting the greatest proportion of the total sample (75%), did not have a web-tag, and as such were of unknown origin. Hereafter, we refer to these birds as 'unmarked adults'. Ringed as goslings, web-tagged and unmarked adults are the three groups we will be considering and comparing in our analyses. Since both adults ringed as goslings and web-tagged adults were hatched at La Pérouse Bay, both groups are, by definition, residents of La Pérouse Bay. In contrast, the unmarked adults are of potentially mixed origin (i.e. they may have been reared at La Pérouse Bay, or be immigrants, either permanent or transient, from another breeding area or even another colony).

2.3 Procedure for comparison

The very unequal samples sizes for the different subsets of the data made comparisons difficult, since the power to resolve differences among groups is

dependent upon differences in sample size. For example, the same amount of time variation detectable with a data set of 9827 animals may be far below significance with a sample size of 632. In particular, we feared that, in a common analysis of the three groups, an important effect specific to the smallest data set could be missed. Therefore, we used a two-stage approach. Each group was initially analyzed separately. Then, for comparisons among groups, we first identified the most parsimonious model acceptable to all groups in a given comparison, and proceeded from this point to test simpler models.

2.4 Model notation

Model notation was based on Lebreton *et al.* (1992). Since survival and capture probabilities were constrained to be bounded 0–1 by means of a logistic transformation, only the linear predictor is shown in the model notation. For example, (ϕ_t, p_t) designates a model in which survival (ϕ) and capture probabilities (p) are time-specific, that is the Cormack–Jolly–Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965). The notation ϕ_{a2} is for a two-age class effect on survival with the following meaning: the survival immediately after the first observation as an adult is allowed to differ from later survivals. We used equivalent notation for recapture probabilities. Effects may be combined in an additive way, that is without interaction: for example, ϕ_{a2+t} indicates that the model was parameterized to allow survival to vary over time in both age classes but with a constant difference (on a logit scale) between the two age classes. With interaction, the notation becomes ϕ_{a2*t} and the survival probabilities are allowed to vary independently within each age class. For example, the model for a ringing effect on survival (Brownie & Robson, 1983) is (ϕ_{a2*t}, p_t) . At the comparison stage, g designates a group effect: for example, $(\phi_{a2*t}, p_{a2+t+g})$ is a model in which survival probabilities vary independently over time in each of the two age classes but are common to both groups (since there is no g subscript for ϕ), while capture probabilities vary over time in each age class of each group with a constant difference (on a logit scale) between the two age classes, the same within each group, the difference between the two groups being itself constant for any combination of age classes and occasions. Finally, for some analyses, we had to use models in which the two age classes behaved differently. Then, two different symbols were used with the age class as a superscript. For instance, ϕ_g^1, ϕ_g^2 meant that survival varied among groups in the first age class but was common to all groups in the second age class.

2.5 Model selection

At each stage, the methodology of model selection followed Lebreton *et al.* (1992). As a first step, we tested the fit of the data to the CJS model (ϕ_t, p_t) —using goodness-of-fit (GOF) tests implemented in program RELEASE (Burnham *et al.*, 1987)—and to a more general model in which both survival and capture probabilities were allowed to differ before and after the first occasion of recapture (ϕ_{a2*t}, p_{a2*t}) ; the GOF test for the second model is described in detail in Viallefont *et al.* (1995) to which we refer the interested reader. In addition, we paid particular attention to one of the components of the overall GOF test in RELEASE: test 3.SR compares for each occasion in succession the fates (seen again or not seen again) of animals entering the experiment (on a given occasion) with those of the animals previously captured. This test, given by Brownie and

Robson (1983) for the detection of a handling effect on survival, has since been shown to be usable for the detection of transients (Pradel *et al.*, in revision). In order to differentiate random fluctuations from the same tendency at all occasions, such as can be expected if transients are among the sample, we also pooled the results of test 3.SR over all occasions.

Once a satisfactory general model had been identified by means of GOF tests, we proceeded to test the significance of the factors in the model and of their interactions by sequential model fitting with program SURGE (Pradel & Lebreton, 1991). SURGE gives, for each model, a relative deviance usable for model comparison. The difference in deviance between nested models follows asymptotically a χ^2 distribution with the difference in number of estimable parameters as number of degrees of freedom. This allows the computation of likelihood ratio tests (LRTs). Alternatively, one can compute the Akaike Information Criterion (AIC) to compare any models (Lebreton *et al.*, 1992). This criterion, unlike LRTs, avoids the pitfalls of multiple testing. Recent work by Burnham *et al.* (1994) suggests that model selection based on AIC is preferable to selection based on LRTs. Consequently, the choice among models was primarily made on the basis of the minimum AIC. Only for models with an AIC that differs by less than 2 (as a rule of thumb) from the minimum AIC were LRTs considered.

3 Results

3.1 GOF tests and identification of the general model

The GOF tests of all three groups, adults ringed as goslings, web-tagged and unmarked adults, generally indicated rejection of the CJS model (Table 1(a)). In each case, the lack of fit was largely due to heterogeneity in the component 3.SR. After pooling over occasions, there was significant evidence of an excessive disappearance of birds after their first observation as adults for the web-tagged and

TABLE 1. GOF tests for each of the three groups of the lesser snow goose data of (a) the CJS model (ϕ_i, p_i) with component 3.SR (sensitive to different fates of newly marked and previously marked individuals at each given occasion) between parentheses and (b) model (ϕ_{a2^*i}, p_{a2^*i}) allowing two age classes and time dependence in probability of survival and recapture

Group	χ^2 -value	Degrees of freedom	P-level
(a) Model (ϕ_i, p_i)			
Adults ringed as goslings	183.97 (34.07)	154 (19)	0.048 (0.018)
Web-tagged adults	83.25 (34.26)	64 (14)	0.051 (0.002)
Unmarked adults	545.22 (255.37)	267 (21)	< 0.001 (< 0.001)
(b) Model (ϕ_{a2^*i}, p_{a2^*i})			
Adults ringed as goslings	153.51	170	0.813
Web-tagged adults	75.65	84	0.731
Unmarked adults	295.57	279	0.237

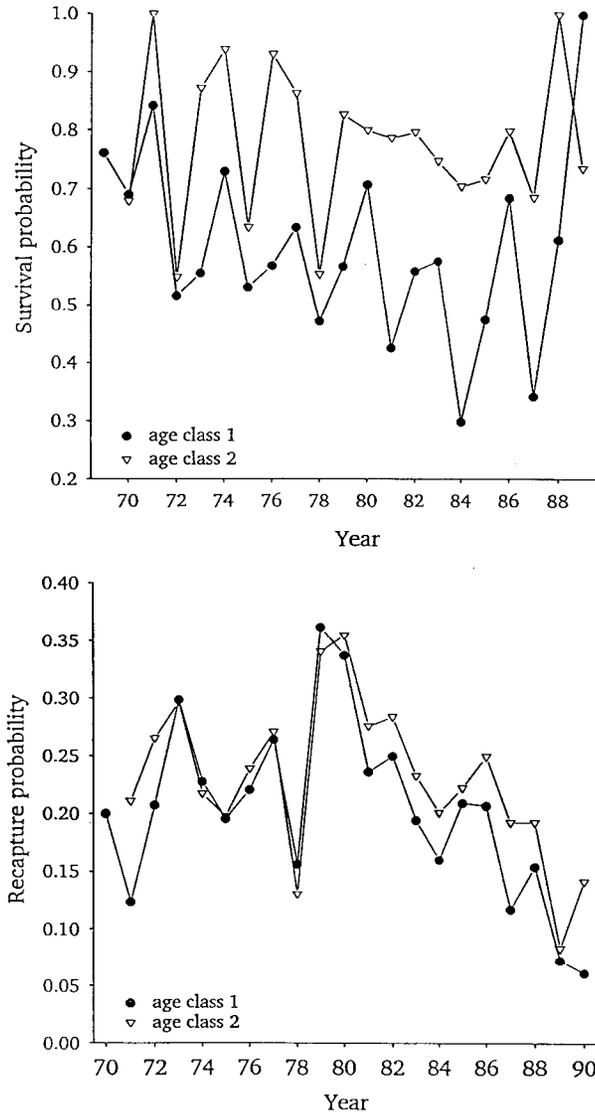


FIG. 2. Comparison of survival and recapture probabilities among two age classes (first age class = first year following initial adult capture, second age class = subsequent years) for unmarked adults.

unmarked adults, but not for adults ringed as goslings (Table 2). In contrast, the GOF test to the more general model (ϕ_{a2^*r} , p_{a2^*r}) was satisfactory for all data sets (Table 1(b)). This model incorporated all known causes of variation: a lower recapture probability after the first adult observation (Viallefont *et al.*, 1995)—modelled as an age effect on p —and the pattern of increased disappearance after the first adult observation—modelled as an age effect on ϕ . It was thus a satisfactory starting point for the separate analyses both from a statistical and biological point of view. The estimates obtained are shown for information in Figs 2 and 3 for, respectively, the unmarked and ringed as gosling adults groups (the web-tagged adult sample was too small to yield meaningful estimates).

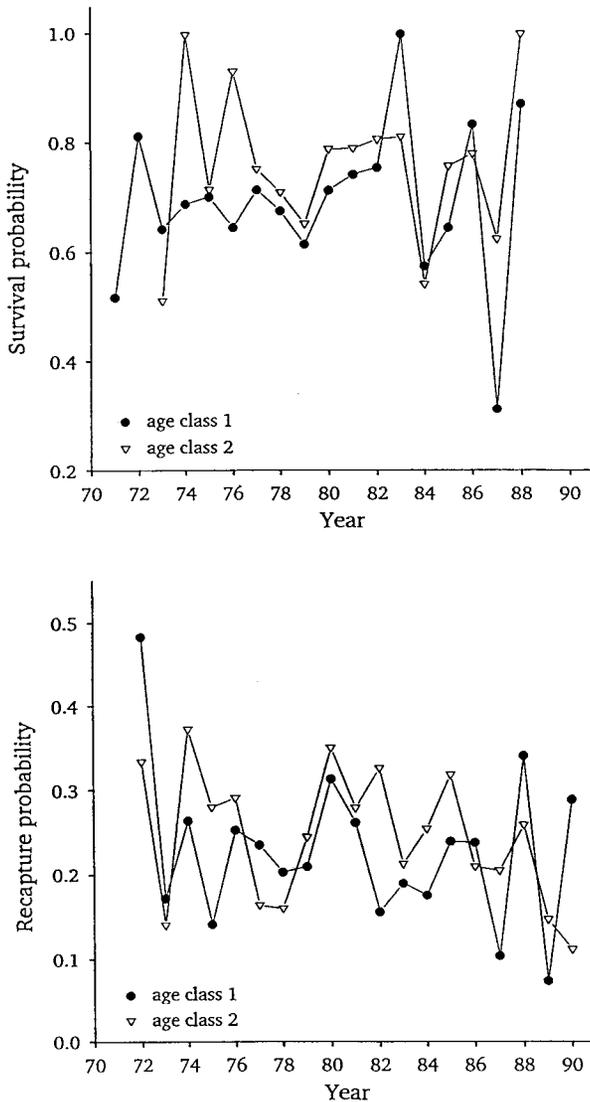


FIG. 3. Comparison of survival and recapture probabilities among two age classes (first age class = first year following initial adult capture, second age class = subsequent years) for adults ringed as goslings.

3.2 Intra-group analysis

For adults ringed as goslings, two models were virtually identical in parsimony and fit, (ϕ_{a_2}, p_{a_2+i}) and (ϕ, p_{a_2+i}) (Fig. 4(a)). This is analogous to the result obtained by Viallefont *et al.* (1995) with a slightly different data set (1 year less of data). For web-tagged adults, the best model was (ϕ_{a_2}, p_i) (Fig. 4(b)). A model with constant ϕ was strongly rejected for this data set. For unmarked adults, two different models were almost equally acceptable on the basis of the AIC, $(\phi_{a_2+i}, p_{a_2+i})$ and $(\phi_{a_2+i}, p_{a_2+i})$ with a preference for the first (Fig. 4(c)). Yet, the LRT strongly favoured the first. (Although survival varies significantly over time in this group, estimates given in Table 3 for comparison are from a model with no time effect.)

TABLE 2. Contingency analysis of capture frequency conditional on prior capture history for each of the three groups of the lesser snow goose data

Group	Seen again	Not seen again	P-level
(a) Adults ringed as goslings			
Seen before	532 (36.5%)	925 (63.5%)	} 0.190
Not seen before	936 (34.5%)	1779 (65.5%)	
(b) Web-tagged adults			
Seen before	110 (38.3%)	177 (61.7%)	} 0.002
Not seen before	178 (28.2%)	454 (71.8%)	
(c) Unmarked adults			
Seen before	1611 (37.4%)	2700 (62.6%)	} < 0.001
Not seen before	2614 (26.9%)	7111 (73.1%)	

TABLE 3. Inter-group comparisons of early (ϕ^1) and late (ϕ^2) survival rate. (Early survival refers to survival rate during the first year following first adult capture. Late survival refers to survival during subsequent intervals.) Groups which do not differ significantly indicated by asterisk. Estimates are from model ($\phi_{a_2, p_{a_2+i}}$) applied to each group separately. This model, although rejected for unmarked adults, is used here for the sake of comparison. LCI and UCI are respectively the lower and upper bounds of the 95% confidence interval

Group	ϕ^1	LCI	UCI	ϕ^2	LCI	UCI
Adults ringed as goslings	0.70	0.64	0.75	0.75*	0.73	0.77
Web-tagged adults	0.54*	0.46	0.61	0.79*	0.74	0.82
Unmarked adults	0.57*	0.55	0.59	0.78*	0.77	0.79

3.3 Inter-group analysis

We started the comparison of unmarked adults with each of the other two groups from the conservative model ($\phi_{a_2+i, p_{a_2+i}}$). For the comparison of ringed as goslings and web-tagged adults, we started with the model ($\phi_{a_2, p_{a_2+i}}$). While recapture rates did not differ significantly between ringed as goslings and unmarked adults (no group effect on p , Fig. 5(a)), they were significantly higher for web-tagged adults (Figs 5(b) and (c)). In contrast, the initial survival (in the interval immediately following first adult capture) of adults ringed as goslings was significantly higher than those of the other two groups (Figs 5(a) and (c)), which themselves did not differ significantly (Fig. 5(b)). Among all three groups, there were no significant differences in apparent survival for later intervals (Figs 5(a)–(c)). The results of the comparisons of survival among groups for both time periods are summarized in Table 3.

In order to avoid potential biases in our analyses due to differences in age structure (because of the relatively high rate of web-tag loss, the web-tagged adults

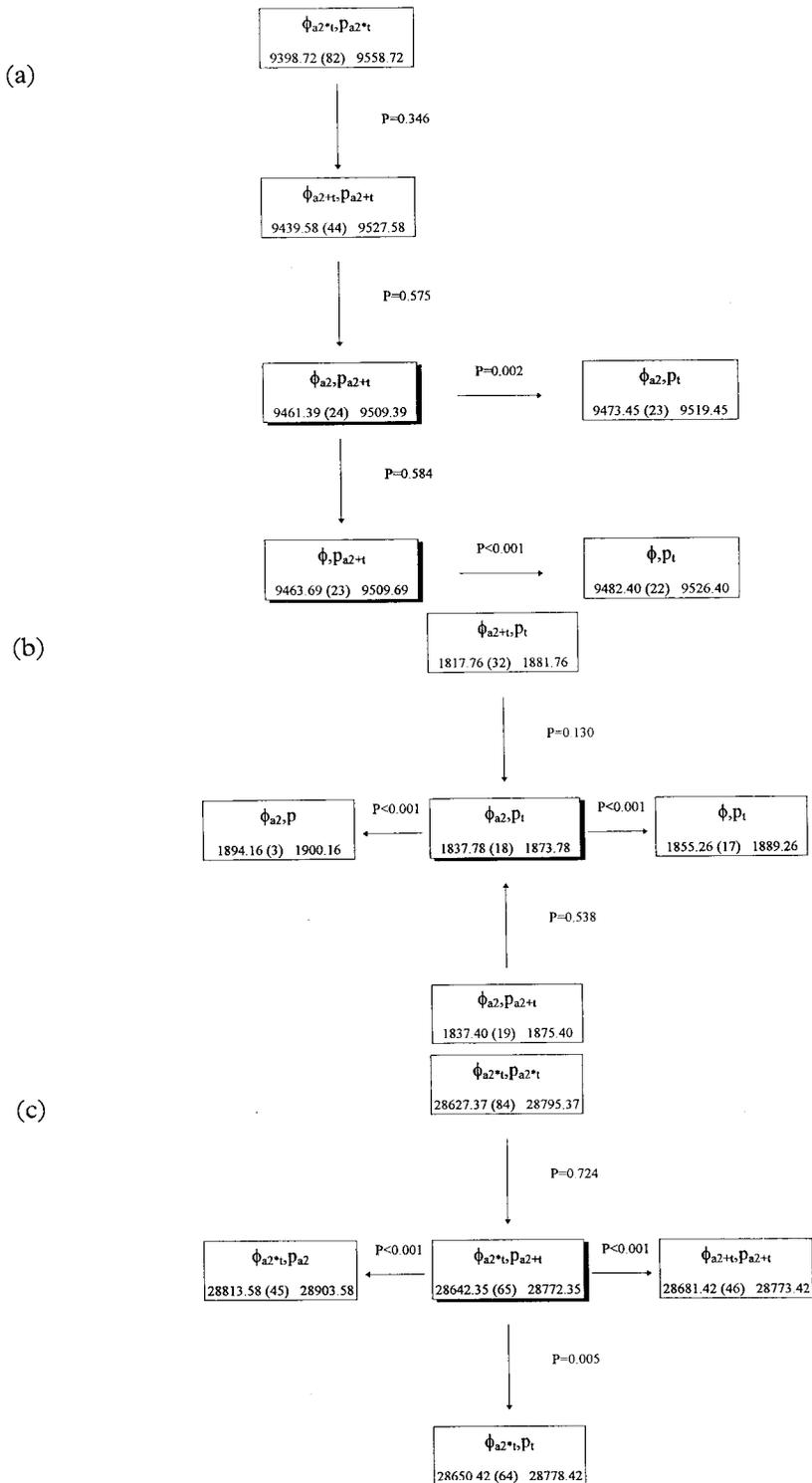


FIG. 4. Schematic representation of order and results of model testing among (a) adults ringed as goslings, (b) web-tagged adults and (c) unmarked adults. Most parsimonious model indicated by shadowed box. Each model is given with model deviance (lower left corner), number of identifiable parameters (in parentheses) and AIC (lower right corner).



FIG. 5. Schematic representation of order and results of model testing among (a) adults ringed as goslings and unmarked adults, (b) web-tagged and unmarked adults and (c) adults ringed as goslings and web-tagged adults. Most parsimonious model indicated by shadowed box. Each model is given with model deviance (lower left corner), number of identifiable parameters (in parentheses) and AIC (lower right corner).

are on average younger than adults ringed as goslings when encountered for the first time as adults), we redid the analysis using a data set restricted to the subsets of ringed as goslings and web-tagged adults seen for the first time breeding at 3 years of age. We used this age class since (a) it comprised the largest proportion

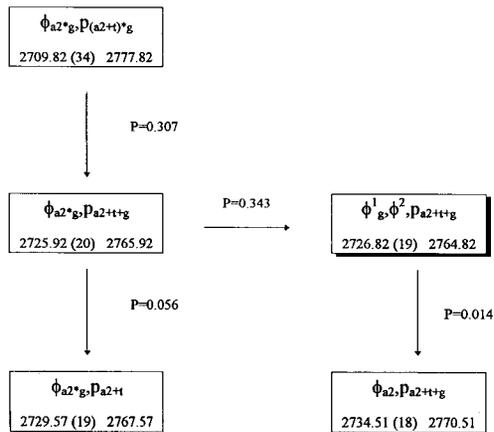


FIG. 6. Schematic representation of order and results of model testing among adults ringed as goslings and web-tagged adults. Sample restricted to those birds captured as adults for the first time at 3 years of age. Most parsimonious model indicated by shadowed box. Each model is given with model deviance (lower left corner), number of identifiable parameters (in parentheses) and AIC (lower right corner).

of the data set for which age at first adult encounter was known and (b) the probability of not breeding in year $(t + 1)$ following breeding in year (t) was minimal for this age class (Viallefont *et al.*, 1995). Results from our analyses of this data set were the same as with the larger data set (Fig. 6), suggesting that our results using the larger data set were not biased by failing to control for age.

4 Discussion

We undertook this study to understand why adult female snow geese from the La Pérouse Bay colony considered as a whole had an apparent survival in the year after their first observation as an adult lower than in subsequent years. This phenomenon was first noted by Francis and Cooke (1993). However, we now have a more complete understanding of the possible basis for this difference: the apparent survival beyond the first year following the first adult observation was not significantly different among birds ringed as goslings, web-tagged and unmarked adults. There was a significant reduction in initial survival for both web-tagged and unmarked adults (with no difference in the magnitude of the reduction between these two groups) but there was no such reduction for adults ringed as goslings. As for capture rate, it was significantly higher for web-tagged adults than for birds from the other two groups which did not differ significantly in this respect. How do these results fit with the different hypotheses presented in the introduction?

Hypothesis (1), heterogeneity of capture, supposes that the two groups in our data with a low initial survival (web-tagged and unmarked adults) are a mixture of birds with high (type C in Fig. 7) and low (type D in Fig. 7) capture probability. In contrast, adults ringed as goslings appear as a homogeneous group made of type C birds. One explanation might be that adults ringed as goslings—thus seen at least twice in the sampling area—are on average more faithful to the sampling area than birds not seen as goslings in the sampling area, and captured (and ringed) initially as adults. This is consistent with the fact that web-tags are placed on goslings at the nest, and not on the rearing grounds where birds are ringed and

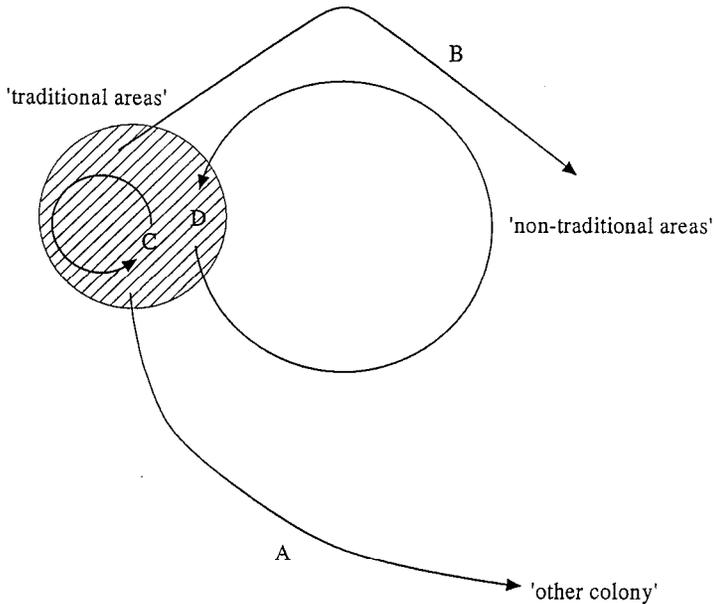


FIG. 7. Hypothetical representation of possible patterns of movement of individual snow geese (see text for complete explanation). 'Traditional' and 'non-traditional' designations correspond qualitatively to Fig. 1.

released. However, such heterogeneity would also be expected to be seen in differences in recapture rate. We would predict that birds which are 'more faithful' to a sampling area (adults ringed as goslings) should have a higher recapture rate than less faithful individuals. However, the significantly higher recapture rate of web-tagged adults conflicts with this hypothesis. As such, we believe that heterogeneity in capture is not a likely explanation.

Having ruled out heterogeneity in capture, we are left with differences in emigration rates. We can approximately estimate the proportion of permanent emigrants from the results presented in Table 3 as $1 - (0.57/0.78)$, or 27%, among unmarked adults and $1 - (0.54/0.79)$, or 32%, among web-tagged adults (Pradel *et al.*, in revision). The emigration of previously unmarked female snow geese contrasting with the apparent fidelity to the site of birds ringed as goslings (who are born at the colony and thus resident) could reflect the presence of transients from other colonies (hypothesis (2)). However, the proportion of emigrants among web-tagged adults (which were hatched at the colony and are thus members of the resident population like the birds ringed as goslings) is comparable. Since true transients (birds from another colony) can only occur in the sample of unmarked adults, the failure to demonstrate significant differences between unmarked and web-tagged adults in apparent survival rate suggests that there is no detectable frequency of true transients in our population.

If the underlying phenomenon was local emigration to new brood-rearing grounds (hypothesis (3)), why should web-tagged adults emigrate and not adults ringed as goslings? We have already argued against the possibility that adults ringed as goslings are more faithful to the sampling area. Could it be that these two groups differ in another respect? About 30% of the goslings captured during the ringing drives are web-tagged. Using the omnibus TEST 1 for comparison of

TABLE 4. Frequency of local dispersal and return of lesser snow goose goslings ringed at La Pérouse Bay (LPB) and Cape Churchill (CC)

Group	Locally dispersed and not returned ^b	Locally dispersed and returned ^c
(a) Including intermediate areas ^a		
Ringed at LPB	165 (97.6%)	4 (2.4%)
Ringed at CC	13 (92.9%)	1 (7.1%)
(b) Excluding intermediate areas ^a		
Ringed at LPB	58 (100%)	0 (0%)
Ringed at CC	5 (83.3%)	1 (16.6%)

^aIntermediate areas = brood-rearing areas located approximately half-way between LPB and CC (see Fig. 1).

^bFrequency of birds who locally dispersed from the ringing site (LPB or CC) and never returned.

^cFrequency of birds who locally dispersed from the ringing site and returned on a subsequent occasion.

groups in RELEASE (Burnham *et al.*, 1987), we compared frequency of return and recapture of adults ringed as goslings which had web-tags, and those which did not. There was no significant difference between these two subgroups ($\chi^2(36) = 38.60, P = 0.35$). Thus, web-tagged adults differ from the adults ringed as goslings because they were not ringed as goslings. This result points strongly to an effect of handling (hypothesis (4)).

In conclusion, we believe that the most parsimonious explanation for our results is that there is a significant effect of handling on the birds, such that 25–30% of birds which are handled for the first time as adults permanently emigrate from the sampling area. Adults which were ringed as goslings do not show this effect following first adult capture, suggesting that either they have become habituated to the procedure after their capture as goslings or only those not affected the first time are left in the adult sample. Of the three groups of recruits distinguished in this study, the group of web-tagged adults is probably the most homogeneous, being made of birds born on the nearby nesting area that feed regularly in the sampling areas. Following the initial trauma of capture, there is virtually no emigration among them: the point estimate of survival (0.792 SE 0.018 model ϕ_{a2}, p_t) is very close to the estimate from recoveries (0.807 SE 0.012) (Francis & Cooke, 1993). By comparison, the lower catchability of goslings marked during the ringing drives tends to indicate that the feeding area is also exploited by birds from other, probably not too distant, nesting areas. The intrinsic heterogeneity of the group of adults ringed as goslings is yet not very strong and not detectable with TEST1 of program RELEASE. Finally, the unmarked adults must include the previous types of birds plus, potentially, transient animals from other colonies. In fact, as there is no difference in initial survival probabilities between web-tagged and unmarked adults, we have no evidence of the presence of transients at this colony. This does not preclude that birds come from other colonies but if they do, they probably stay

thereafter. A limited amount of data on exchanges with the non-traditional brood-rearing areas (Fig. 1) tends to support the idea of predominantly one-way movements (Table 4). This could be further tested by looking at the immigration rates to the colony.

When we started this study, the initial reduction in estimated survival noted by Francis and Cooke (1993) could have been due to heterogeneity of capture under certain conditions, the presence of transient animals from other colonies, local emigration or a direct effect of handling. Another possible interpretation, true age differences in survival, had already been dismissed based on recovery analysis (Francis & Cooke, 1993). The existence of two marking areas (nesting area and brood-rearing area) and of two marking ages (gosling and adult) allowed us to discriminate among the other interpretations. Without at least some individuals where residency was known, there may have been no unambiguous way of differentiating. The main message of this paper is thus a warning against the many possible interpretations of a given capture–recapture model not distinguishable on statistical grounds and a strong recommendation to use several marking and sampling schemes.

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Correspondence: R. Pradel, CEFE/CNRS, CEPE L Emberger, Route de Mende, BP 5051, F-34033 Montpellier Cedex, France.

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