Diagnosing a Shorebird Local Population Decline with a Stage-Structured Population Model

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DIAGNOSING A SHOREBIRD LOCAL POPULATION DECLINE WITH A STAGE-STRUCTURED POPULATION MODEL

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Abstract. The breeding population of Semipalmated Sandpipers at La Pérouse Bay, Churchill, Manitoba declined sharply during the 1980s. Using demographic information collected during eight summers of field work we built a stochastic matrix population model. The model successfully reconstructed the observed decline in the population during the course of the study. The predictions of the model agreed with the observed population level in 1993, 5 yr after the study was completed. Sensitivity analysis showed that the population trend was most sensitive to changes in adult survivorship and to immigration of adults onto the site. We ran simulations to consider five possible reasons for the decline: (1) low adult survivorship, (2) low fecundity, (3) delayed recruitment into the population, (4) low juvenile survivorship, and (5) insufficient immigration. For biologically reasonable values of these parameters, only adult survivorship and immigration rates could account for the observed decline, although juvenile survival also had some impact. These simulations also illustrate that sensitivity is a complex function of the demographic variables, and in particular, sensitivity to adult survival varies across the range of adult survival values that we considered. In addition, we used the model to explore the influence of annual variability in demographic parameters. It is known that the general effect of annual variation is to depress population trends. We showed that the sensitivity of the model to annual variability in survival is tied to the sensitivity of the model to changes in mean values of survival. With the empirical parameter values from this local population, we found that, when survival is high enough to promote stability of the population, the population is highly sensitive to the level of survival, and also to the amount of annual variability in survival. By contrast, the model is not very sensitive to fecundity and is correspondingly insensitive to annual variation in fecundity.

Key words: annual variation; Calidris pusilla; *demography; immigration; matrix population model; Monte Carlo simulation; population trend; Semipalmated Sandpiper; shorebird; stage-structured population model; stochastic demographic model.*

INTRODUCTION

The application of stage- and age-structured population models to populations of conservation interest is increasing (e.g., Lande 1988, Burgman et al. 1988, 1993). Stage-structured population modeling methods make use of data collected at the level of individuals to develop a population-level model using mathematical theories of matrix algebra. Although biologists were introduced to matrix methods by Leslie (1945), the recent availability of microcomputers and matrix-based computer programming languages have made them much more practical and powerful. The theory is being extended, and two recent textbooks (Caswell 1989, Burgman et al. 1993) have made the use of matrix theory in biology more accessible. Through concepts such as sensitivity and elasticity, there are also easy

ways to attribute potential for change among possible parameters in the model.

In this paper we use demographic matrix modeling methods (Caswell 1989) using data collected during eight breeding seasons (1980–1987) on the breeding and population biology of Semipalmated Sandpipers (*Calidris pusilla*) at La Pérouse Bay, near Churchill, Manitoba. The local population declined dramatically during the study, and our model is in part designed to explore possible reasons for this observation. Using a stage-structured matrix model of the population we describe the projected consequences of the demographic structure, and perform a sensitivity analysis of the model to various life history parameters. We generate model predictions with Monte Carlo simulations, and compare the predictions of the model with the observed local trend in the breeding population. We also use the model to distinguish among possible causes for the observed local population decline, and extend the model to explore the effects of annual variability on population trends. Finally we discuss the general implications of

the model. While the model has been specifically tailored to the features of this local population, its form is general. Demographic features of this local population of Semipalmated Sandpipers appear similar to those of other northern-nesting sandpipers, although comparable data are few. Return rates of Semipalmated Sandpipers banded as chicks in this study area (4.5%, Gratto 1988) are low compared to some other studies cited in Thompson et al. (1994). However, the review fails to differentiate between studies where chicks were banded at hatch vs. fledging. Since mortality rates of chicks are usually greatest in their 1st wk of life, this can result in large variations in observed natal return rates (e.g., Semipalmated Sandpipers at La Pérouse Bay banded at < 7 d of age= 4.8% return; banded at > 7 d = 10.0% return; fledging in this species at 16 d; C. L. Gratto-Trevor, *unpublished data*). Thompson et al. (1994) also did not differentiate between studies where researchers actively looked for returning chicks outside the main study area and those that did not. Eliminating studies where chicks were banded at fledging, and those with extensive external searches for returning young, return rates of Semipalmated Sandpipers at La Pérouse Bay fall in the center of the range (Thompson et al. 1994).

About half of the studies with information on age of first breeding in Northern Hemisphere shorebirds report a median age of 1 yr, and the others, a median of 2 yr (Thompson et al. 1994). For calidridine sandpipers, percentages of birds breeding at 1 yr are reported as 0% in Semipalmated Sandpipers elsewhere (Safriel 1971), 29% in Dunlin (*C. alpina*; Soikkeli 1967, Jonsson 1991), 52% in Temminck's Stint (*C. temminckii*; Hilden 1978), and 91% in Least Sandpipers (*C. minutilla*; Cooper 1993). At 23%, Semipalmated Sandpipers at La Pérouse Bay are at the low end of the range, but are probably comparable to other arctic-nesting sandpipers (data are lacking).

It is difficult to find suitable comparisons for the survival rates we use in this paper because the estimates have been calculated with new methods (SURGE [SURvival Generalized Estimation], Lebreton et al. 1992, Sandercock and Gratto-Trevor, *in press*). These new methods are an improvement over the usual approach of using return rates, in that they untangle the element of incomplete resightings from estimates of local survival. However, using uncorrected data, return rates of adult female Semipalmated Sandpipers at La Pérouse Bay (overall 55%) are comparable to those of other calidridine sandpipers (38% in Least Sandpipers, Miller 1977; 49% in Western Sandpipers *C. mauri*, Holmes 1971; 50% in Stilt Sandpipers *C. himantopus*, Jehl 1973; 71% in Dunlin, Soikkeli 1970*a, b*; 72% Temminck's Stint, Hilden 1978).

METHODS

Study site and field methods

Semipalmated Sandpipers were studied at La Pérouse Bay (58°24′ N, 92°24′ W) on the coast of Hudson Bay, 40 km east of Churchill, Manitoba in the summers of 1980–1987 and in 1993. The study area was situated in the Mast River Delta, and was increased from 2 to 3 km² from 1983 onwards. The habitat consisted primarily of low islets of *Salix brachycarpa* or *Betula glandulosa* and mixed sedges and grasses in fresh water. The study area contained the highest breeding densities of Semipalmated Sandpipers in the area, although birds bred at lower densities at the edges of the study area, elsewhere at La Pérouse Bay, and in the vicinity of Churchill. Immigrants likely came from these breeding areas, and also from flocks staging at La Pérouse Bay in the spring before moving to breed farther north.

Incubating birds were captured in walk-in nest traps, and nonincubating birds in mist nets. All adults were given individual color band combinations in addition to stainless steel bands (aluminum bands can become illegible or lost within 2 yr in this species, while stainless steel bands last for life). Except in 1980, all color bands used were ultraviolet stable (less likely to discolor or wear), and 1980 birds were captured in subsequent years and given new color bands. From 1981 to 1987, no color band was lost by any bird. Nestlings were given a stainless steel band and sometimes one color band (to indicate year). They were given individual color combinations if recaught shortly before fledging, or recaptured as adults. Most nestlings (778/846 = 92%) were banded in the 1st or 2nd d after hatch. At this time, tarsus width was fully adult size and tarsus length was 19.6 mm, ≈89% of adult size (Gratto-Trevor 1992); mass at banding was only 16% that of adults.

Survival rates are based on birds seen or captured at nests. If an individually color-banded adult was seen at a nest, it was not always recaptured. Since nestlings were seldom given individual combinations at the time of banding, it was usually necessary to recapture them upon their first nesting attempt. This may have resulted in a slightly greater likelihood of missing known-age birds if the nest was destroyed before the bird was caught. However, since every effort was made to capture these birds as soon as they were noted, very few should have been missed. Males perform flight displays and are more visible than females through most of the breeding season, except during the incubation period. Both parents incubate equally, without notable day/night differences, so there should be no sexual bias in visibility of birds at nests.

Semipalmated Sandpipers are sexually monomorphic in plumage, but within a breeding population, females average slightly larger in size (9% in mass), than males (Gratto 1983). This difference is most pronounced with respect to bill length, and ≈91% of the birds at La Pérouse Bay could be accurately identified to sex by bill length alone. In many instances, sex was verified by behavior: by the presence of an egg in a female's abdomen, copulatory behavior, or by the fact that only males perform flight displays (although both

sexes are territorial). Birds that could not be sexed by size or by behavior were omitted from the survival rate analyses.

There were 634 nesting attempts observed on the study site between 1983 and 1987. At these 634 nests, 475 of the females and 496 of the males were banded and known. Some birds bred in more than one year on the study site; there were 255 unique and banded females and 241 unique and banded males with at least one record of nesting on the site during the study period. Because birds were trapped on the nest, the cases in which one or more of the nesting pair were not marked were generally nests that failed quickly.

After discovery, nests were checked periodically to determine their fate (normally every 1–5 d). Semipalmated Sandpipers do not desert nests after nest visits, or capture, and there was no indication (in this river delta study area) that frequency of nest visitation affected nest predation rates. A nest was considered successful if at least one egg hatched, or if eggs had been pipped strongly 1–2 d before an empty nest was found. In most years, eggs were not floated to determine incubation stage. Egg pigmentation prevents candling. Nests that were depredated before being found could not be distinguished from unused nest scrapes (a male usually makes multiple nest scrapes before the female chooses one) and nest cups from previous years. In this intensive study, nests were usually found early in the 20-d incubation period (mean $\pm$ 1 SD = 4.7 $\pm$ 5.5 d). Nests were checked repeatedly and all but one of the 301 broods found and banded during the study were banded at the nest. While there were undoubtedly early nest failures that were not detected, we believe that there were few of these. From a population modeling perspective, mistaking birds whose nests failed early for nonbreeding birds is a minor concern, because both make the same contribution to the number of chicks produced that year. Further details on methods and the species are described elsewhere (Gratto et al. 1985, Gratto-Trevor 1991, 1992).

Parameter estimation and statistical methods

For our model, we estimated the number of chicks hatched per female in each age class, the proportion of females that bred, annual survival, variation between years in the probability of survival, and the rate of immigration of adult birds from outside the study area.

We found it difficult to estimate the effect of age on egg production and hatching, because there were not enough birds of known age in the youngest age groups to statistically test for effects of age on the number of eggs hatched. As a substitute analysis, we tested for effects of having previously bred on the site on the number of eggs hatched per nest. The distribution of hatched eggs is highly nonnormal and cannot be made normal through transformations; Semipalmated Sandpipers have a typical shorebird clutch size of four eggs, and in the majority of nests either all four eggs hatch,

or the nest fails completely. We analyzed the data using GLIM (version 4.0, NAG [Numerical Algorithms Group]), treating the number of eggs hatched per nest as a multinomially distributed random variable (see Aitkin et al. 1989:235). With the exception of the relevant test statistic, which for this analysis is asymptotically distributed as a chi-squared distribution, the analysis is precisely analogous to an ANOVA. We looked at three categories of breeding experience: birds that were not seen breeding before at the site, birds that had bred in one prior year, and birds that had bred in two or more previous years.

A small number of the 802 birds that were banded as nestlings during 1980–1986 subsequently attempted to breed on the site (16 females and 18 males). We estimated the probability of breeding at a particular age from the pattern of recruitment into the breeding population for these birds (Gratto 1988), and calculated bootstrap estimates of the 95% confidence intervals for these probabilities (n = 1000 samples, Efron and Tibshirani 1993).

Sandercock and Gratto-Trevor (in press) report estimates of survival that they calculated from these data. The analyses were performed with SURGE (see Lebreton et al. 1992 for a review), and estimate local survival, the proportion of birds that both survive and return to the study area. When we use survival in this paper, we are speaking with reference to the study area, and mean local survival. In addition, we used the covariance–variance matrix from that analysis to estimate τ, the annual variation in survival that is ecologically relevant, rather than an artifact of the estimation procedure (Link and Nichols 1994).

We also estimated the survival of chicks between the date of hatching and the date that the chicks were banded. Sandercock and Gratto-Trevor's (in press) analysis calculates nestling survival from the date of banding, and there was generally a delay of a day or two between hatching and banding. Over 90% of nestlings banded were marked on the day of hatch or the following day. In some cases dead chicks were found at the nest. In other cases they were presumed dead if their marked parents were not found with a brood after the nest was empty but eggs should have been hatched. Nests were checked frequently (usually every day or two) as they neared hatch.

Shorebird eggs normally pip for several days before hatching (up to 4 d). Parents with broods are extremely visible due to their intensive distraction displays and vocalizations. After 1980, it was very rare to find a young brood attended by unbanded parents in the study area, so virtually all nests in the area were found if they survived to hatch. By calculating the number of pipped eggs or chicks missing or dead before banding, we obtained an estimate of hatching to banding survival each year.

Finally, we estimated immigration rates onto the study site. Like most studies of wild animals, the study

A. Overall productivity
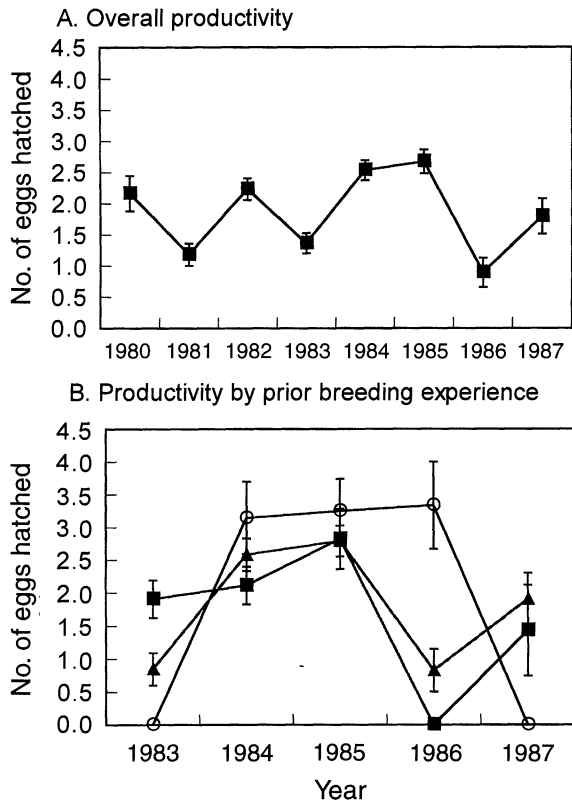

B. Productivity by prior breeding experience

FIG. 1. Annual variability in the mean number of eggs that hatched per nest: (A) the overall pattern; (B) the effects of prior maternal breeding experience on the study site. Error bars indicate the magnitude of the standard error of the mean. Note that birds that are inexperienced on the La Pérouse Bay study site are a mixed group; some may have had prior breeding experience elsewhere, some may have bred previously on the site but not been detected, and some will be breeding for the first time. ○, no known prior breeding experience on the site; ■, 1 yr of experience; ▲, ≥ 2 yr of prior breeding experience.

population was not closed. In fact, very few of the breeding birds were known to have hatched on the study site. Although adult Semipalmated Sandpipers show a high degree of fidelity to the breeding grounds, young birds often disperse from their natal areas during the first and perhaps second years of life. Because immigration is an important component of the local population dynamics, we needed to estimate it and include it in the model. To do so, we first tabulated the number of newly banded birds in each year of the study. In addition, we used SURGE to estimate immigration rates from the banding data. By analyzing the capture histories in reverse order, we estimated the probability that a bird breeding in a given year had also been breeding in the previous year.

These parameters were incorporated in a structured population model. The transition diagram for the model is shown in Appendix A. The model is a modified Leslie matrix, with three stage classes. Immigrants are added

to the oldest stage class. As is typically done in such models, calculations refer to one sex only, in this case females. The 3-yr structure allows us to incorporate the fact that some females did not start to breed until they were 3 yr old. For calculation purposes, a small matrix is easier to work with, and we do not have enough information to distinguish among birds that are older than this. Some results are based on a deterministic matrix calculated from average parameter values, but many come from Monte Carlo simulations of the model.

RESULTS

Estimating demographic variables

There was strong annual variation in the number of eggs hatched per nest ($\chi^2 = 57.94$, df = 8, $P < 0.001$), but no effect of prior breeding experience ($\chi^2 = 2.932$; df = 4; $P = 0.57$). There was a significant interaction between prior experience and year ($\chi^2 = 27.09$; df = 16; $P = 0.04$), indicating that the effect of maternal experience varied among years (Fig. 1B). The annual variation over all 8 yr of the study was approximately uniformly distributed between one and three eggs per nest (Fig. 1A). For each year we chose the number of eggs from this distribution, and used this value as our parameter estimate for all of the stage classes.

Very few birds that were banded as nestlings later returned to breed on the site. Of the 16 females that did so, 4 first bred at age 1, 10 at age 2 and a further 2 at age 3. The probabilities of having bred at each age were calculated as 25% in the 1st yr (95% bootstrapped confidence interval: 0.06, 0.50), 87.5% by the 2nd yr (95% CI: 0.69, 1.0), and 100% by the end of the 3rd yr after hatching. For the mature stage classes (3+ and IMM [immigrants]), we estimated the probability of breeding in any year to be 95% by counting females that were observed to breed in consecutive years relative to those that skipped years. We use these values in the model, and the confidence intervals for our sensitivity analysis.

The results of the SURGE analysis of local survival (Sandercock and Gratto-Trevor, in press) are shown in Appendix B, along with a calculation of τ, the component of annual variability in survival that can be attributed to ecologically relevant variability rather than to sampling error (Link and Nichols 1994). The estimate of annual survival for birds past their 1st yr is 0.563, with annual variability of τ = 0.065. Sandercock and Gratto-Trevor report an overall chick survival rate of 0.094, but this includes a point estimate of 0.01 in 1985–1986. We believe that this very low value reflects delayed recruitment onto the breeding site rather than survival, and so our simulations use the four nonzero estimates of survival rate as representative of juvenile survival in this population. Juvenile survival is affected both by mortality and permanent emigration. In 1984, a year of comparatively low nest

predation, chicks were followed to fledging, and 50% of them survived from hatching to fledging. In the sensitivity analysis we use 50 and 9.4% as high and low estimates of juvenile survival, respectively.

Of 1477 eggs observed, 695 were known to have pipped or hatched. Of these, 582 were banded, 78 were presumed dead, and 35 had an unknown fate. Thus we estimate that the overall survival rate from hatching to banding was between 82 (582/695) and 89% ((582 + 35)/695). Annual estimates ranged from 78 to 100% survival during that short period between hatching and banding. The simulations use 0.90 for this parameter.

Finally, Table 1 shows the population estimate and the number of newly banded females in each year of the study. In Appendix C, we report the results of a SURGE analysis to estimate immigration rates from the banding data. The best model was one that varied with time but not between the sexes. During the course of the study, the proportion of new immigrants dropped from 32 to 19% of the population.

Model results

The dominant eigenvalue of the population transition matrix is denoted by λ and indicates the short-term trend of the population without immigration. We estimate the dominant eigenvalue from these data, using bootstrap estimates to incorporate uncertainty about exact parameter values. The median dominant eigenvalue was 0.661 (95% confidence interval: 0.486, 0.836; bootstrap sample size 1000). Details of parameter estimates and sampling distributions can be found in Table 2. This indicates that, in the absence of immigration, the La Pérouse Bay breeding population would decline rapidly.

The elasticity and sensitivity of the dominant eigenvalue to the parameters of the model provide an indication of the degree to which a change in some component of the model results in a change in the population trend (Caswell 1989). The elasticities for the

TABLE 1. Observed numbers of females on the study site at La Pérouse Bay that were already banded in previous years, observed numbers that were banded during that study season, and a total estimate of the number of paired females, including both banded and unbanded females.

Year	Previously banded females	Newly banded females	Total paired females
1980	0	43	≈86
1981	15	34	91
1982	29	41	93
1983†	50	48	133
1984	48	42	97
1985	58	15	80
1986	42	5	57
1987	29	7	37
1993‡	3	12	23

† Study site expanded from 2 to 3 km² in 1983.
‡ Single study year in 1993.

TABLE 2. Summary of parameters used in simulations: ϕ is the annual survival rate, $\hat{\sigma}$ is the standard deviation of the survival rate estimates between years, uncorrected for sampling variation, and τ is the estimated standard deviation in survival rates due to ecological factors.

A) Annual survival estimates

Adult survival was drawn from a beta distribution with parameters corresponding to mean and standard deviations:

$$\hat{\phi} = 0.563 \qquad \hat{\sigma} = 0.087 \text{ (sampling error)}$$
$$\tau = 0.065 \text{ (annual variation)}$$

Juvenile survival was chosen randomly from: {0.085, 0.159, 0.197, 0.076}
Survival between hatch date and banding = 0.90

B) Probability of breeding

| | Age | | |
	1	2	3+
Median	0.25	0.875	0.95
Lower 95% CI limits	0.0625	0.69	0.95
Upper 95% CI limits	0.5	0.95	0.95

C) Number of chicks hatched per nest during simulated study years

| | Year | | | | | |
	1983	1984	1985	1986	1987	1988–1993
No. chicks hatched	1.36	2.53	2.67	0.89	1.79	U[1.0, 3.0]

(The number of chicks hatched per nest during longer simulations to examine sensitivity followed a uniform distribution on the range [1.0, 3.0]).

D) Immigration during simulated study years

| | Year | | | | |
	1984	1985	1986	1987	1988–1993
No. immigrants	38	14	4	7	7

(During longer simulations to examine sensitivity: seven immigrant female birds per year.)

matrix with average estimates of the various parameters are shown in Appendix A.

Fig. 2 shows the simulated population trajectories from 1983 to 1993 (see Table 2 for parameter values), and the observed number of pairs on the site from 1983 to 1987 inclusive, and in 1993.

We used Monte Carlo simulations to explore the sensitivity of the model to parameter values and to annual variation in those parameters. From the elasticities, it is clear that the population is most sensitive to variation in adult survival. For these simulations we started with the same initial parameters, and varied each of the parameters in turn, presenting the median of 25 yr of simulations. Fig. 3 shows the effects of varying adult survival, the number of eggs hatched per nest, the number of immigrant birds per year, and juvenile survival. In addition, we ran simulations to explore the effects of the probability of breeding at different ages. The simulated trajectories were virtually identical for prob-
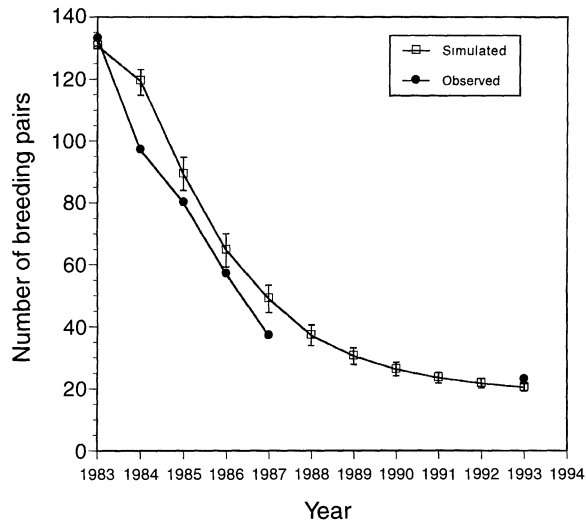
FIG. 2. Number of breeding pairs at the study site as predicted by the simulation (□) and as observed (●). Simulation values are the median of 1000 simulations; error bars indicate the 95% confidence interval within the simulations.

abilities of breeding ranging from (0.062, 0.69, 1.0) to (0.5, 1.0, 1.0) for birds in stage classes 1 through 3, respectively. We also explored the effect of modeling immigration as a proportion of local population size, and found that an immigration rate of >34% was needed to prevent a population decline, given the parameter estimates. Increasing the number of eggs hatched per nesting attempt, and increasing juvenile survival had little effect on the population projection. By contrast, both adult survival and the number of new immigrants per year showed strong effects on the population size.

The effect of variability around two different values of adult survival are illustrated in Fig. 4. Fig. 4A shows the median population size when the expected adult survival rate is 0.86, and the annual variation in survival has standard deviations of 0.065, 0.1, and 0.2. With this combination of parameters, the model is particularly sensitive to adult survival, and increasing annual variability in adult survival can make the difference between population stability and decline. By contrast, in Fig. 4B, the same range of standard deviations has been used, but with a mean value of 0.563. With the parameters we have estimated from the La Pérouse Bay population, annual variation in survival does not make much difference to the overall population trend.

DISCUSSION

Our model reproduces the observed population decline. The Monte Carlo simulations projected the population size during 5 yr of the study and over a subsequent 5-yr interval during which no data were collected on the site. Even over 10 yr, the model predictions are in reasonable agreement with the observed population size.

Sensitivity analysis and further Monte Carlo simulations allowed us to eliminate a number of candidate hypotheses to explain the decline. Within a biologically reasonable range, only increases in adult survival and immigration rates proved influential enough to have averted the observed decline. Increased chick production, accelerated maturity, and increased chick survival all were comparatively ineffective at restoring the simulated population to stable levels. Because we did not test combinations of factors, we can only rule out individual factors with our current model, but our conclusions are very clear. This conclusion is particularly notable because the annual variability in chick production is a prominent feature of the breeding biology of shorebirds. It would be easy to attribute population declines to insufficient fecundity. It is important to note that what we call adult survival is really a mix of survival and site fidelity; from the point of view of the local population, permanent emigration and mortality are equivalent.

As part of the process of identifying parameter values for the model we looked at the role of experience in fecundity. We found evidence for annual variation in the number of eggs hatched, and a significant interaction between prior breeding experience and year, which we found difficult to interpret. The interaction was such that in some years experienced birds hatched more eggs, while in other years experienced birds were less productive than inexperienced birds. Our sample sizes were small and our categories are not entirely clean; some birds that are described as inexperienced may well have had prior breeding experience somewhere else. But both of these factors ought to have made it harder to find effects, not easier. One possible explanation might lie in the timing of breeding. It might be that early- and late-breeding birds differ in prior experience, and that there are other factors that interact with the time of nesting to produce differential mortality. For example, variable weather effects, such as delayed snowmelt, or late storms, may differentially affect early nesters. The timing of breeding can also influence susceptibility to predation (e.g., Alberico et al. 1991). It would be interesting to explore the generality of our observation.

In building this model, we have had to make a number of assumptions, some of which are implicit in the modeling structure, and some of which arise from the estimation of parameters. (1) Survival and fecundity are independent of density on the breeding grounds. While it is possible to include density dependence in models of this type, we had no evidence for density dependence and would have had to invent a function to describe it. We chose instead to omit this factor. (2) Mates are not limiting for females. In each year of the study there were a number of unpaired males, but no unpaired females. Females also tend to start breeding at an earlier age than males. (3) Immigrating birds are 2 yr old or older. This is not strictly true; some im-
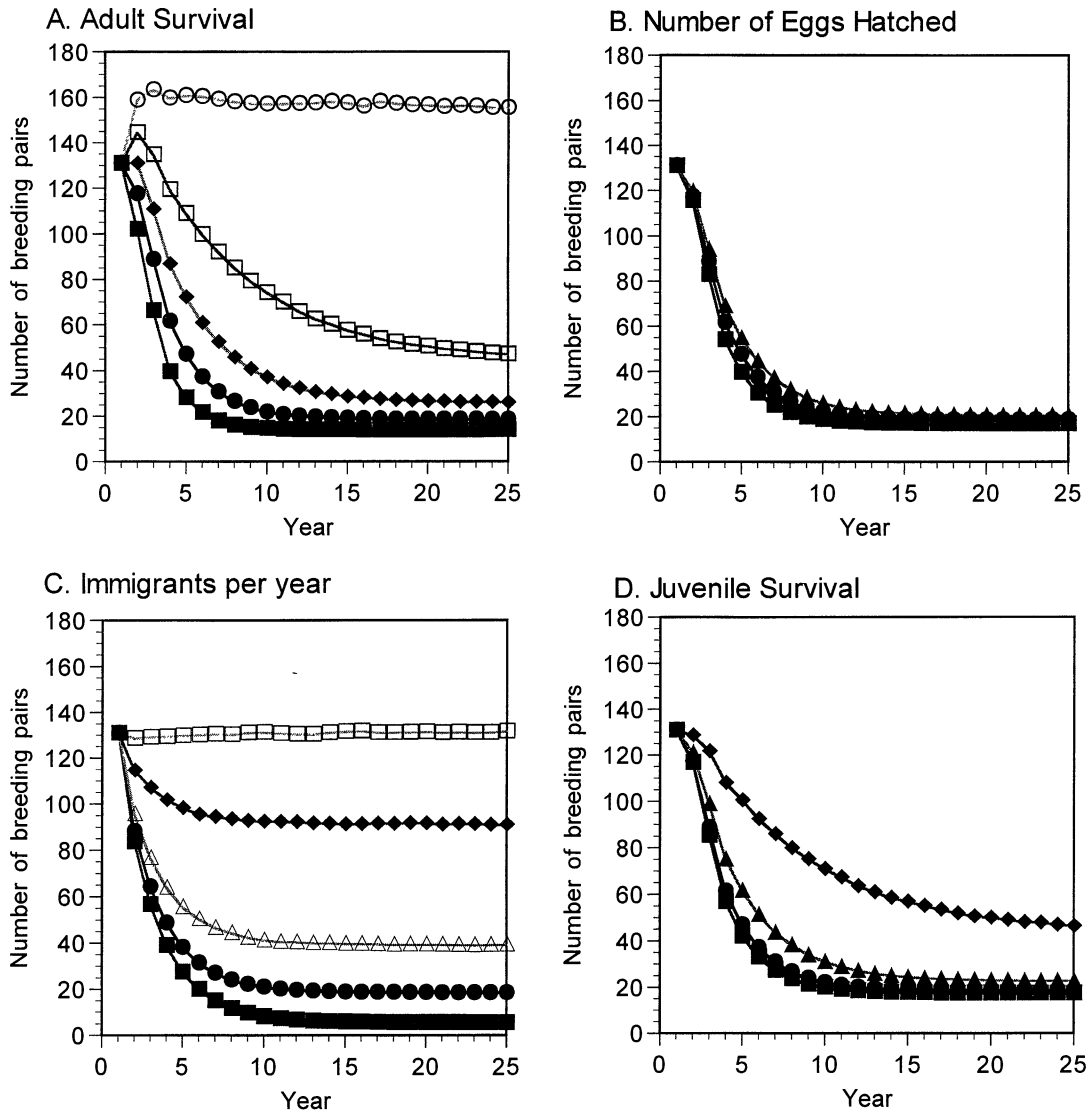
FIG. 3. Sensitivity analysis to changes in (A) adult survival (○, 0.86, □, 0.76; ◆, 0.66; ●, 0.563; ■, 0.45); (B) average number of eggs hatched per nest (▲, 3 eggs/nest; ●, 2 eggs/nest; ■, 1 egg/nest); (C) number of immigrant birds settling per year (□, 50; ◆, 35; △, 15; ●, 7; ■, 2); (D) annual survival of juvenile birds (◆, 0.50; ▲, 0.25; ●, 0.13; ■, 0.09). Values shown for each curve are median values of 1000 simulations over 25 simulated years.

migrants could be identified as yearlings by a partial postjuvenal wing moult (Gratto and Morrison 1981), but there were very few such birds. (4) Given that a bird nests, the expected number of eggs that hatch is independent of the age of the bird. We found a significant interaction effect of prior breeding experience and year on the number of eggs hatched, but in the absence of a clear understanding of the mechanisms involved, we left that feature out of the model. (5) Survival during the first year of age (and, indeed, in all subsequent years) is independent of the age of the parents. Very few field studies provide enough information to address this point, and certainly we were unable to consider it. (6) The absolute number of immigrants per year was

constant following 1987. (7) The natal sex ratio is even. (8) Truncating the explicit age structure at 3 yr of age is an adequate description of the age-specific demographic patterns. In particular, there are no effects of age on survival or fecundity beyond the age of 3. We do not have data to address this question. On the other hand, senescent birds are likely to make up a comparatively small part of the breeding population, so the population-level effects of violating this assumption are not likely to be great. (9) Life history parameters vary between years independently, rather than being correlated. Sensitivities and elasticities are not properties of parameters per se, but depend on the values of all of the parameters in the matrix model. Moreover,
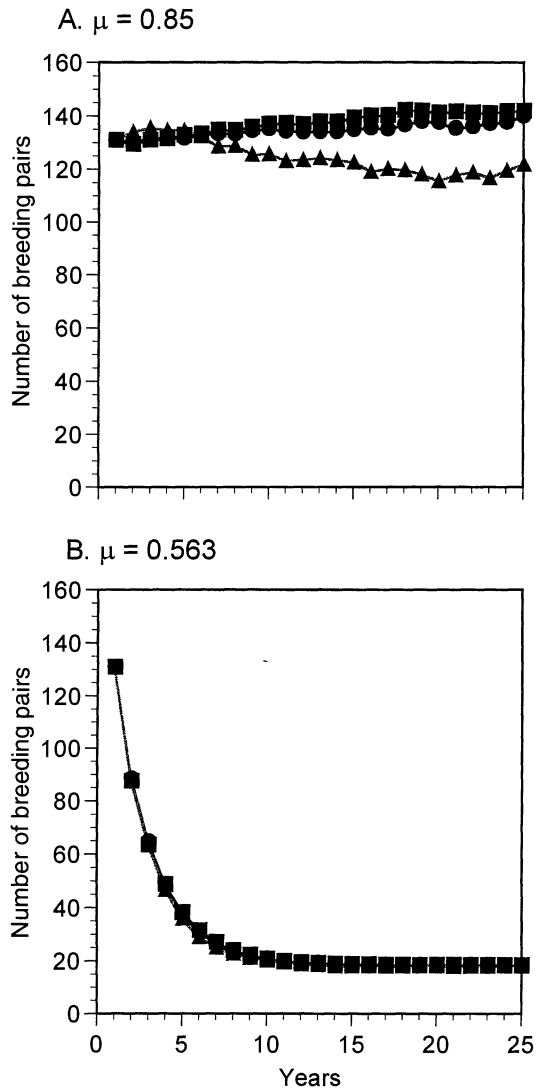
A. μ = 0.85

B. μ = 0.563

FIG. 4. Simulations to explore the effect of annual variability in adult survival on population trends. Values shown are median values from 1000 simulations over 25 yr. In all cases, adult survival was drawn from a beta distribution with parameters α and β corresponding to mean μ and variance τ². (A) μ = 0.85; ■, τ = 0.065, ●, τ = 0.1, ▲, τ = 0.2; (B) μ = 0.563; ■, τ = 0.065, ●, τ = 0.1, ▲, τ = 0.2.

even when all other parameters stay equal, the sensitivity of one parameter does not stay fixed, but responds in a nonlinear way to the value of the parameter itself. This can be seen clearly in Fig. 3A in which the effect of a change in adult survival was dramatically different over the range of survival rates we considered. An increase in adult survival from 0.45 to 0.563 made almost no difference, while raising survival from 0.76 to 0.86 had a dramatic effect.

Our final simulations illustrate the fact that annual variability will always depress population trends, relative to a population with no variability and the same arithmetic mean of parameters (Boyce 1977, Tuljapur-

kar 1980). This is an important point that is often overlooked, particularly if field data are insufficient to provide estimates of annual variability in a demographic parameter. In the course of an ongoing study, plugging early parameter estimates into a population matrix can yield important guidance. A quick analysis of this matrix can indicate parameters that might plausibly range over a variety of biologically meaningful values and that are highly influential on the eigenvalue (as assessed through sensitivity or elasticity calculations). The variability of such parameters is important for two reasons. The first is that, since the variable is highly influential in our assessment of the population, it is important that we minimize our uncertainty, that is, that we take steps to reduce our sampling errors, by, for example, increasing sample size or changing our research designs to best estimate the parameter. The second, and one that is more often overlooked, is that it is important to estimate the annual variability of the parameter as well, and to incorporate this information into our projections and forecasting. We included sampling error in our bootstrap estimates of the dominant eigenvalue, λ, but used the reduced estimate of annual variation, τ, in simulations to explore sensitivity. As Fig. 4 shows, when a parameter is found to be one with high elasticity, and hence one that is highly influential on the population trend, then the amount of year-to-year variability in that parameter can also be highly influential. In our simulations, for the same long-term average survival rate of 0.86, we found that increasing variability in adult survival from year to year led to a change from a stable population to one that was in steady decline.

Most study populations of wild animals in the field are studies of open populations in which immigration and emigration are important components of the population dynamics. The role of metapopulation structure in population persistence is an important one, and is an increasing subject of theoretical and empirical study (Gilpin and Hanski 1991). La Pérouse Bay seems to be a sink for Semipalmated Sandpipers (Pulliam 1988), and the population decline during the 1980s appears to have resulted from a conjunction of net emigration of adults breeding on the site coupled with a decline of immigration. Both factors might be linked to habitat degradation, either locally or at the sites of source populations in the area.

If we are to be able to apply age-structured modeling techniques to more field data sets, we may need to think about how we can alter field methodology to increase the number of individuals that are marked and of known age. For example, most shorebirds disperse away from their natal area comparatively early in life, then settle at a breeding site and return to that breeding site for many years. Thompson et al. (1994) looked at the settlement patterns of Lapwings in Britain and found that 37–73% of the birds settled to breed within 5 km of their natal site. Jackson (1994) documented natal dis-

persal by males and females in Dunlin, Ringed Plovers, and Redshank, and similarly found a range of dispersal distances, with most birds dispersing within 8 km of their natal site. If most birds breed within 8 km of their natal area (and with some further assumptions about the distribution of populations over space), then most incoming adult breeding birds will have hatched within 8 km of their breeding area. In addition, Jackson's data illustrate that, particularly for females, one of the worst places to band nestlings in the hope that they return to the study site is on the study site itself. While we are discussing long distances to extend a study site, there may be ways to focus banding efforts on nestlings in those areas that are most likely to produce adults that later settle in the focal study site. Age-structured population models require data to be collected from birds of known age. If we are to fully harness the power of these developing theoretical methods, it seems important to open the discussion as to how best to collect the data they require.

Our modeling explorations have some important points for shorebird conservation. Firstly, and somewhat counterintuitively, we found that adult survival and immigration, rather than reproduction rates, were most influential on shorebird population trends. While the parameters we used may or may not be the same as those for other shorebirds, it is at least worth noting that in this case, large changes in reproductive output had a surprisingly modest effect on population size. The conclusion that adult survival is most influential on population growth rates has also been arrived at in models of other iteroparous bird species (Lande 1988, Brault et al. 1994, Goudie et al. 1994). Secondly, we found that stable populations can be extremely sensitive to changes in adult survival. A very small shift in adult survival can turn a stable population into a declining population. For migratory shorebirds, stopover sites may be important in survival, and because shoreline development is difficult to reverse, it is essential for shorebird conservation that we be proactive, rather than waiting for declines to occur and be clearly demonstrated. We may not have much time once a decline becomes apparent. Thirdly, we found that variability in survival is also important in this sensitive range. This may have particular relevance for shorebirds that make transcontinental migrations, because the wetlands that are suitable for stopover sites are naturally ephemeral (Skagen and Knopf 1993). Shorebirds are sensitive to the depth of water, so both dry and wet years can cause them problems in finding stopover sites. As the numbers of potential sites decrease, both the chances of finding a suitable site and the variability in the probability of finding a suitable site in a given year will also increase. To the extent that this affects annual survival, it may have a large effect, even with no change in average survival. Moreover, transcontinental and coastal migrant subpopulations may show different population trends, even with the same average

parameter values, because of differences in annual variation.

Our model provides an example of how we can use long-term field data to estimate demographic parameters for a stage-structured population model, and use this model to improve our understanding of the population. The Semipalmated Sandpiper population at La Pérouse Bay has declined, and this decline seems to be related to low adult local survival. We believe that this is more likely the result of net emigration from the site and reduced immigration, rather than increased mortality, potentially through site degradation by a burgeoning population of Lesser Snowgeese (Jeffries et al. 1979). However, populations of Semipalmated Sandpipers around the Churchill area have been declining since the 1950s, which precedes the snowgoose population surge (J. Jehl, *personal communication*). Although annual variation in hatching rate is a prominent feature of the breeding biology, it seems to have little impact on the population trend. The demographic matrix modeling approach has been effective at predicting the decline over a 10-yr period, and is a promising technique for assessing populations of widely dispersed shorebirds.

The recent development of matrix theory and the availability of clear textbooks and powerful computational aids allow us to extract a great deal of information from existing long-term data sets on banded populations. Not only do these methods allow us to address the projected trends of the population we are studying, they also allow us to explore candidate hypotheses about what are the most critical life history parameters for the persistence of the population. If we are to do more than document the declines of populations, we need methods to diagnose the declines and to prescribe effective treatments. When we are working with very incomplete knowledge, exploring likely parameter values can direct us as to which are most likely to be important and to which the population trend is fairly insensitive. This approach is a promising one for organizing research, analyzing data, and exploring the potential effects of change.

of these data. We thank Jim Nichols for comments that led us to substantially improve our model and estimation methods during the review process.

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APPENDIX A

The transition diagram for the population model is shown in Fig. A1. There are three stage classes in the model: yearlings, 2-yr-old birds, and birds ≥ 3 yr old. The s_i are the annual survival rates for birds in stage i. The F_i represent the number of 1-yr-old birds in year $t + 1$ for each individual in stage class i in year t. This model is a prebreeding census model, and so the F_i are affected by not only the number of chicks hatched per female, but also all mortality during the first year of life.

The matrix equation corresponding to this transition diagram is:

$$\mathbf{N}_{t+1} = \mathbf{A}\cdot\mathbf{N}_t + \mathbf{I}_t \quad (A.1)$$

where

$$\mathbf{N}_t = \begin{bmatrix} n_1(t) \\ n_2(t) \\ n_{3+}(t) \end{bmatrix} \quad (A.2)$$

and

$$\mathbf{I}_t = \begin{bmatrix} 0 \\ 0 \\ IMM_t \end{bmatrix} \quad (A.3)$$

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_{3+} \\ s_1 & 0 & 0 \\ 0 & s_2 & s_{3+} \end{bmatrix} \quad (A.4)$$

$\mathbf{N}_t$ is called the population vector, and consists of elements $n_i(t)$, each indicating the number of birds in stage class i in year t. The total population size in year t is the sum of the elements of $\mathbf{N}_t$, $\Sigma\ n_i(t)$. The matrix $\mathbf{A}$ with elements a_{ij} summarizes the population dynamics, and is called the transition matrix. Immigrant birds that were not hatched on the site are added in the vector $\mathbf{I}_t$.

The s_i were taken from a SURGE analysis of data from the same study (Sandercock and Gratto-Trevor, *in press*), and the F_i were calculated using the following formula

$$F_i = 0.5\cdot prbreed_i\cdot nhatch\cdot pr(surv\ h \rightarrow b)\cdot s_0, \quad (A.5)$$

where $prbreed_i$ is the proportion of birds that breed at age i, nhatch is the number of eggs that hatch per nest, pr(surv h $\rightarrow$ b) is the probability of survival from hatching to banding, and s_0 is the rate of survival from banding as a nestling to the first year of life. If the sex ratio is even, half of these birds will be female. These parameters were estimated from data collected at the field site during the study period. Rather than directly estimating the number of nestlings per adult in a particular age class, we calculated the probability of breeding and the number of eggs hatched given that a bird bred, separately. We used this approach for a number of reasons. Firstly, the field collection methods were designed to collect good information on breeding birds, and sightings of non-breeding birds on the site were incidental. Secondly, some birds are seen on the overwintering grounds during the breeding season and presumably do not migrate to the breeding
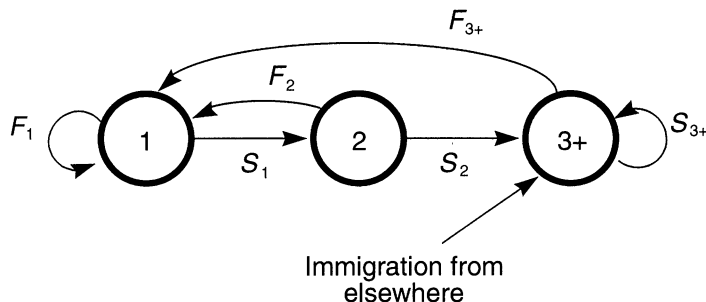
grounds in those years (Naranjo et al. 1994; Mercier, *personal communication*). If this is the case, even a complete census of the breeding ground would miss some birds.

Using the mean parameter values (Table 2), the transition matrix is

$$\mathbf{A} = \begin{bmatrix} 0.02115 & 0.074 & 0.0846 \\ 0.563 & 0 & 0 \\ 0 & 0.563 & 0.563 \end{bmatrix} \quad (A.6)$$

and the corresponding dominant eigenvalue, λ, is 0.639.

Sensitivity was calculated according to

$$\frac{\partial\lambda}{\partial a_{ij}} = \frac{\mathbf{v}_i, \mathbf{w}_j}{\langle\mathbf{w}, \mathbf{v}\rangle}$$

(Caswell 1989:121) where $\mathbf{v}$ and $\mathbf{w}$ are left and right eigenvectors of $\mathbf{A}$, respectively, and $\langle\mathbf{w}, \mathbf{v}\rangle$ is the scalar product of the vectors. The sensitivity matrix is:

$$\left[\frac{\partial\lambda}{\partial a_{ij}}\right] = \begin{bmatrix} 0.1082 & 0.0953 & 0.7067 \\ 0.1187 & - & - \\ - & 0.1062 & 0.7872 \end{bmatrix}. \quad (A.7)$$

Dashes indicate transition elements that must be zero because of the structure of the model, and so whose sensitivity values are not relevant. Using the chain rule (Caswell 1989:127), the sensitivity to each individual parameter is shown in Table A1. The elasticity matrix, which shows the sensitivity measured in terms of proportional changes in matrix coefficients, is

$$[e_{ij}] = \begin{bmatrix} 0.0036 & 0.011 & 0.0936 \\ 0.1046 & - & - \\ - & 0.094 & 0.694 \end{bmatrix}. \quad (A.8)$$

Elasticity is calculated as sensitivity times the corresponding matrix coefficient divided by λ. So, for example,

$$e_{12} = \frac{a_{12}}{\lambda}\left(\frac{\partial\lambda}{\partial a_{12}}\right) = \left(\frac{0.074}{0.639}\right)0.0953 = 0.011.$$

TABLE A1. Sensitivity of λ, the dominant eigenvalue, to small perturbations in each of the demographic parameters in the model, given that the standard parameter estimates are used.

Parameter	Sensitivity
F (chicks hatched per breeding female)	0.0346
s_0 (juvenile survival)	0.7354
s_1 (survival of 1-yr-olds to the next year)	0.1187
s_2 (survival of 2-yr-olds to the next year)	0.1062
s_{3+} (survival of birds 3-yr-old and older)	0.7872
Probability of survival from hatching to banding	0.0768
Probability of breeding at age 1	0.009
Probability of breeding at age 2	0.008
Probability of breeding at age 3 or older	0.0598

FIG. A1. Transition diagram for the stage-structured population model. The model is a prebreeding census model; the youngest stage class in the model is that of 1-yr-old birds that hatched in the previous year. In addition to the 1-yr-olds, the other two stage classes are of 2-yr-old birds, and birds 3-yr-old and older. Arrows denote the transitions in the model, from one stage to another. The s_i are the survival rates from stage i to stage $i + 1$. The F_i are the average number of 1-yr-old birds in year $t + 1$ for each individual in age class i in year t.

APPENDIX B

The results of the survival analysis from Sandercock and Gratto-Trevor (*in press, personal communication*) are shown in Table B1. The overall estimate of annual survival is 0.563 for adults and 0.094 for birds in their first year of life. We have separated the overall variation in estimated survival rates into a component that purely reflects the uncertainty associated with sampling, and a component that reflects the magnitude of ecologically relevant variation. Following Link

and Nichols (1994), we denote the component of variation in annual survival that is of biological (rather than sampling) origin as τ^2, and compute it as:

$$\tau^2 = \hat{\sigma}^2 - \frac{1}{n} \sum_{i=1}^{n} \text{var}(\hat{\phi}_i)$$

$$+ \frac{2}{n(n-1)} \sum_{i<j} \text{cov}(\hat{\phi}_i, \hat{\phi}_j). \quad (\text{B.1})$$

From Table B1, we compute $\hat{\sigma}^2 = 0.00753$ (sample variance of ϕ for the first 6 yr of the study). The variance–covariance table produced by SURGE is shown in Table B2. This table is in units of logit transformation. To calculate $\text{cov}(\hat{\phi}_i, \hat{\phi}_j)$ we use (Lebreton et al. 1992):

$$\times \text{cov}(\hat{\phi}_i, \hat{\phi}_j) = \hat{\phi}_i(1 - \hat{\phi}_i)\hat{\phi}_j(1 - \hat{\phi}_j)$$

$$\times \text{cov}[\text{logit}(\hat{\phi}_i), \text{logit}(\hat{\phi}_j)] \quad (\text{B.2})$$

and so, by substituting the sum of the diagonal elements (sum of variances) and the sum of the off-diagonal elements (sum of covariances) we estimate:

$$\tau^2 = 0.0075 - \frac{1}{6}(0.0191) + \frac{2}{6(5)}(-0.0026)$$

$$= 0.0042. \quad (\text{B.3})$$

Thus we estimate that the actual, year-to-year standard deviation in survival during the course of the study, excluding variability due to sampling alone, is

$$\tau = 0.065.$$

TABLE B1. Results of survival analysis from mark–recapture data collected on birds at La Pérouse Bay and reported in Sandercock and Gratto-Trevor (*in press, personal communication*). The survival estimates were generated using the analysis package, SURGE, and are made up of two components, the actual local survival rate, ϕ_i, and the probability of recapturing a bird given that it was alive, p_i.

Year 1–year 2	Adults		First-year survival (birds hatched on site only)	
	Survival (ϕ_i)	Recapture (p_i)	Survival (ϕ_i)	Recapture (p_i)
1980–1981	0.635	0.531	1.0	0.030
1981–1982	0.593	0.782	0.085	0.211
1982–1983	0.719	0.764	0.158	0.044
1983–1984	0.482	0.902	0.197	0.114
1984–1985	0.620	0.918	0.076	0.000
1985–1986	0.509	0.719	0.01	0.000

TABLE B2. Variance–covariance matrix for the survival parameters from the SURGE analysis of capture–recapture data. The 8 yr of data produce seven estimates of survival, and the matrix shows the covariance of these seven estimates with one another. The diagonal elements are the variances of each estimate.

Survival estimates	Survival estimates						
	1	2	3	4	5	6	7
1	1.74×10^{-1}	-3.51×10^{-2}	3.15×10^{-4}	6.77×10^{-5}	6.48×10^{-5}	-3.1×10^{-5}	7.73×10^{-5}
2		4.97×10^{-2}	-6.69×10^{-3}	-2.10×10^{-4}	1.28×10^{-4}	0.000392	-2.72×10^{-4}
3			7.25×10^{-2}	-9.60×10^{-3}	2.10×10^{-5}	-0.00039	-8.60×10^{-4}
4				2.36×10^{-2}	-1.54×10^{-3}	-0.00012	-4.22×10^{-5}
5					3.25×10^{-2}	-0.00411	5.41×10^{-4}
6						0.051551	-1.42×10^{-2}
7							5.40×10^{-1}

APPENDIX C

This appendix summarizes the SURGE results for a model to describe the capture–recapture history in reverse order. In this case $1 - \phi$ reflects the rate of immigration or birth, rather than mortality. In this case, only birds banded as adults are used, and so this is purely a rate of immigrant influx. Results of the SURGE analysis are summarized in Table C1. The model with the lowest Akaike Information Criterion is ϕ_t, p_t, in which both immigration and resighting change between years, but there are no differences in estimates between the sexes. There were no additional factors that added significant explanatory power to the model, and dropping time from the estimates of either ϕ or p significantly reduced the explanatory power of the model (Table C2). The best model is one in which both ϕ and p depend on time but not sex. The maximum likelihood parameter estimates for the model are shown in Table C3.

TABLE C1. Summary of the results of a SURGE analysis on the capture histories in reverse order.

ϕ	p	Dev.	NP	AIC
ϕ_c	p_c	1443.38	2	1447.38
ϕ_c	p_t	1370.85	8	1386.85
ϕ_c	p_{sex}	1441.22	3	1447.22
ϕ_c	$p_{t,sex}$	1362.80	15	1392.80
ϕ_t	p_c	1365.69	8	1381.69
ϕ_t	**p_t**	**1337.17**	**14**	**1365.17**
ϕ_t	p_{sex}	1363.48	9	1381.48
ϕ_t	$p_{t,sex}$	1327.55	21	1369.55
ϕ_{sex}	p_c	1442.67	3	1448.67
ϕ_{sex}	p_t	1370.04	9	1388.04
ϕ_{sex}	p_{sex}	1441.08	4	1449.08
ϕ_{sex}	$p_{t,sex}$	1362.76	16	1394.76
$\phi_{t,sex}$	p_c	1361.50	15	1391.50
$\phi_{t,sex}$	p_t	1332.92	21	1374.92
$\phi_{t,sex}$	p_{sex}	1359.90	16	1391.90
$\phi_{t,sex}$	$p_{t,sex}$	1323.43	28	1379.43

Notes: In a standard SURGE analysis, the parameter ϕ corresponds to the estimated survival rate. When the capture histories are reversed, ϕ is the probability that a bird present on the site was also present in the previous year, and so $1 - \phi$ represents the rate of immigration or recruitment. The subscripts indicate the model used to generate the estimates. Subscripts c, t, and sex indicate models with constant parameters, parameters that change with time, and parameters that differ between the sexes, respectively. Thus the model denoted by $\phi_{t,sex}$ and p_c is a model in which the immigration rates are estimated separately for each combination of sex and year, but a single resighting rate is estimated throughout the study period and for both sexes; p is the recapture probability, Dev. is the deviance associated with the model, and NP is the number of parameters in the model. The model with the lowest Akaike Information Criterion (AIC) value is indicated in boldface.

TABLE C3. Maximum likelihood estimates and 95% confidence intervals for the parameter estimates of immigration rates and resighting rates for the best fitting model.

Years	Estimate	95% confidence interval Lower limit	Upper limit	SD
A) Probability that a bird on the site was also present in the previous year (ϕ)				
1986–1987	0.819	0.650	0.917	0.067
1985–1986	0.812	0.688	0.894	0.052
1984–1985	0.814	0.720	0.881	0.041
1983–1984	0.665	0.549	0.763	0.055
1982–1983	0.484	0.393	0.576	0.047
1981–1982	0.682	0.460	0.844	0.102

Note: study area expansion this year is probably the reason for the high estimate of immigration.

B) Recapture probabilities (p)				
1985–1986	0.916	0.798	0.968	0.040
1984–1985	0.902	0.800	0.955	0.038
1983–1984	0.754	0.618	0.853	0.060
1982–1983	0.797	0.661	0.887	0.058
1981–1982	0.483	0.220	0.639	0.081
Joint estimates of β (product of ϕ and p)				
1980–1981	0.547	0.225	0.834	0.180

TABLE C2. Statistical comparison of the model with the lowest Akaike Information Criterion with models that (A) have additional explanatory components and (B) have fewer explanatory components. P values correspond to the changes in deviance due to the change in model (ΔDev.), which are asymptotically distributed as a chi-squared distribution with degrees of freedom corresponding to the change in the number of parameters (ΔNP).

Models		Deviance	NP	ΔDev.	ΔNP	P	
ϕ_t	p_t	1337.17	14				
A) vs. models with more parameters							
A1) $\phi_{t,sex}$	$p_{t,sex}$	1323.43	28	13.73	14	0.470	compare with full sex and time model
A2) ϕ_t	$p_{t,sex}$	1327.55	21	9.62	7	0.211	compare with adding sex difference in resighting
A3) $\phi_{t,sex}$	p_t	1332.92	21	4.24	7	0.751	compare with adding a sex difference in immigration rate
B) vs. models with fewer parameters							
B1) ϕ_c	p_t	1370.85	8	33.68	6	0.00001	no time dependence in ϕ
B2) ϕ_t	p_c	1365.69	8	28.53	6	0.00007	no time dependence in p