ESTIMATING POPULATION SIZE IN ASYNCHRONOUS AGGREGATIONS: A BAYESIAN APPROACH AND TEST WITH ELEPHANT SEAL CENSUSES

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ABSTRACT

Many organisms reproduce in temporary aggregations where estimates of colony size can be made by direct counts. When individuals are not synchronous, however, early breeders depart before the last arrive, so counts underestimate the total breeding population. We present a model describing a colony's census as a function of arrival, breeding tenure, and the correlation between them, and we use it to illustrate how variance in arrival and tenure affect the census. Counts of breeding female northern elephant seals (*Mirounga angustirostris*) from 1975 to 2007 were used to test the model. Four of the model's parameters—population size, mean and variance of arrival date, and the correlation between arrival date and breeding tenure—could be estimated from census data using a Bayesian approach; prior estimates of two other parameters—mean tenure and its variance—had to be used to avoid overparameterization. The model's predictions fit observed censuses well and produced reliable estimates of population size and arrival behavior, showing that the maximum census was 8%–16% below the total number of breeding females. This method could be used for estimating abundance in any asynchronous aggregation, given independent information on one of the defining distributions: arrival, tenure, or departure.

Many marine mammals and birds assemble in compact, isolated colonies where direct counts of individuals are possible. These colonies are windows into the population biology of creatures that are otherwise aquatic and difficult to observe, and are especially useful where breeding individuals can be counted so production of offspring can be assessed. Generating an estimate of total colony size works best where breeding is synchronous so that a single count includes all individuals associated with the colony. When there is asynchrony, however, a single count underestimates the entire population because there is never a time when all individuals are present. We produce here a general method for estimating the breeding population in this situation and develop it for the northern elephant seal (*Mirounga angustirostris*). Elephant seals offer several traits ideal for modeling the size of a breeding colony: Females collect in discrete groups that are easy to count, they move little during the breeding period, and nearly every female ashore gives birth to a single pup so that the female population reflects pup production (Cooper and Stewart 1983, Reiter and Le Boeuf 1991, Slip and Burton 1999).

Our model describes the number of animals in a colony as a function of arrival time and breeding tenure of individuals. It incorporates asynchrony as variance in both, and we explore the impact of asynchrony on population counts. We then fit the model's parameters to breeding counts using inversion (Tarantola 2005), searching for model parameters that most closely predict observed censuses. This allows us to test whether the model accounts for observed censuses but, more important, produces useful estimates: total breeding population and the arrival behavior of individuals.

We developed the general framework of this model in the early 1970s and applied it to estimating the population size of northern elephant seals at the Año Nuevo colony in central California. Later, Rothery and McCann (1987) published a similar model independent of our work, and similar modeling approaches have been developed in asynchronous insect populations (Zonneveld 1991). Here we extend these models by adding generality and using a Bayesian approach: We incorporate a variance in tenure and a correlation between arrival and tenure, we estimate the arrival distribution as well as population size, and we account thoroughly for error. We also evaluate the number of censuses needed for good estimates of population size and arrival behavior. Even though breeding asynchrony is widespread (Gochfield 1980, Ims 1990, Barba *et al*. 1995), its impact on population estimates from direct counts is rarely addressed, and our model may be useful for other assemblages of animals or plants.

Model for an Asynchronous Colony

Assume that individuals collect in a breeding colony each season, and call the period of time each individual remains in the colony its breeding tenure. When individuals depart, they do not return until the next season. If individuals are exactly synchronous, then the entire population is present in the colony at the same time. We consider the alternative, where individuals arrive at different times and where some depart before others arrive. In this situation, no count reveals total colony size.

A model for the census. The core of the model states that the number of individuals present in the colony is the number that has arrived minus the number that has

departed. Use $C(T)$ to denote the number of animals present on date T; $F_a(T)$ and $F_e(T)$ the cumulative probability of arrival and departure (e for exit), respectively, on date T; and N the total population using the colony. $NF_a(T)$ is the cumulative number of animals that have arrived by date T, and likewise $NF_e(T)$ the cumulative number departed. Then

$$C(T) = NF_a(T) - NF_e(T). \tag{1}$$

This is equation 2 of Slip and Burton (1999), following Rothery and McCann (1987). Our aim is to estimate N; all we have is $X(T)$, the observed count on date T (an estimate of C). How much do we need to know about F_a and F_e in order to use X to estimate N?

Write $f_a(T)$ and $f_e(T)$ for the probability density functions accompanying the cumulative distributions $F_a(T)$ and $F_e(T)$, so

$$F_a(T) = \int_0^T f_a dx \quad \text{and} \quad F_e(T) = \int_0^T f_e dx. \tag{2}$$

Consider a third probability distribution for breeding tenure, $f_b(t)$: the probability an animal remains t days in the colony (t is a time interval, T a date). Intuitively, there is a simple relationship between arrival, departure, and tenure: Arrival and departure curves will be separated by the tenure, that is, the departure date is the sum of arrival date and tenure.

To be general, there must be a variance in breeding tenure. To accommodate this, the departure distribution must be calculated with an integral:

$$f_e(T) = \int_0^\infty f_b(t) f_a(T - t) dt. \tag{3}$$

The right side is a convolution of the distributions of arrival and tenure. It states that the probability of departing on date T is found from the probability of arriving t days earlier, summing over all values of t. Imagine that the average tenure is 20 d, but some animals stay 19 or 21 d. Then the number departing on date 25 is the number arriving on date 4 multiplied by the probability of staying 21 d, plus the number arriving on date 5 multiplied by the probability of staying 20 d, plus the number arriving on date 6 multiplied by the probability of staying 19 d.

One additional generalization is needed. Equation (4) rests on the assumption that the breeding tenure does not correlate with arrival date. If it does, then $f_b(t)$ must be written as $f_b(t|T)$, or the probability that an animal arriving on date T remains t days. Then

$$f_e(T) = \int_0^\infty f_b(t|T - t) f_a(T - t) dt. \tag{4}$$

Combining Equations (1)–(4) produces a model for the census as a function of the distribution of arrival dates, $f_a(T)$, and the distribution of breeding tenure, $f_b(t)$:

$$C(T) = N \int_0^T f_a dx - N \int_0^T \int_0^\infty f_b(t|x - t) f_a(x - t) dt dx. \tag{5}$$

Rothery and McCann (1987) used a similar approach for estimating the breeding population of southern elephant seals but did not incorporate variance in tenure nor the correlation between arrival and tenure. Then $f_e(T) = f_a(T - \mu_b)$ because the number departing on date T is the same as the number arriving μ_b days earlier where μ_b is the tenure (which in the simple case is a constant for all animals on all dates). Only one distribution, $f_a(T)$, is required to predict $C(T)$:

$$C(T) = N \int_0^T f_a(x)dx - N \int_0^T f_a(x - \mu_b)dx. \qquad (6)$$

Variance in Arrival and Departure

Synchrony in behavior, breeding or otherwise, is defined by variance in dates, and the equations above describe variance in arrival, tenure, and departure. Recognizing departure as the sum of arrival and tenure allows a precise relationship between the variance of the three distributions to be derived. Call the variance in arrival σ_a^2 and the variance in breeding tenure σ_b^2, and because we allow a correlation between the two, their covariance, $cov(a, b)$, is nonzero. Departure date $e = a + b$, and the variance in departure date, σ_e^2, is

$$\sigma_e^2 = \sigma_a^2 + \sigma_b^2 + 2cov(a, b). \qquad (7)$$

This relates synchrony in departure (or the termination of breeding) to synchrony in arrival (onset) and synchrony in tenure. It demonstrates that no qualitative generalization is possible. Any variance in tenure, σ_b^2, tends to make departure more variable than arrival, but the covariance can be negative and thus reduce the variance in departure relative to arrival.

Specifying the Model

The model is generic to this point, making no assumptions about functions describing arrival, tenure, or departure, nor the correlation between arrival and tenure. To illustrate or test, we need to specify distributions. Consider a normal distribution to describe arrival. Furthermore, assume that breeding tenure, b, is linearly related to arrival date, a, and normally distributed at a given arrival date, that is, $b = q(a - \mu_a) + \mu_b + \epsilon$, where μ_a is mean arrival date, μ_b is mean tenure, $\epsilon \sim Norm(0, k^2)$, and k^2 is the variance in tenure at a fixed arrival date; $k^2 \leq \sigma_b^2$ because of the correlation between b and a.

If k^2 is constant across arrival dates—homoscedasticity—then

$$\sigma_e^2 = (1 + 2q)\sigma_a^2 + \sigma_b^2. \qquad (8)$$

This follows from $cov(a, b) = q\sigma_a^2$ and $\sigma_b^2 = q^2\sigma_a^2 + k^2$. Given homoscedasticity, the distribution of breeding tenure, f_b, is normal, and thus, the distribution of departures, f_e, is also normal because departure date $e = a + b$. The mean of the departure distribution, μ_e, is $\mu_a + \mu_b$, and its variance is given by Equation (8). Given these assumptions and the six model parameters—total colony size N, mean arrival date μ_a, SD of arrival σ_a, mean tenure on the colony μ_b, its SD σ_b, and the regression

slope q between a and b—arrival and departure distributions are fully specified (Table 1).

Censuses can then be simulated by subtracting one cumulative normal distribution (departure) from another (arrival), following Equation (1). If every individual remains on the colony for exactly the same period ($\sigma_b = q = k = 0$), the departure distribution has the same variance as the arrival distribution but has a mean displaced from the arrival mean by the tenure. This is the model of Rothery and McCann (1987). The resulting census curve is unimodal and symmetric, but the shape depends on whether arrival and departure overlap: With overlap, the census is bell-shaped (dashed curves in Fig. 1); without such overlap, the census curve is broad and flat-topped, with the entire population present for a time.

If there is variance in tenure, then departures are more spread than arrivals and the right tail of the census is extended (solid curves, Fig. 1). On the other hand, with a negative relation q between arrival and tenure, departures have less variance than arrivals, and the census declines abruptly (dotted curves, Fig. 1). Interestingly, σ_b and q can interact to restore a symmetrical census, that is, a negative correlation of just the right magnitude can balance the variance in tenure and produce a departure distribution identical to arrival. This holds if $q = -\frac{1}{2}\frac{\sigma_b^2}{\sigma_a^2}$ (Equation 8). Thus, the parameters σ_b and q interact, they cannot both be estimated from census data alone. We expand on this problem below.

There is another crucial parameter interaction: total colony size N and mean tenure μ_b. The interaction is illustrated by producing near-identical census curves for different values of N and μ_b (Fig. 2). One set of curves was calculated with $N = 1,000$, the other with $N = 1,155$. In order to produce matching censuses, μ_b was adjusted downward by a corresponding 15%, N and μ_b interact linearly. (We produced the two matching census curves using parameter-fitting procedures described later.) Given many $N > 1,000$, we assert that there is a $\mu_b < 30$ that will produce a matching census. Again, this means that N and μ_b cannot both be estimated using census data, one must be known from independent information.

Applying the Model

The northern elephant seal. Our analysis of the model employs data from the northern elephant seal's Año Nuevo rookery in central California (37°06′N, 122°20′W). The elephant seal was overhunted in the nineteenth century but has recovered since, and we are interested in documenting its recolonization (Le Boeuf *et al.* 1974, Le Boeuf 1981, Cooper and Stewart 1983, Stewart *et al.* 1994).

Breeding Colonies

Elephant seal females form tight aggregations while breeding (Le Boeuf *et al.* 1972, Reiter *et al.* 1981, McMahon and Bradshaw 2004). Pregnant females haul out sometime between early December and mid-February, give birth about 6 d later, and nurse their pups about 25 d (Reiter *et al.* 1981, Ortiz *et al.* 1984). The nursing period, and hence tenure, varies with female age and arrival (Reiter *et al.* 1981). While nursing, females move little and do not enter the water; however, prior to birth, females sometimes move. Toward the end of the nursing period, females copulate then return to sea, leaving weaned pups behind, and migrate long distances to feeding grounds (Le Boeuf *et al.* 1993, 2000).

Table 1. Parameters of the colony census model, assuming a normal distribution for arrival dates and tenure on the colony, and a linear correlation between arrival and tenure. All six parameters were fitted, two with a restrictive prior. The column *parameterization* gives the probability distributions; all are normal, with mean and SD given in parentheses. Arrival and tenure distributions were defined, and the departure distribution and the predicted census were calculated from them.

| Parameter	Symbol	Parameterization	Fitted parameter (prior)	Calculation
Observed census on date T	X_T			
Total breeding population	N		N(flat > 0)	
Arrival	A		μ_a(flat > 0)	
Probability density	$f_a(T)$	$f_a = \text{Norm}(\mu_a, \sigma_a)$	Σ_2(flat > 0)	
Breeding tenure	B	$b = q(a - \mu_a) + \mu_b + \varepsilon$	$\mu_b[\text{Norm}(31.06, 0.271)]$	$k^2 = \sigma_b^2 - q^2\sigma_a^2$
Probability density	$f_b(t)$	$\varepsilon \sim \text{Norm}(0, k^2)$	$\sigma_b[\text{Norm}(3.77, 0.193)]$	
		$f_b = \text{Norm}(\mu_b, \sigma_b)$	$q[\text{flat over} (-0.51, 0.32)]$	
Departure	E			$\mu_e = \mu_a + \mu_b$
Probability density	$f_e(T)$	$f_e = \text{Norm}(\mu_e, \sigma_e)$		σ_e from Equation 8
Predicted census on date T	C_T			from Equations. 1, 2
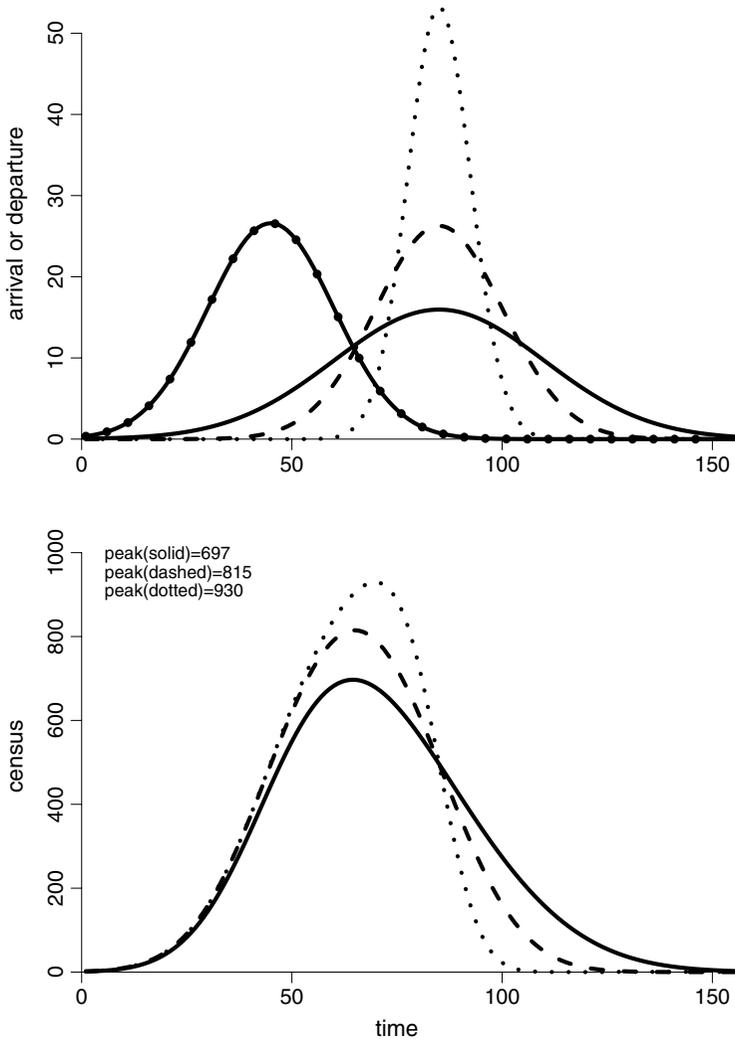
Figure 1. Simulated censuses in an asynchronous breeding colony, with arrival and breeding tenure normally distributed and a linear correlation between arrival and tenure. These illustrate the impact of altering the departure distribution while the arrival distribution is not changed. (A) Arrival (animals d^{-1}) is the single-beaded curve on the left, peaking at day 45; three alternate departure distributions (also animals d^{-1}) peak at day 85. Departure is tighter than arrival (dotted), more spread than arrival (solid), or has the same variance as arrival (dashed). The total colony size in all three simulations was $N = 1,000$. Arrival curve has mean $\mu_a = 45$ and SD $\sigma_a = 15$. Three departure curves, all based on mean breeding tenure $\mu_b = 40$: (1) solid curve based on an SD of tenure $\sigma_b = 0.5 \, \mu_b$ and correlation $q = 0$ between arrival date and tenure; (2) dotted curve based on $\sigma_b = 0$ and $q = -0.5$; (3) dashed curve, based on $\sigma_b = 0.5 \, \mu_b$ and $q = -0.5$. (B) Corresponding census curves (total animals present each day). With tight departure, females leave fast and the census declines abruptly (dotted); with spread departure, the census declines more slowly than it increases (solid); a symmetrical census occurs when variance in departure matches variance in arrival (dashed).
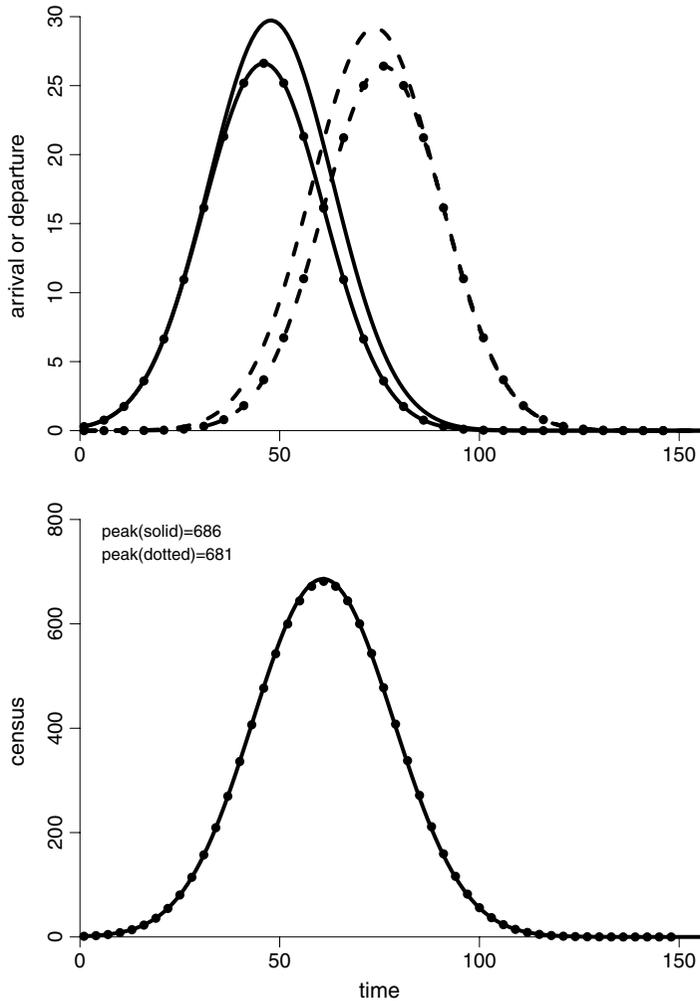
Figure 2.   A demonstration that near-identical census curves can result from quite different colony sizes. (A) Arrival and departure (animals d^{-1}). Two alternate arrival functions to the left (solid curves, one is beaded) and two departure functions to the right (dashed, one is beaded). In the unbeaded arrival curve, $\mu_a = 47.8$, $\sigma_a = 15.5$; in the beaded, $\mu_a = 46$, $\sigma_a = 15$. The unbeaded departure curve results from $\mu_b = 26$, $\sigma_b = 0.02 \, \mu_b$, $q = -0.018$; the beaded from $\mu_b = 30$, $\sigma_b = 0.02 \, \mu_b$, $q = 0.007$. For the unbeaded (taller) curves, the total colony size was $N = 1,155$, while for the beaded (shorter), $N = 1,000$. (B) Census curves (total animals present each day), one beaded and one not; they are nearly identical on every day.

Census Methods

We carried out counts of elephant seals at Año Nuevo regularly throughout the breeding season, December through March, from 1968 to 2007 (Le Boeuf *et al*. 1974, Reiter *et al*. 1978, Le Boeuf 1981). Pups were first recorded on Año Nuevo Island in 1961 (Poulter and Jennings 1966), and a single pup was born on the adjacent

mainland in 1975 (Le Boeuf and Panken 1977). By 1995, single counts on the mainland exceeded 1,900 females, with 500 more on the island. We focus our test of the model on mainland groups, which are counted more frequently than island groups due to easier access.

Observers can stand 5 m from female aggregations without causing disturbance, and most of the beaches at Año Nuevo have 3–6-m cliffs or dunes adjacent, providing elevated viewing angles from which all animals can be seen. Animals move seldom enough that counts of every individual are possible. Adult females, adult and subabult males, and pups differ in size and color and can be counted separately (Le Boeuf *et al*. 1974). The main limit to census accuracy is keeping count in large groups: For beach harems that are long and linear, this is not difficult. The largest group, however, is more than 10 females deep and includes up to 700 females, so it is necessary to use imaginary lines through objects in the harem or in the distance as placeholders.

Breeding Tenure of Females

Because the breeding tenure of females at the colony is critical to the model, we use an expanded data set to revisit estimates originally published by Reiter *et al.* (1981). In each season, tagged females were dye marked on arrival and their subsequent presence on the rookery recorded (Le Boeuf *et al*. 1972, Reiter *et al*. 1981). Data are available since 1968, but only subsequent to 1980 have daily sightings of marked females been computerized. The time between first and last observations of individual females in those years provides an estimate of the breeding tenure: An animal first seen on 10 January and last seen on 29 January was present 20 d. This estimate is biased, though, because animals may be present but unobserved before the first or after the last observation.

We judged the magnitude of the bias by simulating female sightings, assuming each individual has a sighting probability, p, per day. In the simulation, each animal has a known arrival date, a, drawn from a normal distribution with mean 0 and variance 10, and a known breeding tenure, b, drawn from a normal distribution with mean 31 and variance 14.4. The departure date was determined as $e = a + b - 1$. For each day during the tenure, a random draw on the sighting probability, p, determined whether the simulated animal was seen; call the first sighting date $\hat{a}$ and the last $\hat{e}$. An estimate of the breeding tenure is $\hat{b} = \hat{e} - \hat{a} + 1$, and an estimate of the sighting probability is $\hat{p} = \frac{s}{\hat{b}}$, where s is the total number of days sighted. The bias of estimated tenure is $\hat{b} - b$, which we can prove is $\frac{2(1-p)}{p}$. Unfortunately, the true sighting probability p is not known, only the biased estimate $\hat{p}$. In simulations, animals for which $0.9 \leq \hat{p} < 1$ had a bias of ~0.1 d, consistent with $\frac{2(1-\hat{p})}{\hat{p}}$ as long as $\hat{p} \sim p$. For simulated females with $p = 1$, the bias was quite high because animals with shorter tenure were more likely to be seen every day. This suggests that we can get a nearly unbiased estimate of tenure using those females seen at least 90% of the days present but not 100%.

There were 191 female breeding records meeting these criteria: 14 in 1980, 17 in 1994, 25 in 1995, and 146 in 1996; no other year had >7. Because there was considerable overlap in confidence limits (based on standard *t*-tests) among those 4 yr, all data were combined in one large sample. Because our overall approach is Bayesian, we used a Gibbs sampler to estimate mean tenure, μ_b, and its SD, σ_b (Gelman *et al.* 1995). The posterior distribution of each parameter appeared normal and can be described by the estimated mean and standard errors; these became prior

distributions when fitting the model (Table 1). We also used a standard Gibbs sampler for normal regression (Gelman *et al.* 1995) to estimate the slope of the regression between tenure and arrival, q, and the variance in tenure at a given arrival date, k^2. In this sample, the correlation was weak, $k^2 \sim \sigma_b^2$, and we used the latter in subsequent calculations.

Fitting the Model to Seal Censuses

As illustrated earlier (Fig. 1, 2), specifying distributions of arrival and tenure allows a census curve C to be predicted, given six parameters (Table 1). We need the inverse though: We want to estimate the six parameters given observed censuses, X. To accomplish this, we sought the parameters that created the closest fit of all predicted censuses C to the observations X, where closeness of fit was defined by likelihood: the probability of observing X given C. We adopted a Bayesian approach, using the likelihood function to estimate posterior distributions for each of the parameters.

Likelihood

The probability of an observed count $X(T)$ on date T is given by a Poisson distribution with mean $C(T)$, where $C(T)$ is the model's predicted count on date T given the six model parameters (Equation A1 in the Appendix). The logarithm of this likelihood was summed across all dates on which censuses were carried out in one season. This total log-likelihood is thus a function of the six model parameters as well as the observed counts, and it gives a measure of how well any set of parameters describe the data. In a maximum-likelihood approach, the parameters producing the highest likelihood possible are located. A Bayesian approach differs by seeking not just the one best parameter set but all parameter combinations that fit the data reasonably well, where "reasonable" has a quantitative grounding in probability. Before embarking on the Bayesian calculation, we tested the model with standard numerical searches to locate optimum parameter values, using the *optim* function in the computer language R and its default Nelder–Mead algorithm (Bates *et al*. 2004).

With six parameters, however, the model is overparameterized: Two parameters are redundant because of the parameter interactions described earlier (N and μ_b; q and σ_b). This was evident during optimizations in which all six parameters were allowed to vary. The two redundant pairs were highly correlated, and the likelihood surface was flat over a wide range of each. By fixing two of the parameters, mean tenure μ_b and its standard deviation σ_b, the optimization worked consistently and had repeatable best estimates for the remaining four parameters. Fixing parameter values, however, ignores uncertainty in our knowledge of those parameters.

In a Bayesian framework, uncertainty in the redundant parameters can be handled using prior probability distributions based on independent quantitative information. As described above, normal posterior distributions for mean tenure μ_b and its standard deviation σ_b were estimated from marked females, and these became priors in model fitting. This means that the likelihood calculation for these two parameters must be expanded: It includes the Poisson likelihood multiplied by the prior probability (see the Appendix). This allows us to set the two extra parameters using independent data, so the model can be fitted, but also incorporates uncertainty in this prior knowledge. For the other four parameters, we assumed flat priors over all plausible values (see the Appendix for parameter limits).

A Gibbs Sampler and Credible Intervals

Instead of the optimization method, we employed a Gibbs sampler to generate model fits, allowing the priors to be incorporated and statistical confidence in all parameters to be calculated. The Gibbs sampler makes use of the same likelihood formulation given above, but instead of simply identifying the optimum, it samples the surface of the posterior distribution near the optimum. Its output is a chain of parameter values that represent a sample from the joint posterior distribution of the parameters. In all seasons, the sampler converged in 250–500 steps, and we used the parameter combinations from step 1,001 to 5,000. For each parameter, the mean plus 2.5th and 97.5th percentiles were taken from these 4,000 values. The mean values represent our single best parameter estimates, while the percentiles reveal confidence in each parameter, known in Bayesian analysis as credible intervals. These intervals incorporate uncertainty in the model, counting error, plus uncertainty in prior knowledge of μ_b and σ_b. Details of the sampler are given in the Appendix.

A Simpler Census Model

The model of Rothery and McCann (1987), described in Equation (6), was also fitted. It has three parameters, N, μ_a, and σ_a. To compare models, we used the Deviance Information Criterion (DIC), a measure of fit analogous to the Akaike Information Criterion that is easy to apply in a Bayesian framework (Burnham and Anderson 2002). DIC uses the log-likelihood of every parameter combination evaluated in the Gibbs sampler and penalizes for the number of parameters. Spiegelhalter *et al.* (2002) offer a detailed presentation, and the Wikipedia article (http://en.wikipedia.org/wiki/Deviance_information_criterion) provides a convenient formula.

Census Years

We have census data for every year from 1975 to 2007 at the Año Nuevo mainland, and we fit the model using all censuses between 19 December and 10 March in all but 3 yr. Censuses outside those dates often include nonbreeding or juvenile females. The model was not fitted in 1975 and 1976 because there were just one and three females respectively in those years. In 1983 a key assumption of the model was violated because a big storm at peak season inundated the Año Nuevo Island harem, and many females who had already pupped there moved to the mainland (Le Boeuf and Condit 1983). To complete the table of estimates, we calculated the total 1983 breeding population using a multiplier for individual counts prior to the storm on 27 January (unpublished data).

Rarefaction

In some seasons, fifty or more counts were available and in others as few as eight. To examine how the number of counts affected estimates, we rarefied samples. The interval from 1 January to 1 March was divided into five (or seven) equal sections, and one, two, or three censuses were chosen at random from each section. This produced five to fifteen well-spaced censuses to which we refit the census model. We examined rarefied data in 1980, 1984, and 1995, three seasons that had more than forty censuses.

Results

Breeding Tenure

The Gibbs sampler estimated mean breeding tenure in the sample of 191 closely observed females as $\mu_b = 31.06$ d, with a standard deviation $\sigma_b = 0.1212\mu_b$. The Gibbs chains also produced standard errors of those estimates, 0.271 and 0.193 d respectively (simply the standard deviation of each Gibbs chain). These parameters defined Gaussian prior distributions for μ_b and σ_b used in model fitting (Table 1). Both arrival date and breeding tenure were unimodal and symmetrically distributed, and there was a negative but nonsignificant correlation between them, $q = -0.05$, that is, tenure was 0.05 d shorter for every 1-d delay in arrival. García-Aguilar (2004) observed a mean tenure of 31 d and a weak negative correlation between arrival and tenure on a Mexican rookery.[1]

Breeding Season Censuses

The number of breeding females on the rookery followed a unimodal curve with a broad peak from 27 January to 2 February, and the general shape was maintained despite large variation in the peak count (Fig. 3). In 1978, the census rose abruptly compared to its descent. In other years, the census declined more rapidly than it ascended, although the difference is subtle and barely detectable by visual inspection. Consider 2004 as an example: The peak count as estimated from the model was on 29 January; the observed count 25 d earlier, on 4 January, was 425, but 25 d later (23 February), it was only 234.

Fits of the Model

The model produced a close fit to the census data throughout each season (Fig. 3). In nearly all years, the fitted parameters were consistent, predicting a census peak between 29 January and 1 February (Fig. 3, Table 2). In some years, discrepancies between observed and predicted counts were notable, for instance in 1993 and 1998, especially near the peak. Counts were higher than the model's prediction as often as they were lower, though. Since 2001, the model predicted every census closely with as few as eight censuses.

The peak census was eighty-three in 1978, and the estimated total female population was only eighty-one. This apparent anomaly is due to fluctuations in the counts: There was just one count of eighty-three, and most counts near the peak were eighty to eighty-one, suggesting that eighty-three was either an error or included two to three females that appeared only briefly. Because females arrived synchronously that year (the lowest SD of arrival of any season), departures were barely underway by 1 February and there was no overlap between arrival and departure (Fig. 3). Similarly, 1993 had a peak count higher than the estimated population, but the peak was a substantial outlier (Fig. 3).

[1] Personal communication from M. C. García-Aguilar, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), Km. 107 Carretera Tijuana–Ensenada, Código Postal 22860, Apdo. Postal 360, Ensenada, B.C. Mexico, August 2006.
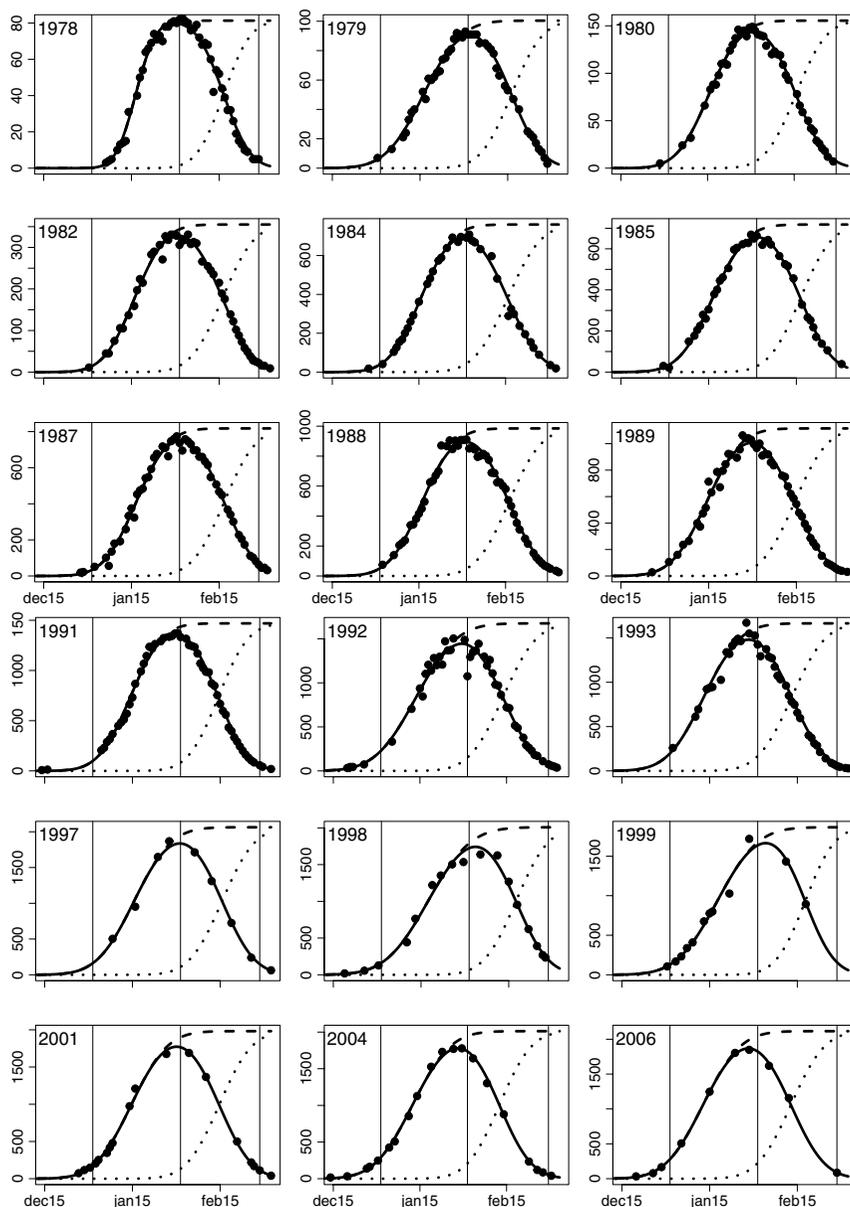
Figure 3.   The census model's predicted daily counts, calculated from the mean of each parameters' posterior distribution, compared to observed counts of breeding female elephant seals at the Año Nuevo mainland. The general shape and timing of the census curve was maintained from year-to-year despite twentyfold variation in colony size (note variation in scale of the vertical axis). The census model handled the entire range and was able to pick up small differences in shape, such as the abrupt rise in 1978. Seasons were chosen (eighteen of the thirty we tested) to illustrate both consistent data and good fits (*i.e.*, 1984, 2004) as well as erratic data with poorer fits (*i.e.*, 1993, 1998). Observed censuses (points) and best fits of the model (solid curves). Cumulative arrival (dashed) and departure (dotted) curves as estimated by the model. Vertical lines are at 1 January, 1 February, and 1 March.

Table 2. Size of the breeding colony of female elephant seals at the Año Nuevo mainland, 1975–2007. *N* (number of breeding females), mean (μ_a), and standard deviation (σ_a) of arrival date (in January), and the slope of the correlation between arrival date and breeding tenure (*q*) were estimated from the model (mean of posterior distributions); 95% credible intervals (CI) for *N* are shown (limits for other parameters were calculated but are not shown). The model also produced an estimate for the peak female count during each season along with the date of that count, and these are compared to those observed. The number of censuses throughout the breeding season and during peak season (17 January–4 February) is given. The 1983 estimate was not modeled but calculated using correction factors applied to counts before the storm on 27 January.

	Abundance		Arrival (Jan)		Correlation	Peak date		Peak census		No. censuses	
Year	*N*	CI	Mean	SD	arr.–tenure	Obs.	Pred.	Obs.	Pred.	Total	Peak
1975	1	not modeled									
1976	3	not modeled									
1977	16	14–18	13.4	9.9	−0.262	26 Jan	30 Jan	16	15	42	16
1978	81	78–85	16.5	5.6	0.159	02 Feb	30 Jan	83	80	53	19
1979	100	96–105	16.2	10.5	−0.265	31 Jan	02 Feb	93	90	46	19
1980	155	150–161	15.5	9.0	−0.146	31 Jan	31 Jan	149	143	45	19
1981	296	287–306	17.0	7.2	−0.153	29 Jan	01 Feb	343	287	32	13
1982	355	345–366	16.1	8.6	−0.070	29 Jan	31 Jan	331	328	51	16
1983	503	383–624								46	15
1984	760	742–778	15.6	8.9	−0.036	02 Feb	31 Jan	708	691	37	13
1985	718	702–736	16.4	9.3	−0.145	30 Jan	01 Feb	669	656	39	14
1986	850	832–869	15.7	8.4	−0.017	02 Feb	31 Jan	818	788	40	16
1987	818	802–835	16.7	9.0	−0.104	31 Jan	01 Feb	774	751	57	18
1988	985	965–1,006	16.1	9.2	−0.094	01 Feb	01 Feb	911	892	57	17
1989	1,115	1,094–1,137	14.3	9.6	−0.134	27 Jan	30 Jan	1,063	1,005	53	17
1990	1,208	1,187–1,233	13.5	10.3	−0.137	27 Jan	29 Jan	1,094	1,064	61	16
1991	1,469	1,445–1,496	14.2	8.9	−0.154	31 Jan	30 Jan	1,373	1,360	55	15
1992	1,675	1,641–1,721	13.6	11.5	−0.240	27 Jan	30 Jan	1,504	1,444	47	16
1993	1,665	1,632–1,701	12.9	10.1	−0.147	28 Jan	29 Jan	1,672	1,473	45	13
1994	1,665	1,632–1,701	14.8	10.7	−0.266	03 Feb	31 Jan	1,554	1,484	50	16
1995	2,093	2,056–2,135	16.0	11.3	−0.315	29 Jan	02 Feb	1,922	1,849	40	10
1996	1,821	1,782–1,865	15.1	9.8	−0.124	03 Feb	31 Jan	1,543	1,633	22	4
1997	2,063	2,007–2,117	15.6	10.3	−0.197	28 Jan	01 Feb	1,868	1,832	9	2
1998	2,009	1,960–2,053	17.5	11.8	−0.310	30 Jan	03 Feb	1,535	1,742	18	4
1999	1,865	1,809–1,928	17.7	11.3	−0.358	29 Jan	04 Feb	1,718	1,662	12	2
2000	1,885	1,833–1,933	17.0	10.7	−0.199	01 Feb	02 Feb	1,630	1,653	18	6
2002	1,976	1,913–2,041	13.2	10.4	−0.165	29 Jan	29 Jan	1,738	1,740	12	1
2003	2,162	2,101–2,228	11.7	10.0	−0.159	28 Jan	28 Jan	1,902	1,933	10	2
2004	2,012	1,963–2,059	12.3	10.7	−0.226	30 Jan	29 Jan	1,778	1,776	19	5
2005	2,032	1,973–2,094	13.2	10.8	−0.234	29 Jan	29 Jan	1,795	1,788	9	2
2006	2,115	2,062–2,173	12.7	10.4	−0.174	29 Jan	29 Jan	1,848	1,868	10	2
2007	1,985	1,929–2,047	13.6	9.9	−0.201	26 Jan	30 Jan	1,760	1,795	8	2

Estimated Colony Size

In 1977, the first year for which the model was fitted, only sixteen females were counted at the peak of the season, and the model estimated sixteen for the total colony size. In 2003 the peak count was over 1,900 females and the total colony size over 2,200 (Table 2). Credible intervals on estimated colony size were ±2%–4% in most years and only above 4% in a few years (Table 2). Uncertainty in the breeding tenure generally caused less than half the uncertainty in colony size. Ignoring it, credible intervals were ±1%–3%.

Estimated Arrival

In the late 1970s and early 1980s, the mean arrival date was 15–17 January, but it crept forward and after 2000 was 12–15 January. Credible intervals for mean

arrival were ± 0.3–0.6 d in most years. In 1978 female arrival was most abrupt, visually evident in Figure 3. Correspondingly, the SD of arrival date in 1978 was 5.6 d (credible intervals ± 0.7 d). In most years, the SD was 9–11 d (credible limits ± 0.2–0.6 d).

Estimated Correlation Between Arrival and Breeding Tenure

The fitted slope q of the correlation was usually negative, often between -0.10 and -0.25 (Table 2), and in most years, credible limits excluded zero. These are slightly steeper than the estimate of -0.05 based on marked females. The negative correlation was necessary to accommodate the tendency for censuses to decline more rapidly than they rose, as described above for 2004. In 1978 there was a positive correlation: Late-arriving females remained longer, and the census clearly declined more slowly than it ascended (Fig. 3).

Estimated Breeding Tenure and Its Standard Deviation

In all years, estimated values of μ_b and σ_b were dominated by the prior distributions: Credible intervals on each broadly overlapped the independent of estimates of $\mu_b = 31.06$ and $\sigma_b = 0.1212\mu_b$. This is what should result given that these two parameters are redundant to the model: Census data alone provide little information about tenure, so the priors dominate.

Overlap in Arrival and Departure

The total colony size, N, exceeded the estimated peak census by 8%–16% in most years, meaning there was 8%–16% overlap between arrival and departure. Three early years had less overlap, especially 1978, where the estimated peak was only one less than N (eighty *vs.* eighty-one; the observed peak, eighty-three, was an outlier). The degree of overlap was strongly associated with the variance in arrival dates. When $\sigma_a = 9$, the overlap was only 8%, but at its broadest $\sigma_a = 12$, overlap was 16%. Since 1992 the standard deviation in arrival was always >10 d and the overlap between arrival and departure >10%.

The Model of Rothery and McCann

In all 30 yr, the full model was a better fit (higher DIC) than the Rothery and McCann (1987) model in which every female has the same breeding tenure. This demonstrates that the correlation parameter, which was usually negative, improved the fit of the model. In nearly all years, arrival according to the full model was later and more variable than according to the simple model (mean arrival differed by half a day, with a standard deviation differing by 0.5–1 d). The two models, however, produced nearly identical estimates of population size, differing by <2% in most years and never by >3%.

Rarefaction

With random subsets of censuses spaced evenly during January and February, the estimated breeding population was accurate with as few as five censuses. For

instance, the estimate from all thirty-seven censuses in 1984 was 754 females; with five different random sets of five censuses, the estimates were 750, 752, 758, 770, and 797. As expected, the variance of the estimates (calculated with the Gibbs sampler) was inversely related to the number of censuses. In the 1984 example, the coefficient of variation was 2.5% with five censuses but 0.9% with thirty-seven censuses.

DISCUSSION

Synchrony in breeding is commonly measured using the variance of reproductive onset (Gochfield 1980), but breeding tenure and departure also influence synchrony. If tenure is much longer than the variation in onset, synchrony is high because all breeders will be present together; likewise, departure can be more or less synchronous than arrival. We present a framework for quantifying the interaction of all sources of asynchrony and describing the resulting population of a colony through time. The previous model of colony size under asynchrony (Rothery and McCann 1987) covered a specific case, where departure matches arrival, and can produce only a symmetric census curve.

Our modeling approach allows colony size and arrival behavior to be estimated from counts alone. It can describe asymmetry in a census curve by fitting both the variance in arrival date and the correlation between arrival and breeding tenure. Independent estimates of breeding tenure as well as its variance must be available. Counts alone cannot yield estimates of both population size and tenure, and uncertainty in the estimate of tenure produces error in the estimate of colony size, a fact that has been disregarded in previous modeling attempts.

The fact that asynchrony is relevant to estimates of colony size appears to be frequently ignored. In temperate breeding birds, this is probably because the length of the individual breeding period substantially exceeds the SD in initiation dates (SD typically <12 d; see Burger 1979, Brown and Brown 1987, Murphy and Schauer 1996), and colony size can be estimated by simply counting nests. But in tropical birds, the SD of hatching dates can be up to 40 d (Reville 1988, Webster 1994). At another extreme, individual mayflies breed for 30 min (Sweeney and Vannote 1982) while the whole population breeds over 12–16 d. In all cases, our model could precisely define the overlap among breeders and determine whether all are present together. Nevertheless, the only cases we know where careful modeling has been used to assess the impact of asynchrony on population estimates are in pinnipeds (Rothery and McCann 1987, Trites 1992, Slip and Burton 1999) and insects (Zonneveld 1991). One very different case that poses the same problem is flower production. For example, Aizen (2001) showed daily flower counts following a bell-shaped distribution over 36 d, while individual flowers lasted 3.65 ± 0.21 d. From these data, we could estimate flower-opening date (arrival) and total flower production (colony size) using our model.

Galimberti and Sanvito (2001) tested the simpler model of Rothery and McCann (1987) and concluded that it predicted colony size of elephant seals well. The simpler version does not incorporate variation in the breeding tenure nor correlation between tenure and arrival. The fact that it is still adequate for estimating elephant seal abundance appears to be fortuitous: Modest variation in breeding tenure is counteracted by a tendency for late arriving females to spend less time in the colony. The analytical formulation for the variance in departure dates in Equation (7) shows exactly how the two terms counteract. Departure would be more variable than arrival due to variance in breeding tenure. In elephant seals, the SD in arrival is about 10–11 d, and the SD

in tenure is about 4 d, so the SD in departure would be 11–12 d in the absence of any correlation between tenure and arrival. But the negative covariance term diminishes the SD in departure: If the correlation were −0.08, it would just balance the variance from tenure, so that departure and arrival would have identical variances. The correlation was generally stronger than this so that seals departed more rapidly than they arrived, which is why the simpler model was a poorer fit.

Errors in our female counts near peak season were evident in many years, not surprising given the size and density of the largest harems (700 females in 5,000 m^2). We believe that the model describes the female census accurately, and that the discrepancies are unbiased counting errors; indeed, the model reveals these errors. The large number of counts in certain years served to overcome these occasional errors. In the 3 yr tested, predictions based on five well-spaced counts produced accurate estimates of colony size and arrival time. Barring large errors, we conclude that five to seven counts are sufficient; the risk with few counts, of course, is that a single large error has a big impact.

Other errors could result if the model's assumptions were faulty. We describe the arrival date and breeding tenure of female elephant seals as normally distributed, largely because observations of individuals support this. Symmetrical and bell-shaped reproductive onset has been described in squirrels (O'Donoghue and Bouton 1995), ungulates (Sinclair *et al*. 2000), many birds (Burger 1979, Wiklund 1984, Brown and Brown 1987, Webster 1994), mayflies (Sweeney and Vannote 1982), and plants (Rabinowitz *et al*. 1981), and the normal distribution has been used in models for birds (Birkhead and Biggins 1987) and trees (Bronstein *et al*. 1990). In butterflies, Zonneveld (1991) justified a normal distribution of emergence dates but used a logistic for mathematical convenience. Skewed distributions of reproductive onset, though, are seen in birds (Burger 1979, Brown and Brown 1987, Murphy and Schauer 1996, Galetto *et al*. 2000) and plants (Rabinowitz *et al*. 1981, Malo 2002). In gray seals, *Halichoerus grypus* (Boness *et al*. 1995), and northern fur seals, *Callorhinus ursinus* (Trites 1992), the distribution of birth dates was right skewed. The model we presented, though, can accommodate any distributional form and could be tested where onset is skewed. Galimberti and Sanvito (2001) noted a different discrepancy in the arrival distribution of southern elephant seals: fatter tails than a normal distribution accommodates. We looked closely at the earliest and latest arrivals at Año Nuevo, and it appears that a few females arrive earlier than a normal distribution predicts but that the latest arrivals are accommodated. We have not evaluated how slight nonnormality would impact estimates from the model.

We also based our estimates on the assumption that breeding tenure in female elephant seals is consistent from year to year. Breeding tenure is crucial because there is a linear interaction in the model between tenure and estimated abundance: Overestimating tenure by 10% will cause a 10% underestimate of N, *etc*. (Galimberti and Sanvito 2001). Evidence from marked females suggested that a mean breeding tenure of 31 d held in four different years, and García-Aguilar (2004) observed marked females in a harem 1,000 km to the south in Mexico and also found a mean tenure of 31 d in two different years. Moreover, our estimates of N incorporate uncertainty in our knowledge of breeding tenure. But other colonies, particularly new ones with only a few females, may differ in mean tenure, and we must remain cognizant of this as a source of error.

In many species of animals or plants, documenting the tenure—whether breeding tenure in a colony of seabirds or flower life span on a tree—may be difficult and time-consuming. An obvious example would be where censuses are made from airplanes,

so nothing is known about individual behavior. It would be useful to develop a tool for estimating breeding population that circumvented the need for independent knowledge about breeding tenure. Our model could work without knowing the distribution of breeding tenure, as long as either arrival or departure distributions are known, and these might be easier to estimate in some species. Perhaps even less information is necessary; for instance, the date of the first departure might add enough information to allow the full model to be fit. In the meantime, the model can be applied to any situation, regardless of the degree of asynchrony and symmetry, as long as a few counts are available throughout the breeding period and given independent evidence on the length of time individuals remain in a colony.

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APPENDIX: A GIBBS SAMPLER FOR FITTING THE CENSUS MODEL

The Gibbs sampler is based on the likelihood of observing X animals given the model's prediction, C:

$$P[X|C(\theta)] = \text{Pois}(X, \text{mean} = C) = \frac{C^X}{C!}e^{-c}. \qquad (A1)$$

P is the conditional probability of observing X given C because C is calculated from the six model parameters, here designated θ (Equation 1, Table 1), P is conditional on $C(\theta)$. The log of the likelihood for all counts (in one season) is the sum of the log

likelihoods for each day:

$$L = \sum_T \ln P\left[X_T | C_T(\theta)\right]. \tag{A2}$$

To bound the parameter search, the likelihood function was set to 0 when a parameter fell outside predefined limits. Except for the correlation parameter, q, all parameters were bounded below by 0 but had no upper bound; q was constrained to the range $(-0.51, 0.32)$, chosen because those values prevent the expected tenure for any arrival date from being <15 or >45 d.

The tenure parameters, μ_b and σ_b^2, were constrained by tight priors, and the likelihood of Equation A2 must be multiplied by the priors for those two parameters (steps 6 and 7 below). For other parameters, the prior was assumed to be flat, apart from upper and lower bounds. We had no justification for prior information on four of the parameters, and the Metropolis algorithm does not require it; because the Gibbs chains converged, we can be secure that the estimated posterior distributions were proper.

The Gibbs sampler proceeds as follows.

1. Choose initial parameter values $\theta^{[1]}$. Initial values are arbitrary as long as the likelihood can be calculated. In practice, we used these initial values: population size, $N^{[1]} = 1.14X_{\max}$ (where $X_{\max}$ is the maximum count); mean arrival, $\mu_a^{[1]} = 43$ (where day 1 = 1 December, so day 43 is 12 January); SD of arrival, $\sigma_a^{[1]} = 11$; the slope of the correlation between tenure and arrival, $q^{[1]} = -0.17$; mean tenure, $\mu_b^{[1]} = 31.06$ and its standard deviation, $\sigma_b = 0.1212\mu_b$. The superscript [1] indicates that these values are step 1 in the Gibbs chain.
2. Update N using a Metropolis step (Gelman *et al.* 1995).
a. Choose a candidate $N^{[test]}$ by making a random draw from a normal distribution with mean $N^{[1]}$ and standard deviation $S_N^{[1]}$. S_N is called the step size; it requires an elaborate calculation, described below.
b. Define $\theta^{[1]} = (N^{[1]}, \mu_a^{[1]}, \sigma_a^{[1]}, q^{[1]}, \mu_b^{[1]}, \sigma_b^{[1]},)$, the six parameter values at step 1, and $\theta^{[test]} = (N^{[test]}, \mu_a^{[1]}, \sigma_a^{[1]}, q^{[1]}, \mu_b^{[1]}, \sigma_b^{[1]},)$. That is, five parameters are held at their current values while the candidate N is tested.
c. Let $L^{[1]} = \sum_T \ln P(X_T | C_T(\theta^{[1]}))$, the likelihood of the data given parameters $\theta^{[1]}$; $L^{[test]} = \sum_T \ln P(X_T | C_T(\theta^{[test]}))$, the likelihood of the data given $\theta^{[test]}$.
d. Define $\Delta L = e^{L^{[test]} - L^{[1]}}$, the likelihood ratio, and draw a random number, r, between 0 and 1. If $r < \Delta L$, then accept $N^{[test]}$ and set $N^{[2]} = N^{[test]}$; otherwise reject it and set $N^{[2]} = N^{[1]}$. This means that the new value of N is always accepted if it improves the likelihood but can also be accepted if it reduces the likelihood by a small enough amount.
3. Update μ_a using the same algorithm but choosing a candidate $\mu_a^{[test]}$ and deciding to accept it or reject it based on the likelihoods of

   $\theta = (N^{[2]}, \mu_a^{[1]}, \sigma_a^{[1]}, q^{[1]}, \mu_b^{[1]}, \sigma_b^{[1]},)$ and

   $\theta^{[test]} = (N^{[2]}, \mu_a^{[test]}, \sigma_a^{[1]}, q^{[1]}, \mu_b^{[1]}, \sigma_b^{[1]},)$.
4. Update σ_a with the same algorithm.
5. Update q with the same algorithm.

6. Update μ_b, again with the Metropolis algorithm, however, the likelihood formulation differs because there is a prior probability. Define the prior log-likelihood as $L_p^{[1]} = \ln[\text{Norm}(\mu_b^{[1]}, \text{mean} = 31.06, \text{SD} = 0.271)]$, which is the log of the probability of observing $\mu_b^{[1]}$ given the prior normal density. The log-likelihood of the data given $\mu_b^{[1]}$ comes from Equation A2; call it L_D. The total log-likelihood of $\mu_b^{[1]}$ is $L^{[1]} = L_D + L_p$. The Metropolis step is conditioned on $L^{[1]}$ and a log-likelihood $L^{[\text{test}]}$ calculated in the same way for the randomly chosen candidate $\mu_b^{[\text{test}]}$.

7. Update σ_b using the Metropolis step, including the prior probability $\text{Norm}[\sigma_b^{[1]}, \text{mean} = 0.1212, \text{SD} = 0.0062]$ in the likelihood.

8. Return to step 2 and update $N^{[2]}$ to $N^{[3]}$, *etc.*

The loop of steps 2–7 was repeated 5,000 times for each season.

The step size S for each parameter is critical for efficient chains. If it is too large, many steps are rejected and convergence is slow. On the other hand, steps that are too small are dangerous: Most steps are accepted and the parameter space may not be adequately covered. The optimal acceptance rate is 25%, given six parameters (Gelman *et al*. 1995). By adjusting step-size based on each acceptance, it is possible to assure any acceptance rate desired.[2] For each parameter, arbitrarily assign an initial step-size $S^{[1]}$, and let δ be a number just greater than 1. At each step through the loop, adjust the step size to $S^{[2]} = \delta^3 S^{[1]}$ if the new parameter value is accepted but to $S^{[2]} = \delta^{-1} S^{[1]}$ if it is rejected; the acceptance rate will converge on 25%. In practice, we used $\delta = 1.01$, and initial step sizes for parameters $\theta = (N, \mu_a, \sigma_a, q, \mu_b, \sigma_b)$ were $S = (100, 4, 1, 0.05, 1, 0.01)$.

Step-size adjustment was stopped at the end of the burn-in (1,000 steps), as suggested by Gilks *et al.* (1998); the mean step of the previous 100 runs (901–1,000) was held for the rest of the Monte Carlo chain. The final post-burn-in acceptance rate was >0.16 and <0.35 (most 0.22–0.28), and chains were graphed to check for adequate mixing and convergence. The distribution of each parameter's output was evaluated, and all were bell-shaped with a strong mode.

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[2] Personal communication from H. Muller-Landau, 100 Ecology Building, University of Minnesota, 1987 Upper Buford Circle, St Paul, MN 55108, April 2006.