

Incorporating uncertainty in spatial structure for viability predictions: a case study of California sea lions (*Zalophus californianus californianus*)

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Abstract

In recent years, population viability analysis has become a popular tool to assess the relative risk of extinction among populations. Viability estimates for spatially structured populations require movement data that are often unavailable. In this paper, a diffusion approximation model was used to explore the effects of different spatial scenarios resulting from assumptions about movement rates. Census data for 13 breeding islands occupied by California sea lions *Zalophus californianus californianus* in the Gulf of California were used to explore three potential scenarios: unlimited movement between sites (panmictic population), limited movement (several clusters of populations) and no movement between islands (isolated islands). Predicted viability estimates were different for each scenario, but contrary to expectations, the mean extinction risk estimates were generally lowest when movement was unlimited (panmictic scenario). However, despite an extensive dataset, the confidence of the viability predictions for each scenario was low. In some cases, uncertainty in predictions within a scenario was greater than differences between scenarios. Therefore, it is recommended that in situations where movement rates and spatial structure are unknown, extinction risk estimates should reflect both the confidence intervals for each risk estimate and the uncertainty resulting from different spatial scenarios. This study also provides the first estimate of population viability (considering spatial structure) for California sea lions in the Gulf of California and an evaluation of population status based on the IUCN criteria for species listing.

Introduction

Decisions about allocations of resources for species conservation often rely on quantitative determination of a population's current status and probability of future persistence. In recent years, population viability analysis (PVA) has become a popular tool to assess the relative risk of extinction. However, the validity of these models has been debated by several authors (Ludwig, 1999; Brook *et al.*, 2000; Coulson *et al.*, 2001; Ellner *et al.*, 2002; McCarthy, Andelman & Possingham, 2003). One of the simplest forms of PVA is the diffusion approximation (DA) model proposed by Dennis, Munholland & Scott (1991). It is an exponential growth model described by the discrete annual rate of increase (λ) and an error term that includes the stochastic variation around λ . The model provides analytical solutions for a number of risk metrics, such as mean and median times to extinction and the probability of decline to threshold abundances. This approach has been used in conservation applications for a variety of species, such as grizzly bears (Dennis *et al.*, 1991), gray whales (Gerber, DeMaster & Kareiva,

1999), Mount Graham red squirrels (Buenau & Gerber, 2004) and red-cockaded woodpeckers (Morris *et al.*, 1999). Because it is a commonly used approach, several studies have examined its reliability when key assumptions are violated. For example, Holmes (2001) and Holmes & Fagan (2002) modified and tested a DA method for datasets corrupted by observation error or fluctuations in age structure. This method improved predictions for all but rapidly increasing populations. Sabo, Holmes & Kareiva (2004) found that DA predictions were robust to violations of the density independence assumption except when populations are recovering rapidly. Wilcox & Possingham (2002) demonstrated that model performance varied with life history, and suggested that life histories should be considered when using DA as a management tool. However, to our knowledge, no studies have explored how assumptions about movement affect predictions from this simple PVA, although others have explored the influence of model structure in viability predictions (Pascual, Kareiva & Hilborn, 1997). Here, we examine a situation in which multiple patches have been sampled, yet the movement rates between patches are

unknown. In such circumstances, it is possible to group patches in different ways (e.g. considering each patch as an isolated population or in one panmictic population).

In light of the sparse data often available for species of conservation concern, conservation biologists often make simplifying assumptions in spatially complex situations, where populations are distributed across multiple sites (Morris *et al.*, 1999). For example, analyzing multi-site populations requires estimation of movement rates between sites, as movement can significantly affect the viability of a population (Madsen, Stille & Shine, 1996; Lunney *et al.*, 2002). Yet, movement rates are often unknown and difficult to obtain (e.g. Baguette, Petit & Queva, 2000). Movement patterns and rates are frequently determined with mark–release–recapture studies, but such studies are often implausible for endangered species because of small sample sizes and risks associated with capturing and marking (Mech & Shannon, 2002). In such cases, studies from similar species are often used to estimate movement. However, real movement rates can be easily under- or overestimated using this method (Gaines & Bertness, 1993; Baguette *et al.*, 2000; Lindenmayer *et al.*, 2003). Therefore, in spatially complex situations, multiple sites are often ignored (all sites are pooled and considered as one population), or assumptions about movement rates are based on preliminary data, related species or rules of thumb.

In this paper, we examine the extent to which assumptions about movement and hence the grouping of different sampled patches may influence standard risk metrics in PVA. This is one common type of assumption made by managers and other modellers when considering the viability of a population with limited data on movement rates. To examine this question, we use 30 years of abundance data for 13 patches occupied by California sea lions *Zalophus californianus californianus* in the Gulf of California. This species represents an interesting case study for exploring the effects of assumptions about movement in viability predictions for several reasons. First, despite the extensive abundance data available, information about movement rates is limited. For example, based on population structure and genetic analyses, California sea lions are usually separated into groups (Maldonado *et al.*, 1995; Schramm-Urrutia, 2002), suggesting that movement is somewhat limited. However, male migration from the Channel Islands (California) to Oregon demonstrates the ability of this species to move over large distances (Mate, 1975). Similarly, a mark–recapture study in one rookery suggested little or no movement between rookeries within the Gulf area (Hernandez-Camacho, 2001). Yet, we have occasionally found individuals several hundred kilometers away from their natal colony in the Gulf (unpubl. data). Moreover, studies from other otariid populations that could be used to infer movement rates have suggested different rates depending on which sex was studied (Raum-Suryan *et al.*, 2002; Trujillo *et al.*, 2004). California sea lions are also an interesting case study because population status is currently unknown, which makes this species a potential subject for PVA. Census data on the entire Gulf of California depict an

increase in resident populations in recent years (Zavala-Gonzalez & Mellink, 2000). However, PVA performed on each individual rookery suggests that some islands have rapidly declining populations (Szteren, Auriolos & Gerber, 2004). Therefore, a PVA of California sea lions will require making one of several conflicting assumptions about movement rates and therefore grouping.

In this study, we explore the effect of alternate assumptions about spatial structure on extinction risk estimates using three scenarios that vary only in the degree of movement expected between sites, and thus in the spatial structure considered. The scenarios we consider include (1) unlimited movement between sites, so that all sites were considered as one panmictic population, (2) movement only within clusters of sites, where some sites were pooled into panmictic cluster populations, but clusters were treated as isolated from each other, and (3) no movement between sites, where each sampled island was considered as an isolated population. These scenarios represent distinct alternatives that are likely to be selected by practitioners or researchers when calculating the viability of a population with unknown movement rates (e.g. York, Merrick & Loughlin, 1996). Thus, we illustrate the consequences of commonly used assumptions about movement in PVA and discuss the importance of incorporating uncertainty into models used for conservation and management.

Materials and methods

Data

Census data of sea lion abundance for 13 breeding rookeries (Fig. 1) found in the Gulf of California were considered. The 13 breeding colonies have been censused at irregular intervals since the late 1960s, resulting in a variable number of abundance estimates for each rookery and year. The DA model used allows for censuses completed in non-consecutive years, but two of our three scenarios (panmictic and cluster) require data for all rookeries for each year. Data for all 13 sites were only available for 1 year (1997), so it was necessary to estimate missing counts for islands not censused every year.

To estimate missing data points, we first log transformed available count data and performed a linear regression on the transformed data. Values missing from the log-transformed data were then estimated based on $y = mx + b$, where y represents the estimated data point, m is the slope, x is the missing year and b is the intercept. The resulting dataset represents the best fit from the regression analysis; we refer to this as the *mean dataset*. To better understand the range of variability around this mean estimated dataset, we then estimated two additional datasets: one based on the lower 95% confidence limit and the other based on the upper 95% confidence limit of the regression. Missing data points were estimated using lower or upper 95% confidence limits for each data point following methods for computing confidence intervals (CIs) in linear regression (Zar, 1999). All three datasets were then back-transformed to the

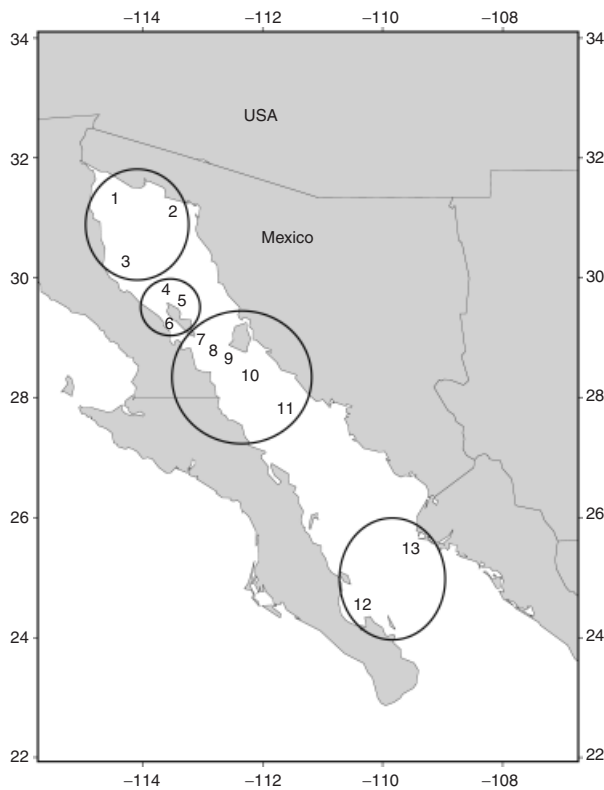


Figure 1 Map of the Gulf of California, Mexico. The breeding colonies are: 1. Rocas Consag, 2. San Jorge, 3. Los Lobos, 4. Granito, 5. Cantiles, 6. Machos, 7. Partido, 8. Rasito, 9. San Esteban, 10. S.P. Martir, 11. S.P. Nolasco, 12. Los Islotes and 13. Farallon de San Ignacio. Shaded circles represent the clusters used in the cluster model.

original units and used to estimate viability for each spatial scenario.

Abundance data for the panmictic scenario (which represent stock population size) were calculated by summing the population size for each rookery in each selected year. The cluster scenario involved more complicated techniques. Here, we assumed some islands were connected in clusters, within which sea lions moved, but that clusters were isolated from each other. We established these clusters using an agglomerative hierarchical cluster analysis. In this analysis, clusters are created by grouping individual sites into larger clusters until all sites are part of one large cluster. Sites were grouped using similarity in two variables: distance in kilometers from one island (Consag) to all others (to maintain some spatial order in the clustering), and standardized population trends (population growth values for each year minus the mean, divided by the standard deviation). The distance between clusters was determined using squared Euclidean distances. Ward's method (Ward, 1963) was then used to compare cluster distances. This approach calculates the union of all possible pairs of clusters at each step and repeats the process until all clusters are grouped into one large cluster. Then the groups that result in the smallest increase in the combined

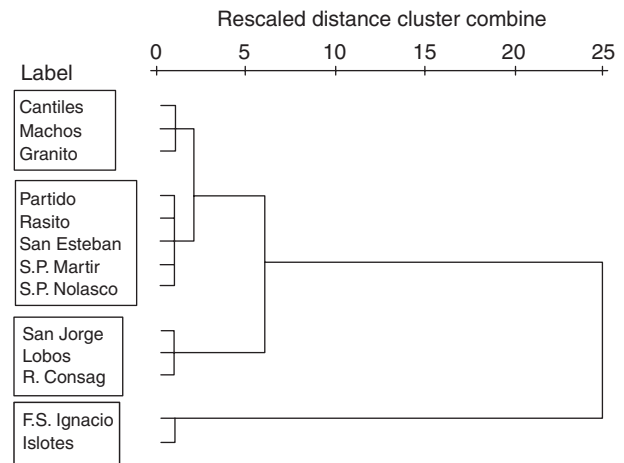


Figure 2 Results from the hierarchical cluster analysis with distance coefficients between groups rescaled from 0 to 25. The analysis suggested grouping the islands into four clusters (circled): the first cluster corresponds to the North-Midriff area, the second cluster is the South-Midriff area, the third cluster is the Northern area and the last cluster is the Southern area. See Fig. 1 for map location of the clusters and islands.

error-sum-of-squares are selected. The resultant clusters (Fig. 2) represent the groups of islands in which we expect movement (see Pedernera *et al.*, 2004 for empirical support for this clustering pattern). Count data from all sites within each cluster were totalled and then each cluster's viability was estimated independently (allowing no movement of individuals between clusters). Finally, for the rookery scenario, viability was estimated independently for each island.

Expected results

Based on previous work on Steller sea lions (York *et al.*, 1996), we expected to find variability in extinction risk estimates among each scenario. In particular, we predicted that the rookery scenario would yield the lowest risk estimates as some thriving populations could persist over long periods of time (Szteren *et al.*, 2004). The panmictic scenario was predicted to generate the highest risk estimates because differences in trend for individual islands are masked by the general trend for the entire population. In this case, the positive growth of thriving populations is reduced by the negative growth of declining rookeries, resulting in lower viability. Finally, an intermediate estimate of viability was predicted when using the cluster grouping.

Population viability model

Population viability under each scenario was estimated using the DA approach developed by Dennis *et al.* (1991). As mentioned, the DA model uses linear regression to estimate the general trend and variability in population growth (based on a time series of counts) and then uses this information in stochastic estimation of long-term population viability. In our model, extinction was considered to

occur when population size decreased below a quasi-extinction threshold ($N_q = 650$). This threshold represents an estimated minimum number of individuals needed to maintain a viable population in the entire Gulf region and was obtained by considering a threshold of 50 individuals per rookery (hence a total of 650 for the 13 rookeries in the Gulf).

For each scenario, five standard risk metrics were estimated: the stochastic lambda value (λ), the cumulative probability of quasi-extinction (CPE) and the probability of an 80% (P_{80}), a 50% (P_{50}) and a 30% (P_{30}) reduction in population size within three generations (15 years). These probabilities of decline are used by the World Conservation Union (IUCN) as criteria to classify species at risk (2001 Categories and Criteria v. 3.1). For example, if a population size reduction of 80% is projected or suspected within 10 years or three generations, the IUCN considers the taxon as critically endangered; a projected reduction of 50% within 10 years or three generations is classified as endangered, and a projected reduction of 30% in 10 years or three generations is considered vulnerable. Thus, our analyses also provide a basis for determining the status of this population based on the IUCN criteria.

Extinction risk metrics and their bootstrapped 95% CIs were calculated using the DA (Dennis *et al.*, 1991; Morris & Doak, 2002). In the panmictic scenario, abundance data for the Gulf population were summed and a single set of risk estimates was obtained. However, in the cluster and rookery scenarios, we ran the DA model for each cluster or rookery, and thus obtained multiple risk estimates. To compare among our three scenarios, we required a single risk estimate for the entire Gulf (the minimum grouping unit considered in the panmictic scenario) and thus overall values had to be computed. Overall Gulf λ values for the rookery and cluster scenarios were calculated as the weighted mean,

$$\lambda = \sum (N_s/N_t)\lambda_s \quad (1)$$

where λ_s is the rookery or cluster value obtained from the DA, N_s is the population size (from the last count) for the rookery or cluster and N_t is the total population size in the Gulf (from the last count). This weighted λ reflects the expectation that a combined growth rate will be more influenced by the growth of a large population than the growth of a small one. The overall CPE and P_{80} , P_{50} and P_{30} for the rookery and cluster scenarios were estimated using the mean μ and pooled σ^2 (Dennis *et al.*, 1991; Zar, 1999) and their 95% CI (Morris & Doak, 2002). Pooled $\sigma^2 = \sum SS_i / \sum v_i$, where SS_i is the sum of squares for site i and v_i is the degrees of freedom for site i (Zar, 1999, p. 124).

Results

Testing our estimation methodology

Estimated and empirical datasets provided similar results for our risk metrics for individual rookeries (Table 2).

Estimates of λ were similar in both analyses (paired t -test, $t_{12} = 1.188$, $P = 0.258$), and were not consistently higher or lower for any given dataset. Probabilities of population size reduction were generally lower with our estimated dataset because in all cases the number of census counts was higher in that dataset. Increasing the number of counts had the effect of making the system appear more stable than the original dataset, and thus reduced the probability of decline. However, only differences in P_{30} were significant (paired t -test, $t_{12} = 2.364$, $P = 0.036$). The results for P_{80} (paired t -test, $t_{12} = 1.696$, $P = 0.116$) and P_{50} (paired t -test, $t_{12} = 1.743$, $P = 0.107$) were not significantly different between both datasets.

We also examined the difference in variability for our three estimated datasets to the variability generated by the bootstrapped CIs. The differences in prediction between the three estimated datasets were notably smaller than the range of predictions determined with the bootstrapped CIs for the mean estimated dataset (Fig. 4). This suggests that any biases associated with our estimation technique are small in comparison with the significant uncertainty in model predictions. Therefore, we focused on the mean dataset for all comparisons of viability.

Comparing viability estimates

Viability estimates were considerably different for each scenario, but in contrast to our predictions, CPE (Fig. 3) and the probabilities of population reduction (Table 1) suggest the highest viability for the panmictic grouping and the lowest for the rookeries scenario. Interestingly, estimated λ values agreed with our predictions, and were highest in the rookery scenario (Table 1). This contradiction in predictions from λ and other risk metrics is probably because of the method by which λ was estimated for the rookery and cluster scenarios. In these cases, we used the weighted mean of λ , which was influenced by large populations with high λ values (e.g. San Esteban). In addition,

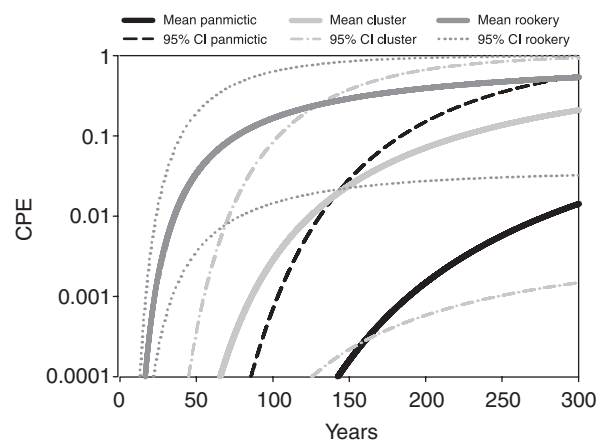


Figure 3 Mean cumulative probability of extinction (CPE) with bootstrapped 95% confidence interval (CI) predicted by each scenario. We considered a quasi-extinction threshold of 650 individuals. The lower 95% CI for the panmictic model falls on the x-axis.

Table 1 λ values, probability of 30% (P_{30}), 50% (P_{50}) and 80% (P_{80}) size reduction in three generations (15 years) and resulting IUCN status for each of the three spatial scenarios

Scenario	Range of λ values obtained for datasets with estimated points ^a	Stochastic λ (and bootstrapped 95% CI) ^b calculated using DA method	IUCN criteria		
			P_{80}	P_{50}	P_{30}
Panmictic	1.000–1.003	1.000 (0.979–1.022)	0.00	0.01	0.18
Clusters	1.005–1.007	1.004 (0.973–1.035)	0.00	0.08	0.40
Rookeries	1.017–1.021	1.016 (0.948–1.083)	0.05	0.42	0.68

λ estimates for cluster and rookery scenarios represent weighted averages, and P_{30} , P_{50} and P_{80} were calculated using the probability of extinction with a quasi-extinction threshold representing a 30, 50 or 80% reduction from the initial population size. Tables 2 and 3 provide values for individual islands and clusters.

^aValues represent the range of λ values estimated for three datasets including estimated points: mean, upper and lower values from 95% CI (mean, upper and lower values from 95% CI; Zar, 1999).

^bValues represent the mean stochastic λ calculated from the mean dataset and the bootstrapped 95% CI that represents the variability in λ (Dennis *et al.*, 1991).

CI, confidence interval; DA, diffusion approximation.

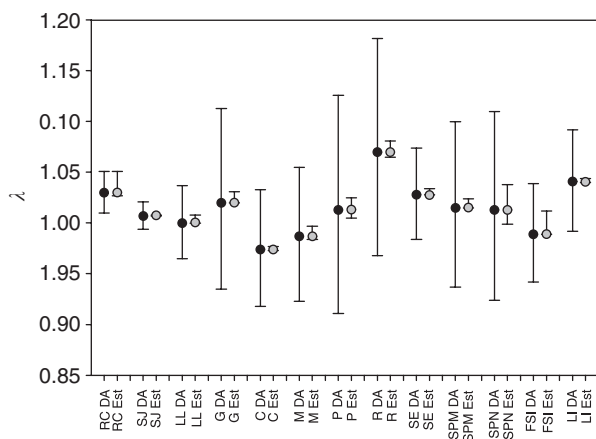


Figure 4 Comparison of the range of λ values from (a) mean and bootstrapped 95% confidence intervals (CIs) based on the diffusion approximation (DA, black circles), and (b) mean, upper and lower 95% CI estimated datasets (Est, gray circles). All values obtained using our estimation approach fall within the range of bootstrapped CIs. Rookeries are abbreviated as follows: RC, Rocas Consag; SJ, San Jorge; LL, Los Lobos; G, Granito; C, Cantiles; M, Machos; P, Partido; R, Rasito; SE, San Esteban; SPM, San Pedro Martir; SPN, San Pedro Nolasco; FSI, Farallon de San Ignacio; LI, Los Islotes.

some individual rookeries had surprisingly high values of λ , which may be an artifact of not considering migration from other rookeries to these islands.

Differences between models were less apparent when we considered the 95% CI for the studied risk parameters. In general, differences between scenarios were small compared with the uncertainty in predictions observed within a single scenario. For example, by the end of the time frame explored, the bootstrapped 95% CI for the CPE in the cluster scenario encompassed both the mean CPE predictions for the other two scenarios. Uncertainty in CPE was greater in the rookery model, in which the probability of extinction at 300 years ranged from nearly zero to over 98%. Differences in λ values among grouping

scenarios were also small compared with the CI of each scenario's predictions. Uncertainty in λ was substantial in all scenarios and in all cases ranged from a deterministic prediction of extinction ($\lambda < 1$) to a predicted increase ($\lambda > 1$) (see Table 1).

Probabilities of population reduction (P_{80} , P_{50} and P_{30}) were generally small for all three scenarios, and did not meet the criteria for classification under the IUCN (Table 1). However, in the rookery scenario, there was nearly a 50% probability of a 50% decline for the entire Gulf population in the next 15 years (three generations), suggesting that the population may not be completely out of risk if rookeries are highly isolated. In contrast, results from the panmictic scenario, where movement was assumed to occur among all rookeries, suggest a negligible risk of population reduction for that same time frame. When data were analyzed independently for each cluster (Table 3) and rookery (Table 2), we found a high probability of population size reduction for some sites. For example, seven of the 13 rookeries had a higher than 50% probability of halving their populations in the next 15 years, and one rookery (Partido) had nearly a 30% probability of reducing its population by 80% in only three generations (Table 2).

Discussion

Effects of spatial structure on viability predictions

Even for our substantial dataset (several decades of multiple sites sampled), assuming different movement rates resulted in widely variable estimates of extinction risk. Contrary to our predictions, the panmictic scenario had the lowest risk of extinction, and the rookery scenario had the highest risk of extinction (ignoring overlap of CIs). These results suggest that movement between rookeries could ensure persistence of this population. Even limited movement (i.e. cluster scenario) considerably improved viability estimates (e.g. CPE) compared with the isolated scenario (i.e. rookery). Variation in viability estimates among distinct spatial

Table 2 λ values, probability of 30% (P_{30}), 50% (P_{50}) and 80% (P_{80}) size reduction in three generations (15 years) and resulting IUCN status for the rookeries scenario using the estimated mean dataset (Est.) and the empirical dataset that contains only actual counts (Emp.)

Island	Stochastic λ (and bootstrapped 95% CI) ^a calculated using DA method		IUCN criteria					
	Emp.	Est.	P_{80}		P_{50}		P_{30}	
			Emp.	Est.	Emp.	Est.	Emp.	Est.
Rocas Consag	1.031 (0.999–1.065)	1.030 (1.010–1.051)	0.00	0.00	0.00	0.00	0.08	0.00
San Jorge	1.017 (0.987–1.031)	1.007 (0.994–1.021)	0.00	0.00	0.00	0.00	0.09	0.00
Los Lobos	0.989 (0.950–1.076)	1.000 (0.965–1.037)	0.03	0.00	0.36	0.13	0.65	0.46
Granito	1.004 (0.933–1.126)	1.020 (0.935–1.113)	0.17	0.14	0.56	0.55	0.78	0.77
Cantiles	0.979 (0.919–1.031)	0.974 (0.918–1.033)	0.11	0.11	0.63	0.63	0.85	0.85
Machos	1.032 (0.923–1.056)	0.987 (0.923–1.055)	0.13	0.12	0.60	0.59	0.82	0.81
Partido	1.047 (0.909–1.189)	1.013 (0.911–1.126)	0.29	0.31	0.67	0.70	0.83	0.86
Rasito	1.047 (0.969–1.174)	1.070 (0.968–1.182)	0.09	0.10	0.42	0.44	0.66	0.68
San Esteban	1.033 (0.978–1.089)	1.028 (0.984–1.074)	0.00	0.00	0.15	0.08	0.42	0.31
S.P. Martir	1.019 (0.934–1.116)	1.015 (0.937–1.100)	0.15	0.12	0.56	0.53	0.77	0.76
S.P. Nolasco	1.038 (0.908–1.186)	1.013 (0.924–1.110)	0.27	0.21	0.65	0.62	0.82	0.81
Farallon de San Ignacio	0.982 (0.903–1.040)	0.989 (0.942–1.039)	0.19	0.02	0.71	0.41	0.88	0.72
Los Islotes	1.054 (1.003–1.120)	1.041 (0.992–1.092)	0.00	0.00	0.07	0.07	0.27	0.28

^aValues represent the mean stochastic λ calculated from the mean dataset and the bootstrapped 95% CI that represents the variability in λ (Dennis *et al.*, 1991).

CI, confidence interval; DA, diffusion approximation.

scenarios has been found in some previous studies, but the results conflict with evidence for higher viability in isolated patches (Quinn & Hasting, 1987; York *et al.*, 1996), panmictic populations (Forney & Gilpin, 1989; Durant, 2000), metapopulation systems (Lunney *et al.*, 2002) and even complex effects dependent on population size (where smaller populations suffered the effects of migration more than larger populations; Lindenmayer & Lacy, 1995). It appears that the effect of movement in viability predictions is dependent on model structure and the species considered, and no single approach can be considered as most conservative.

In addition, we found that despite the large amount of data available, each scenario provided a wide range of estimates, from a relatively safe future to a considerable risk of decline. In fact, uncertainty associated with predictions from a single scenario was often greater than differences in predictions among scenarios (Fig. 3; Table 1). In our case, the effect of assumptions about movement between rookeries appears to be relatively small compared with the uncertainty in a single model prediction. In fact, while we

estimated viability over extensive periods of time in the future, which has the effect of increasing uncertainty (Beissinger & Westphal, 1998), uncertainty was significant even in the first 100 years. For imperiled species for which more limited data are often available, even greater uncertainty should be expected, which could further confound estimates of extinction risk. Ellner *et al.* (2002) found that reliable predictions of long-term extinction probabilities are likely to require a substantial quantity of data. As a result, they suggest that reliable predictions of extinction probabilities can be made only for short-term time horizons. We further suggest that for population of conservation concern for which data are available for multiple sites but movement rates are unknown, bootstrapped CIs for the most plausible grouping scenario should be explored. If CIs for that scenario are relatively small, we recommend exploration of additional spatial scenarios to incorporate uncertainty associated with unknown movement patterns. If CIs are large, uncertainty associated with different movement patterns might be ignored until additional data are collected and viability can be assessed with greater confidence.

Our estimation methodology

Our approach for the estimation of data points is a relatively simple technique that may be applied in situations where movement patterns are unknown. The DA method requires less data than many other models. For example, although a true metapopulation model may provide the best estimates of population viability when considering movement, this technique requires estimates of actual movement rates, which may often be unavailable. However, the DA method assumes count data are available for all patches sampled, a condition that may not be met by many datasets for which several patches were sampled at irregular intervals. Here, we suggest a simple estimation method for missing patch data that appears robust to variation in data among patches. In our case, using this estimation approach allowed us to explore different spatial structures, and showed the associated range of viability predictions, making this a helpful initial approach. Nevertheless, one important caveat should be considered before using this method. The estimation approach effectively reduces the variability found in the data, a problem we examined by estimating datasets using lower and upper 95% confidence limits. In our case, upper and lower confidence limits were not dramatically different from the mean, which suggests that the mean estimated values are not unreasonable. However, in other situations, this reduction in variability may be more important, especially when estimating a larger proportion of the dataset and/or when empirical estimates are more variable. For these reasons, it is important to examine datasets based on mean, lower and upper 95% CIs to identify the impact of using this approach. If variability between the three datasets is high, we suggest estimating viability for each dataset to explore the range of predictions.

Viability estimates for California sea lions

This paper provides the first estimate of population viability for California sea lions in the Gulf of California that considers the spatial structure. Our results suggest that this population is likely to be increasing in abundance overall; however, we also found that the current data are inadequate

to provide a very confident estimate of viability. This suggests that determining the status of this population will require additional monitoring of all breeding colonies in the Gulf. In addition, recent genetic analyses (Schramm-Urrutia, 2002) and studies of distribution patterns of infectious diseases (Pedernera *et al.*, 2004) suggest that movement could be limited between rookeries, and thus some rookeries or clusters might be truly isolated. Under these circumstances, overall estimates of viability for the entire Gulf might not adequately represent the risks for this population. Instead, individual results from rookeries or clusters might need to be considered. When we estimated viability for individual rookeries or clusters (Tables 2 and 3), some groups were predicted to reach extinction within a few decades (CPE results for each rookery or cluster are not shown). For example, seven rookeries were found to have a greater than 50% probability of a 50% decline in the next 15 years (Table 2). Although these values do not meet the criteria for classification under the IUCN, it is worth noting that more than half of the breeding colonies in the Gulf could experience a large reduction in population size in the near future.

Our results should be interpreted with caution, and future analyses are needed to determine the status of this species. First, it is important to note that our goal was to compare estimates of population viability from scenarios with different assumptions about movement. Thus, although our results provide reasonable bounds for uncertainty in extinction risk metrics, we do not provide a single estimate of extinction risk for California sea lions. Additionally, our simple model ignores complexity in movement patterns likely to be observed in nature. For example, dispersing individuals are unlikely to distribute themselves equally among patches because of variation in access and in preferences (Fahrig & Paloheimo, 1988). Currently, we are studying the spatial structure of this population in more detail and the results should allow for a more accurate prediction of status. Second, we did not quantitatively explore movement by varying movement rates; instead, we represented three alternative population structures expected to be the result of different movement patterns. This approach does not consider the influence of sources and sinks on

Table 3 λ values, probability of 30% (P_{30}), 50% (P_{50}) and 80% (P_{80}) size reduction in three generations (15 years) and resulting IUCN status for the cluster scenario using the estimated mean dataset

Cluster	Range of λ values obtained for datasets with estimated points ^a	Stochastic λ (and bootstrapped 95% CI) ^b calculated using DA method	IUCN criteria		
			P_{80}	P_{50}	P_{30}
Northern	1.005–1.008	1.005 (0.992–1.018)	0.00	0.00	0.00
North-Midriff	0.979–0.982	0.978 (0.939–1.019)	0.01	0.43	0.76
South-Midriff	1.009–1.015	1.010 (0.974–1.047)	0.00	0.08	0.35
Southern	0.999–1.019	1.005 (0.978–1.032)	0.00	0.03	0.25

^aValues represent the range of λ values estimated for three datasets including estimated points: mean, upper and lower values from 95% CI (mean, upper and lower values from 95% CI; Zar, 1999).

^bValues represent the mean stochastic λ calculated from the mean dataset and the bootstrapped 95% CI that represents the variability in λ (Dennis *et al.*, 1991).

CI, confidence interval; DA, diffusion approximation.

population viability. The scenarios used here were chosen because they represent commonly assumed population structures and include the two extreme cases: a panmictic population and several completely isolated patches. We suspect that incorporating more complexity into movement would provide a greater range of predictions.

Conclusions

This paper suggests a relatively simple method to explore a range of spatial scenarios for irregularly sampled patches. The viability of populations for which movement rates are unknown should be explored under several realistic scenarios, using multiple risk parameters and ideally considering bootstrapped variability estimates to examine uncertainty (Gerber & VanBlaricom, 2001). Different scenarios should include the range of potential movement rates for the species based on natural history and data from related species. Including this range is likely to result in several alternative estimates that should be considered before making any decision regarding management of a population.

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CORRIGENDUM

Incorporating uncertainty in spatial structure for viability predictions: a case study of California sea lions (*Zalophus californianus californianus*)

M. Gonzalez-Suarez, K. E. McCluney, D. Auriolos & L. R. Gerber

In Gonzalez-Suarez *et al.* (2006), the following error was published on page 224:

The empirical λ values in Table 2 (second column) were calculated using census data from 1979 to 2002. However, they should have considered census data from 1979 to 2004 to make them comparable to the other values provided. The results of the paper are not changed by this.

The corrected version of Table 2 is printed below.

We apologize for this error.

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- Dennis, B., Munholland, P.L. & Scott, J.M. (1991). Estimation of growth and extinction parameters for endangered species. *Ecol. Monogr.* **61**, 115–143.
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Table 2 λ values, probability of 30% (P_{30}), 50% (P_{50}) and 80% (P_{80}) size reduction in three generations (15 years), and resulting IUCN status for the rookeries scenario using the estimated mean dataset (Est.) and the empirical dataset which contains only actual counts (Emp.)

Island	Stochastic λ (and 95% CI) ^a calculated using DA method		IUCN criteria					
	Emp.	Est.	P_{80}		P_{50}		P_{30}	
			Emp.	Est.	Emp.	Est.	Emp.	Est.
Rocas Consag	1.031 (0.999–1.065)	1.030 (1.010–1.051)	0.00	0.00	0.00	0.00	0.08	0.00
San Jorge	1.009 (0.987–1.031)	1.007 (0.994–1.021)	0.00	0.00	0.00	0.00	0.09	0.00
Los Lobos	1.011 (0.950–1.076)	1.000 (0.965–1.037)	0.03	0.00	0.36	0.13	0.65	0.46
Granito	1.025 (0.933–1.126)	1.020 (0.935–1.113)	0.17	0.14	0.56	0.55	0.78	0.77
Cantiles	0.973 (0.919–1.031)	0.974 (0.918–1.033)	0.11	0.11	0.63	0.63	0.85	0.85
Machos	0.987 (0.923–1.056)	0.987 (0.923–1.055)	0.13	0.12	0.60	0.59	0.82	0.81
Partido	1.040 (0.909–1.189)	1.013 (0.911–1.126)	0.29	0.31	0.67	0.70	0.83	0.86
Rasito	1.067 (0.969–1.174)	1.070 (0.968–1.182)	0.09	0.10	0.42	0.44	0.66	0.68
San Esteban	1.032 (0.978–1.089)	1.028 (0.984–1.074)	0.00	0.00	0.15	0.08	0.42	0.31
S.P. Martir	1.021 (0.934–1.116)	1.015 (0.937–1.100)	0.15	0.12	0.56	0.53	0.77	0.76
S.P. Nolasco	1.038 (0.908–1.186)	1.013 (0.924–1.110)	0.27	0.21	0.65	0.62	0.82	0.81
Farallon de San Ignacio	0.969 (0.903–1.040)	0.989 (0.942–1.039)	0.19	0.02	0.71	0.41	0.88	0.72
Los Islotes	1.060 (1.003–1.120)	1.041 (0.992–1.092)	0.00	0.00	0.07	0.07	0.27	0.28

^aValues represent the mean stochastic λ calculated from the mean dataset and the 95% CI that represents the variability in λ (Dennis *et al.*, 1991). CI, confidence interval.