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TREND DETECTION IN SOURCE–SINK SYSTEMS: WHEN SHOULD SINK HABITATS BE MONITORED?

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Abstract. We determine the power of population monitoring in source or sink habitat to detect declining reproductive success in source habitat using a stochastic population model. The relative power to detect a trend in the source by monitoring either the source or the sink varies with life history parameters, environmental stochasticity, and observation uncertainty. The power to detect a decline monitoring either source or sink habitat is maximized when the reproductive surplus in the source is low. The power to detect a decline by monitoring the sink increases with increasing reproductive deficit in the sink. If environmental stochasticity in the source increases, the power in the sink goes down due to a lower signal-to-noise ratio. However, the power in the sink increases if environmental stochasticity is increased further, because increasing stochasticity reduces the geometric mean growth rate in the source. Intriguingly, it is often most efficient to monitor the sink even though the actual reproductive decline occurs in the source. If reproductive success is declining in both habitats, censusing the sink will always have higher power. However, the probability of Type 1 error is always higher in the sink. Our results clearly have implications for optimal population monitoring in source–sink landscapes.

Key words: environmental stochasticity; habitat selection; life history parameters; observation uncertainty; population monitoring; population trend; reproductive success; source–sink dynamics; statistical power.

INTRODUCTION

In contemporary population ecology, the analysis of time series data plays a central role (Royama 1992, Dennis et al. 1998, Stenseth 1999, Bjørnstad and Grenfell 2001, Turchin 2003), and the application of various statistical modeling techniques to such data has revealed a number of important insights for at least three areas of applied theoretical population ecology: fisheries management (Quinn and Deriso 1999), pest control (Berryman 1999), and conservation biology (Burgman et al. 1993). Ecological time series data collection and analysis are often the result of long-term monitoring programs (e.g., the Breeding Bird Surveys in North America [James et al. 1996] and Great Britain [Greenwood et al. 1995]), where the primary concern is the detection of adverse trends (e.g., Jassby and Powell 1990, Thomas 1996). When designing monitoring programs aimed at detecting changes such as long-term decline, the issue of statistical power must be investigated, e.g., to determine sample size, precision and an acceptable level of Type I and Type II errors (Gerrodette 1987). This is particularly important for threatened species or resource management, where the “cost” of failing to detect a negative trend or impact

may be high (Peterman 1990, Taylor and Gerrodette 1993, Mapstone 1995).

In a recent paper, Shea and Mangel (2001) investigate how observation error, length of the time series of data, and autocorrelation in vital rates affect the power of trend detection in population models of coho salmon (*Oncorhynchus kisutch*). They shed light on important questions about whether one is likely to observe a trend in one life history stage (e.g., adults) by sampling another (e.g., juveniles). Even though age- and/or size-structured models have a long and successful history in ecology (Caswell 2000), demographic rates may vary more between same-aged individuals living in different habitats than between different-aged individuals in the same habitat (Bowers 1994). A conceptual framework for habitat-structured populations is given by source–sink theory (e.g., Holt 1985, Pulliam 1988, Pulliam and Danielson 1991), in which the persistence of populations in sink habitats, with a finite rate of increase (λ) below unity in isolation, is only possible if there is sufficient immigration of individuals from source habitats ($\lambda > 1$). Individuals may occur in sink habitats due to environmentally constrained dispersal (Diffendorfer 1998), imperfect knowledge (Delibes et al. 2001), pre-emptive habitat selection (Pulliam and Danielson 1991), unstable population dynamics in source habitats (Holt 1997), or use as a temporary refuge before occupying a better habitat (Morris 1991). However, populations can persist in a system of only

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sink habitats if there are temporal fluctuations in habitat quality (Jansen and Yoshimura 1998). Even though the existence of source-sink dynamics is indeed difficult to demonstrate in practice (Watkinson and Sutherland 1995), there is ample evidence that they may occur in a number of species and on spatial scales of relevance for monitoring and environmental decision making (e.g., Brawn and Robinson 1996, Dias 1996, Boughton 1999, McCoy et al. 1999).

Apart from having a number of interesting implications for harvesting decisions and reserve design (e.g., Tuck and Possingham 1994, Lundberg and Jonzén 1999, Tuck and Possingham 2000), source-sink dynamics may also complicate the interpretation of monitoring data by uncoupling local production and population trends (Brawn and Robinson 1996). For instance, if we observe a negative population trend in a sink habitat, this may be due to (1) a local trend caused by a demographic change in the sink, (2) a global trend in demographic rates that can be detected in both sources and sinks, or (3) an effect of a demographic change in a source habitat that is manifested in a sink habitat via decreased dispersal from the source (see this paper). It has been shown previously that global trends may be more easily detected in relatively poor habitats than in better habitats (Bowers 1996). In practice, poor habitats often occur in the periphery of a species' distribution (Brown 1984) and monitoring edge populations that fluctuate heavily may be difficult due to the noise that has to be accommodated to find a real trend (Bowers 1996).

In this paper, we use a stochastic two-habitat source-sink model of a territorial species to investigate how the power of detecting a negative trend in abundance due to declining reproductive success in the source habitat varies between source and sink habitats, in relation to life history parameters resulting in a reproductive surplus or deficit, environmental stochasticity and observation uncertainty. We also study the power of trend detection when the reproductive success declines in both habitats. Finally we demonstrate how the probability of a Type I error (i.e., finding a non-existing trend) depends on the demography in the source and the sink.

METHODS

Model

As a starting point, let us consider two habitats, one source (habitat 1) coupled with a sink (habitat 2). A habitat is defined as a source or a sink depending on whether the geometric mean of λ_i (the finite rate of increase in habitat i) is larger or smaller than unity. We denote the number of individuals in the source and the sink N_1 and N_2 , respectively. In the source, there are a limited number of territories (\hat{u}) and if $N_1 > \hat{u}$, the surplus will disperse to the sink. The sink, on the other hand, is considered to have an unlimited number of

territories, but the habitat quality is not good enough for a self-supporting population. Hence, without any immigration from the source, the sink will go extinct. There is no backflow from the sink to the source, i.e., the sink is a "black-hole sink" (Holt and Gaines 1992). One may object to the use of black-hole sinks because emigration to such habitats is unlikely to be an evolutionary stable strategy, ESS, (Holt 1997, Morris 1991). However, we find at least three different reasons why our simple model can be motivated. First, dispersal to sink habitats may not have evolved as an ESS on its own account, but rather as a necessary consequence of other processes (Morris 1991). Second, dispersal to sink habitats can evolve as an ESS on its own account if there is some back dispersal from the sink to the source (Morris 1991; Holt 1997). The back dispersal may be small and negligible compared to the overall dynamics and therefore it would not affect the overall dynamics studied in this paper. Third, and most importantly, we know that habitat deterioration may turn previous source habitats into sinks on ecological time scales, but very little is known about the time that it takes for actively dispersing individuals to respond to the new situation by habitat selection. We therefore think that Pulliam's model is a valid simplification for source-sink dynamics in territorial species that suits the purpose of this study.

The model used here is the two-patch version of the source-sink model presented by Pulliam (1988) and we will assume that the per capita birth rate distinguishes a source from a sink. Following Pulliam (1988), λ_i is defined as

$$\lambda_i = P_a + P_j \beta_i \quad (1)$$

where P_a (per capita adult survival) and P_j (per capita juvenile survival) are habitat independent, and β_i is the per capita birth rate in each habitat, respectively.

Now, we will introduce environmental stochasticity by replacing β_i with a lognormal stochastic variable such that the per capita birth rate in habitats i in year t is

$$\beta_{i(t)} = b_i \exp[\varepsilon_i(t) - 0.5\sigma_i^2] \quad (2)$$

where b_i is the expected value of the process, henceforth referred to as the average per capita birth rate to distinguish it from the geometric mean of β_i . The environmental stochasticity is generated by drawing random numbers from a bivariate normal distribution, $\varepsilon_{i(t)} \sim \text{MVN}(0, \Sigma)$, with standard deviation σ_i , but we let Σ be a diagonal variance-covariance matrix. Hence, we assume the environmental stochasticity in the two habitats to be independent. Putting the pieces together, we can write the temporal dynamics of the population in the source (N_1) and the sink (N_2) as

$$N_{1(t+1)} = N_{1(t)} \lambda_{1(t)} - I_{(t)} \quad (3)$$

$$N_{2(t+1)} = N_{2(t)} \lambda_{2(t)} + I_{(t)} \quad (4)$$

where $I_{(t)}$ is the emigration of surplus individuals from

the source to the sink. This model system has no explicit density dependence, but regulation takes place through competition for a limited number of territories in the source and the fact that the sink population will decline in the long term (Pulliam 1988).

Finally, no observations are perfect and most analyses of ecological data have to deal with observation uncertainty in some way (Hilborn and Mangel 1997). We assume that the observation errors in the source and sink are lognormal and independent, but with the same standard deviation, i.e.,

$$N_{i,\text{obs}} = N_i \exp(w_i - 0.5\sigma_{\text{obs}}^2) \quad (5)$$

where w_i is a normal random deviate, with standard deviation σ_{obs} , in habitat i . The observations take place just before the onset of the breeding season.

Population decline and trend detection

We simulated the model system for 200 years. After this baseline period we let the average per capita birth rate in the source (b_1) decline linearly over a time interval T . This procedure was iterated 1000 times. Using the observed (with error, as before) time series of length T from the source and the sink, we tested for a significant decline in abundance in the source and sink at the 5% level ($\text{Pr}\{\text{Type I error}\}$). We applied a simple linear regression model to abundance and used a one-tailed t test (Sokal and Rohlf 1995) against the null hypothesis that the slope was not significantly different from zero over the time interval T . We tried different values of T , but because the effect of the length of the time series has been investigated before (e.g., Shea and Mangel 2001), we only present the results for $T = 10$ years. As an estimate of statistical power ($1 - \text{Pr}\{\text{Type II error}\}$), we used the proportion of iterations where a significantly negative trend was found. Several trend analysis methods exist (reviewed by Thomas (1996)) and the choice is somewhat subjective. However, for our purposes, the method, *per se*, is not of interest and we have therefore chosen linear regression for its simplicity and common usage in ecology (e.g., Shea and Mangel 2001). Furthermore, detecting nonlinear behavior in 10-year time series is very difficult, especially in the face of environmental stochasticity and observation error.

We were also interested in how often we falsely detect a decline when there is no decline ($\text{Pr}\{\text{Type I error}\}$). Therefore we repeated the simulations without inducing a trend in the average per capita birth rate in the source, and used the proportion of iterations where a significantly negative trend was found as a measure of the probability of a Type I error ($\text{Pr}\{\text{Type I error}\}$). Finally, we repeated all of these steps assuming a decline in both the source and the sink; specifically, we let the average per capita growth rate in both the source and sink, b_1 and b_2 , decline linearly over time. In the results presented here, we fixed adult (P_a) and juvenile (P_j) survival to 0.6 and 0.2, respectively, and we varied

the reproductive surplus in the source and the deficit in the sink by varying the average per capita birth rate (b_i) in the source and the sink. The presented values (given in each figure legend) are representative and are chosen to illustrate our general results.

RESULTS

Managers and agencies responsible for nature conservation and regulation are interested in whether with equal per habitat, monitoring in source vs. sink habitat is more likely to detect a real decline. The answer depends on the magnitude of decline that we are interested in detecting, the standard deviation of the observation error, and the reproductive surplus and deficit in the source and sink, respectively (Fig. 1). The overall effect of observation uncertainty, not surprisingly, is to mask the negative trend and thereby decrease the power. In general, a large decline is easier to detect in the source simply because a large decline increases the probability that the source actually becomes a sink. Note that the reproductive decline can force the source to become a sink, but this new sink is different from the original sink habitat in the sense that it is not supported by immigration. However, when the difference in reproductive outputs between the source and the sink increases, it becomes relatively more efficient to census the sink (compare Fig. 1E and F).

The effect of the demographic parameters on the statistical power is shown in more detail in Fig. 2. The chance of detecting a negative population trend (of 25% over 10 years) in the source falls as the per capita reproductive surplus before the decline increases (Fig. 2A) and, not unsurprisingly, is unaffected by the demographics of the sink (Fig. 2B). In the sink, the power of finding a negative trend almost always increases as the per capita reproductive deficit in the sink ($1 - \lambda_2$) increases, but there is a hump-shaped relationship when the per capita reproductive surplus in the source is low (Fig. 2D). The power in the sink is also influenced by the demography in the source, such that increased surplus production in the source decreases the power in the sink (Fig. 2C).

Whereas the effect of observation error on power is straightforward, the influence of environmental stochasticity is far more complicated. Increasing the standard deviation of the environmental stochasticity in the source (σ_1) increases power in the source (Fig. 3A), but has a highly nonlinear effect on power in the sink, such that power first goes down and then goes up when σ_1 is increased (Fig. 3C). Increasing the standard deviation of the environmental stochasticity in the sink (σ_2), on the other hand, has only a local effect (as did the average growth rate), i.e., it does not affect the probability of finding a trend in the source. The effect of increasing environmental variability in the sink on power in the sink can be either positive or negative, depending on the magnitude of the reproductive deficit (Fig. 3D).

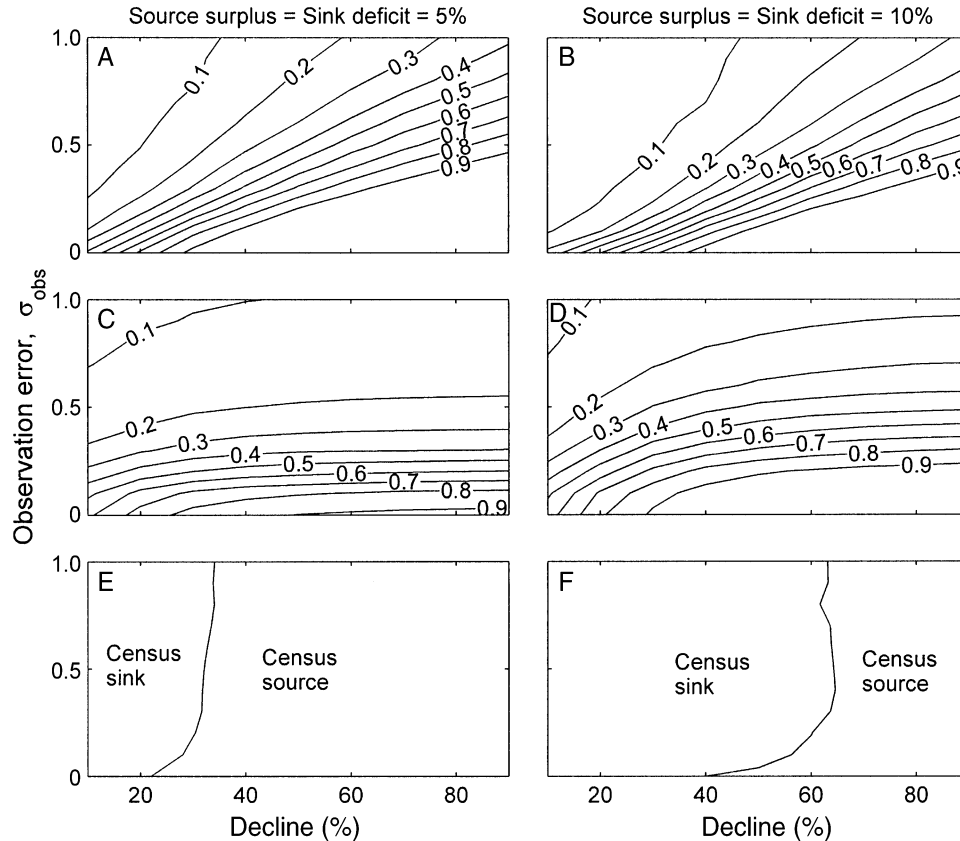


FIG. 1. Contour plot showing the power of detecting a negative population trend due to decreasing average per capita birth rate in the source (b_1) by using a 10-yr census window in the source (A, B) or the sink (C, D) as a function of the magnitude of decline over the 10-yr period and the standard deviation of the observation error. For instance, a 50% decline means that b_1 in the end of the 10-yr period has declined by 50% from the baseline value before the 10-yr period. The lines in the lower panels divide the parameter space in regions where power in the source is higher or lower than in the sink. In the left panels (A, C, E), $b_1 = 2.25$ (before decline) and $b_2 = 1.75$, which gives a 5% reproductive surplus in the sink and a 5% deficit in the sink when $P_a = 0.6$ and $P_j = 0.2$. In the right panels (B, D, F), $b_1 = 2.5$ (before decline) and $b_2 = 1.5$, which gives a 10% reproductive surplus in the sink and a 10% deficit in the sink for the same values of P_a and P_j as in (A, C, E). The standard deviation of the environmental stochasticity is set to 0.2 in both habitats, i.e., $\sigma_1 = \sigma_2 = 0.2$.

The probability of finding a false population trend when there is no decrease in reproductive success ($\Pr\{\text{Type I error}\}$), is generally higher than that specified in the null hypothesis test. This is due to temporally correlated residuals, which has the effect of underestimating the true variance such that the null hypothesis is rejected more often than expected (Bartlett 1935, Bence 1995). The $\Pr\{\text{Type I error}\}$ is also higher in the sink than in the source habitat. In the source, the $\Pr\{\text{Type I error}\}$ falls as the reproductive surplus increases because population sizes below carrying capacity (number of territories) become less likely. In the sink, a maximum is reached when the reproductive surplus in the source is low (Fig. 4C and D) and the reproductive deficit in the sink is $\sim 15\%$ (Fig. 4D). This optimum is the result of an increasing coefficient of variation (which tends to mask any trend) and a stronger dependence on immigration from the source (which tends to increase the occurrence of a trend) as the reproductive deficit increases.

All of the main conclusions remain valid when we assume a trend in average per capita birth rate across both habitats (both b_1 and b_2 decline), except for the important difference that power in the sink always exceeds power in the source, regardless of the magnitude of reproductive decline.

Finally, we notice that in real ecological systems, the survival probability for dispersing individuals should depend on the distance between the sink and the source. It is also reasonable to think that the spatial correlation of environmental stochasticity should decrease with distance. So far, we have assumed independent error terms and that all individuals leaving the source end up in the sink. We relaxed both assumptions, but neither spatially correlated stochasticity nor survival probability below 1.0 had any effect on the results. The fact that survival has no effect on the probability of finding a trend in the sink can be understood by analyzing the deterministic version of the source-sink model. Let us assume that a fraction s of the dis-

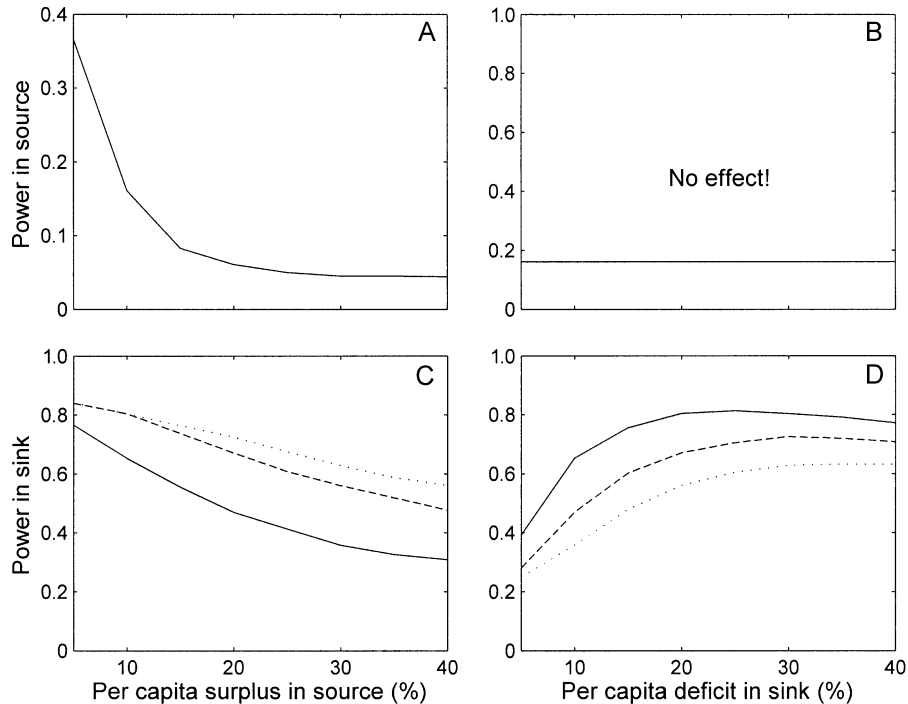


FIG. 2. The power of detecting a negative population trend due to a 25% decline in the average per capita birth rate in the source (b_1), by using a 10-yr census window in the source (A, B) or the sink (C, D). The per capita reproductive surplus in the source refers to the arithmetic mean surplus before the decline. In panel (A), the per capita reproductive deficit is set to 10%, as was the per capita surplus in the source in panel (B). In panels (C, D), we let the sink deficit (C) or source surplus (D) be 10% (solid lines), 20% (dashed lines), or 30% (dotted lines). The other parameter values are $P_a = 0.6$, $P_j = 0.2$, $\sigma_1 = 0.2$, $\sigma_2 = 0.2$, and $\sigma_{\text{obs}} = 0.2$. Hence, survival is fixed, and we set the reproductive surplus ($\lambda_1 - 1$) and deficit ($1 - \lambda_2$) by varying b_i in the source and the sink.

persers survive and reach the sink. The equilibrium population size in the sink (where \hat{u} is the number of territories) is

$$N_2^* = \frac{s\hat{u}(\lambda_1 - 1)}{1 - \lambda_2}. \quad (6)$$

If one were to let λ_1 decrease by, say, a fraction p , the relative change in equilibrium population size in the sink would not be a function of survival:

$$\frac{N_{2,\text{new}}^* - N_{2,\text{old}}^*}{N_{2,\text{old}}^*} = -p \frac{\lambda_1}{\lambda_1 - 1}. \quad (7)$$

DISCUSSION

Using a spatially explicit simulation model, Bowers (1996) found that a region-wide decrease in survivorship could be detected earlier in poorer than in better habitats when testing for a change in average abundance. In this paper, we have focused on local habitat deterioration resulting in population decline due to decreased per capita reproductive output in source habitat. That is important because declines in demographic parameters in source habitat are likely to be serious from a conservation and/or sustainable harvesting perspective. It would be prudent to know where monitoring is most likely to deliver early warning of serious

decline in demographic rates. Because source–sink dynamics complicate the relationship between local reproduction and global population trends (Brawn and Robinson 1996), it is generically useful that we found some rules of thumb for where it would be most efficient to monitor demographic change in a source–sink system. First of all, one must decide the minimum decline that one would like to detect. Unless this value is very high and the demographic difference between the source and the sink is very low, the answer would be to sample in the sink. When the magnitude of the reproductive decline in the source is very high, the source becomes a sink, but a different sink than the original sink habitat because there is no immigration. This is also the reason why detecting large declines becomes easier in the original source habitat. In the original sink habitat, a trend due to reproductive decline in the source is only detectable because of changes in the number of immigrants, and once there is no surplus produced in the source, there is no longer any signal in the sink for detecting further declines in the previous source habitat.

Secondly, increasing the observation error not only decreases the overall power but also shifts the maximum power from the source to the sink. The exact breakpoint, however, is dependent on the demographic

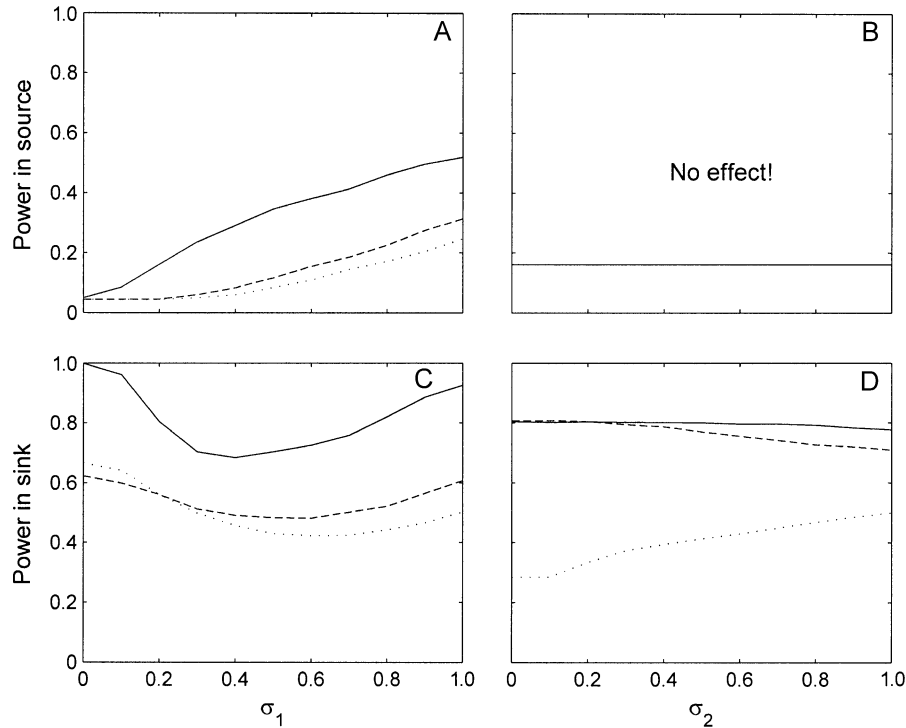


FIG. 3. The power of detecting a negative population trend due to a 25% decline in the average per capita birth rate in the source (b_1), by using a 10-yr census window in the source (A, B) or the sink (C, D) as a function of the standard deviation of the environmental stochasticity in the source (σ_1) or the sink (σ_2). In (A), b_1 (the per capita reproductive surplus in the source before decline) is set to 2.5 (solid lines), 3.5 (dashed line), or 4 (dotted line) and $b_2 = 1$. In panels (C, D), $b_1 = 2.5$, and b_2 is set to 0.5 (solid line), 1 (dashed line), or 1.8 (dotted line). The other parameter values are $P_a = 0.6$, $P_j = 0.2$, and $\sigma_{\text{obs}} = 0.2$.

parameters. Hence, to design a monitoring program for maximizing the probability of trend detection in such a system requires clearly stated objectives and at least some prior knowledge of the demographic details of the monitored population. To measure the demographic parameters that influence whether a reproductive surplus or deficit exists requires season-long productivity data (Powell et al. 1999). This may seem an arduous task, but at least a rough estimate of surpluses and deficits may be achieved by testing a range of plausible values for unknown demographic parameters where data are scarce or non-existing (see e.g., Brawn and Robinson 1996). An alternative and somewhat pragmatic view would be to monitor the habitats close to the periphery of a species' distribution, where it may be more likely to find sink populations. Some authors have tried to estimate to what extent a landscape consists of source and sink habitats, based on habitat selection studies and knowledge about the species' natural history (e.g., Beshkarew et al. 1994). Even if it is challenging to determine whether a reproductive surplus or deficit exists, we think it is an important lesson that detecting a reproductive decline in source habitats may often be easier by monitoring the sink population. This necessarily has ramifications for how we think about the design of monitoring programs and the in-

terpretation of survey data from such programs, independent of whether we are able to correctly identify reproductive surpluses and deficits.

The effect of environmental stochasticity on statistical power is indeed very interesting. Bowers (1996) suggested that even though population trends due to large-scale environmental change may occur in relatively poorer habitats (e.g., sinks) before they are visible in the best habitats (sources), heavy population fluctuations in the poorer habitat might cause a signal-to-noise ratio problem for trend detection. We have shown here that the relationship is more complicated (Fig. 3). In stochastic environments, the geometric mean of the growth rate will determine whether a population increases or decreases. The geometric mean is discounted by the variance of the growth rate (e.g., Caswell 2000, Bascompte et al. 2002) and, hence, the geometric mean declines when the magnitude of environmental stochasticity is increased. That explains why the power in the source actually increases as a function of σ_1 (Fig. 3A). The effect of σ_1 on censusing in the sink is first to decrease the power by decreasing the signal-to-noise ratio due to "noisy" immigration from the source. However, when σ_1 is increased even more, the geometric mean of the growth rate in the source decreases to the extent that the immigration to

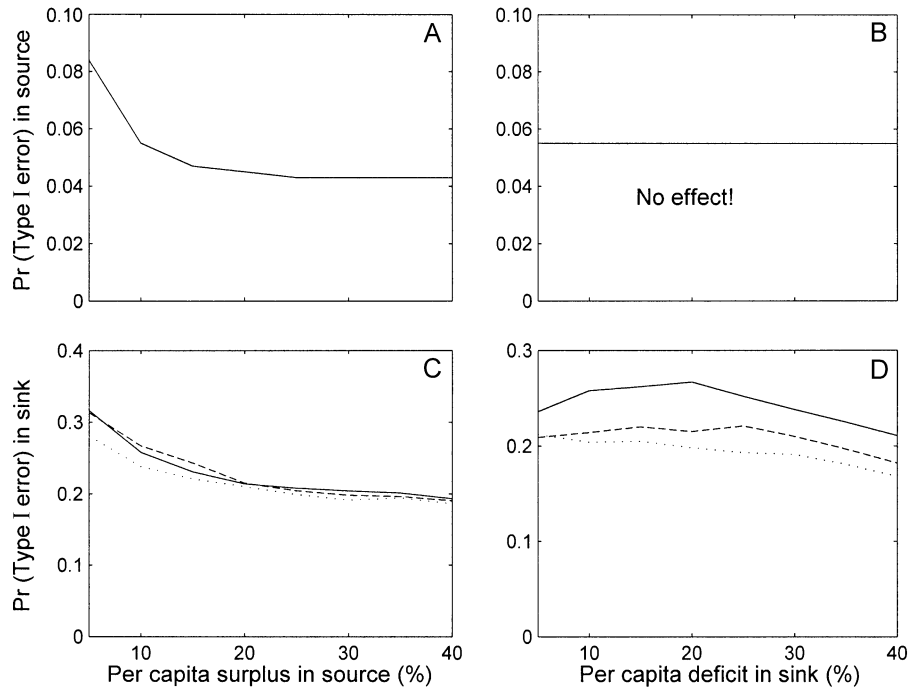


FIG. 4. The probability of detecting a negative population trend when there is not one ($\text{Pr}\{\text{Type I error}\}$), using a 10-yr census window in the source (A, B) or the sink (C, D). In panel (A), the per capita reproductive deficit is set to 10%, as is the per capita surplus in the source in panel (B). In panels (C, D), we let the sink deficit (C) or source surplus (D) be 10% (solid lines), 20% (dashed lines), or 30% (dotted lines). The other parameter values are $P_a = 0.6$, $P_j = 0.2$, $\sigma_1 = 0.2$, $\sigma_2 = 0.2$, and $\sigma_{\text{obs}} = 0.1$. Hence, survival is fixed, and we set the reproductive surplus ($\lambda_1 - 1$) and deficit ($1 - \lambda_2$) by varying b_i in the source and the sink.

the sink is low enough for a trend to become visible (Fig. 3C).

Even though the magnitude of environmental stochasticity, which is difficult to measure without long time series available, obviously has some interesting impact on the power of trend detection, the effect is often minor compared to the effect of the magnitude of the surplus and deficit in reproductive output. Furthermore, it only marginally influences the relative power in the source and the sink (compare Fig. 3A and 3C).

Our finding that the $\text{Pr}\{\text{Type I error}\}$, in both the source and the sink, tended to be higher than the expected $\text{Pr}\{\text{Type I error}\}$ has wider implications for the analysis of time series data where the residuals are not independent (Edwards and Coull 1987). This is an important consideration for monitoring programs where there is a "cost" associated with a Type I error if the $\text{Pr}\{\text{Type I error}\}$ is likely to be much higher than we expect. Mapstone (1995) suggests that we should aim to set the ratio of the $\text{Pr}\{\text{Type I error}\}$ and $\text{Pr}\{\text{Type II error}\}$ to the ratio of the "costs" associated with committing a Type I and a Type II error, respectively. Our finding that this ratio ($\text{Pr}\{\text{Type I error}\}/\text{Pr}\{\text{Type II error}\}$) tends to be lower in the source than in the sink therefore has implications for specifying the critical $\text{Pr}\{\text{Type I error}\}$ for rejecting the null hypothesis. As such, for a given set of "costs," it may often be ap-

propriate to specify a higher critical $\text{Pr}\{\text{Type I error}\}$ for monitoring source populations, compared to monitoring sink populations. Hence, in conclusion, the results that we present here indeed could be helpful in practice and we encourage ecologists to test our general predictions in system-specific models before starting detailed monitoring schedules. Such a schedule should be explicit about how to weight the consequences of $\text{Pr}\{\text{Type I error}\}$ and $\text{Pr}\{\text{Type II error}\}$ (Mapstone 1995). We have shown here that both $\text{Pr}\{\text{Type I error}\}$ and statistical power are often higher when monitoring in a sink compared to a source habitat.

Our conclusions are based on a model relevant for territorial species; one should therefore be careful before extending the results to species with different forms of density dependence and habitat selection. However, the similarities between our results and the results presented by Bowers (1996), who built on a spatially explicit model very different from the simple model implemented here, suggest that sampling in poor habitats to detect population change may be a good strategy in general.

Our results are also related to the more general discussion of how structured populations of individuals making evolutionarily stable habitat selection choice respond to habitat change (e.g., Kokko and Sutherland 1998, Pen and Weissing 2000, Kokko et al. 2001). Just as we found that the decline in average reproductive

success in the source may sometimes have a larger effect on the sink than the source population, habitat loss (starting from the best habitats), under a number of alternative assumptions about optimal territory choice, can have a larger effect on floaters than the breeder population (Kokko et al. 2001). As pointed out by Kokko and Sutherland (1998), this may cause problems for monitoring if only the number of territories is counted. The surplus production in terms of floaters potentially could be estimated if censuses were taken outside the breeding season. In the same vein, we suggest that monitoring sink populations may often be more efficient than only monitoring the source habitats. However, when censusing sink habitats, one cannot distinguish whether the adults are incoming dispersers or individuals that grew locally. Therefore, it is not similar to counting the number of floaters. In the face of uncertainty about habitat qualities, monitoring both sources and sinks may be a bet-hedging strategy. This is outside the scope of this paper, but we think there is room for future studies that sort out the most efficient strategy for a given study system. It is clear that the seasonal and spatial structure of the environment has potential consequences for the conclusions we draw about the status of natural populations, and this should be mirrored by the implemented monitoring strategies.

In conclusion, we have shown that stochastic dynamics in a source-sink environment have a number of implications for population monitoring. We provide a framework for estimating the power of trend detection as a function of biological and environmental parameters, as well as parameters set by the monitoring system, e.g., observation error and the magnitude of decline that must be detected. We would also encourage managers making decisions about monitoring schemes to consider what levels of Type I and Type II error are acceptable, and to plan their monitoring scheme in awareness of the benefits and trade-offs associated with monitoring sink populations.

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