
Reliability of Elasticity Analysis: Reply to Mills et al.

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Introduction

Matrix population models and analysis of proportional sensitivities (elasticity analysis) of population growth to changes in demographic rates are an important tool with which to examine life histories. In recent years elasticity analysis has also been used as a tool in conservation decision making. Therefore, it is necessary to critically examine areas where possible pitfalls may arise when elasticities are used to provide direction in population management. It is equally important, however, that such examinations are sound and well founded.

In a recent paper, Mills, et al. (1999) examines situations where elasticity analysis may give misleading information for application in management. They sought to evaluate how well “elasticity values alone predict the effects of realistic changes in vital rates on population growth.” They did this by addressing three general questions using one hypothetical example and three real data sets.

In general we sympathize with the objective of the study, but we are concerned with the judgments of elasticities that Mills et al. provide. Although we agree with much of the interpretation of the results in each particular case, we disagree with the general conclusion that “elasticities are accurate only under a very constrained scenario.” We argue that this overall assessment is unfounded.

Ranking of Elasticities Changes When Vital Rates Undergo Large Changes

Mills et al. claim that changes in one demographic rate can change the qualitative ranking of elasticity values. They base this conclusion mainly on the case that led to

the biggest changes in the values of the elasticities for each of the three empirical examples (as a “worst-case scenario”). Nevertheless, their simulation results show that the rankings of elasticity values did not change in any of the three examples and that the quantitative changes were small (their Fig. 2). Their results thus support the notion that elasticities provide robust qualitative predictions for relatively large changes as well as for small changes. Although we argue that the ranking of elasticities was relatively robust in this study, we think that managers should de-emphasize rankings. Instead, conservation biologists should be interested in the actual change in population growth rate that can be achieved through different measures. Hence, it is the quantitative correlation between predicted and actual changes in growth rates that is crucial. The shift in ranking of the elasticities reported for the hypothetical example is therefore of little significance because the actual elasticity values changed little (<0.10) as a function of the wide range of vital rates that were applied.

Inaccuracy of Elasticities in Predicting Future Changes in Population Growth When Perturbations are Large or Affect More than One Vital Rate

Mills et al. state that “proportional changes predicted by elasticities of the mean matrix can be misleading when the underlying relationships are nonlinear and changes in vital rates are realistically large in size.” We are not sure what the authors imply here. “Underlying relationships” are nonlinear and elasticities are local estimates of this function (e.g., Boyce 1977; Caswell 1997; de Kroon et al. 2000). Deviations between “predictions” and “realistic changes” therefore follow directly from this fact. Also, deviations caused by multiple changes in two transition rates follow directly from the local nature of elasticities. The relevant question then is not a qualitative but a quantitative one: at what point are these devia-

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tions important from a conservation point of view (e.g., when do they result in misleading predictions)?

Mills et al. judged the fit between predicted and actual values for the three empirical examples after “realistically large” changes in vital rates as “excellent,” “correspond closely,” and “accurate” for Prairie Chicken (*Tympanuchus cupido*), desert tortoise (*Gopherus agassizii*), and killer whales (*Orcinus orca*), respectively (their Fig. 3). We agree with this interpretation and with the interpretation that the fit was also good when two vital rates were changed simultaneously (“excellent,” “fairly predictable,” and “accurate” according to Mills et al.) (their Fig. 5). Hence, the simulations seem to provide no basis for their warning against using elasticities to predict changes in future population growth when large or simultaneous changes in vital rates occur, but instead they demonstrate that elasticities, in spite of their local definition, are robust enough to also predict the effects of large and simultaneous relative changes.

Our argument indicates that the conclusions are in the eye of the beholder and underscores the need to make a statistical treatment of the results. It is not appropriate to sort out only the worst cases and make inferences from this, as done by Mills et al. Rather than focusing on arbitrarily chosen cases, we need to consider the overall performance of elasticities. In taking a conservation action we will never be 100% sure about its effects. It is of little use to say that elasticities can yield inaccurate estimates. Instead, we need to know how often such inaccuracies occur and the magnitude of the discrepancies. Even simple statistics, such as correlation coefficients, help a lot in making such assessments. For example, we examined (de Kroon et al. 2000) the responses of elasticities for three animal and three plant examples and found that the degree of nonlinearity was not large. Elasticities were highly significantly correlated with the percent change in lambda as caused by reductions in parameter values as large as 50% (R^2 values of 0.687 and 0.946 for the animal and plant species, respectively). Our results also show that a linear approximation (percent change in $\lambda \approx$ percent change in transition element \times elasticity) predicted larger changes in lambda quite accurately (Heppell 1998; Caswell 2000), with the exception of one transition with a very high elasticity (0.61). We (de Kroon et al. 2000) conclude that elasticities also provide accurate quantitative estimates of large changes in vital rates, which is equally apparent from the simulation results of Mills et al.

Misleading Nature of Predictions Based on Elasticities When Vital Rates Change to Their High or Low Values Observed in Nature

Mills et al. fail to make a clear distinction between problems that arise because elasticities are local estimates

and problems that are due to the fact that the proportional changes examined by elasticities are different from the actual variation in transition rates. Elasticities do not say anything about the contribution of vital rates to variance in lambda. Several recent papers stress the importance of distinguishing between prospective methods, such as elasticity analysis, that examine the functional dependence of lambda on its vital rates and which are independent of observed variation in those rates and retrospective methods that examine the importance of variation in vital rates on variation in lambda (Caswell 1997, 2000; Horvitz et al. 1997). Hence, when the changes predicted by elasticities are compared with changes corresponding to the actual variation in transition rates, it is important to remember that discrepancies do not arise because elasticities make inaccurate predictions but because we want to know something in addition to the metric provided by elasticities.

Not unexpectedly therefore, the fit between predicted and observed values that Mills et al. found is poorer when vital rates are allowed to vary according to observed minimum and maximum values recorded in the field (their Fig. 6). It is hardly surprising, however, that elasticities that examine the effects of similar proportional changes do not agree with entirely different changes that are not proportional. For example, Mills et al. compared the effects on population growth of a 5% increase in survival with a 123% increase in reproduction for desert tortoises in class 6. It is misleading to regard such a mismatch as “quite misleading.” Mills et al. conclude that “Therefore, elasticities from a mean or ‘best guess’ matrix are not enough, by themselves, to accurately predict how population growth will change as vital rates change.” But when Mills et al. used simulations that incorporated the actual magnitude of the variation by weighing elasticities by the proportional change in the vital rate, the changes in population growth rate again correspond well with the predictions (“much closer,” “scatter reduced,” and “improved considerably,” according to Mills et al., their Fig. 7). The results of their study therefore suggest that elasticities are accurate in predicting the effect of specified vital rate changes, but of course elasticities cannot say anything about the size of the change in vital rate.

The change in vital rates that we will be able to achieve may be constrained by biological factors, technical difficulties, monetary costs, or political considerations. Measures directed toward high-elasticity transitions will therefore often be much less effective than indicated by their elasticities. This is especially true if vital rates that are associated with high elasticities are more difficult to perturb than low-elasticity transitions, as analyses of the actual variation in vital rates seem to suggest (Ehrlén & van Groenendael 1998; Pfister 1998; Saether & Bakke 2000). Whether the actual causes of observed variation in vital rates are random (due to envi-

ronmental stochasticity) or manageable (e.g., related to habitat quality that may be manipulated) will determine the importance of this variation for population management (Wisdom & Mills 1997; Caswell 2000; Mills et al. 1999). Elasticities therefore cannot be the sole tool to identify the life-cycle phases to which effort should be directed (Ehrlén & van Groenendael 1998). An evaluation of the elasticity landscape for the purpose of conservation should be accompanied by knowledge about the actual transition values, their biological constraints on variation, and management options (what transitions can most easily be enhanced).

There is one other problem with the way in which Mills et al. use the range of transitions. Like several others, their study shows that the actual range of observed transition rates is not proportional to their mean. The range of variation, however, does not tell us how much transition rates vary on average. The authors themselves point this out: "Wide confidence limits can be generated by poor data or by real variation. Conversely, a limited range of conditions during sampling may not accurately reflect the possible scope for a rate." These are the serious and real problems with using range or confidence limits. For example, even if we accept the conclusions of Mills et al., we do not know how relevant their minimum and maximum values are. Do they occur once every 5 years or once every 50 years? If the observed variation in transition rates is relevant and manageable, then a better option is to include it by rescaling the sensitivities to give the effects of a change in standard deviation units (van Tienderen 1995; Ehrlén & van Groenendael 1998; Ehrlén 1999).

Conclusion

We fully agree with Mills et al. that the results of elasticity analyses must be applied to conservation issues with great caution. Therefore, we welcome a critical examination of how elasticities can be used. To really be of guidance to management work, however, the conclusions of such examinations must be clear and well founded. In the examples put forward by Mills et al., we found that elasticities provide accurate estimates not only for small changes in one vital rate but also for larger changes and for multiple changes. Their simulations also indicate that it is sometimes important to account for unequal variation in transition rates when making man-

agement decisions. Unequal variation, however, is not a problem of elasticities. We therefore conclude that the general statement made by Mills et al., that elasticities can give inaccurate predictions of the response of lambda, remains unfounded. Hence, there seems little reason to doubt that elasticities, in spite of their limitations and when applied cautiously, are a central and important tool in conservation biology (Benton & Grant 1999; de Kroon et al. 2000; Heppell et al. 2000).

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