Use of Substitute Species in Conservation Biology

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Abstract: *In conservation biology, researchers often want to study the reasons why an endangered population is faring poorly but are unable to study it directly for logistical or political reasons. Instead they study a species that substitutes for the one of concern in the hope that it will cast light on the conservation problem. Here we outline the assumptions underlying this approach. Substitutes can be different populations or species and may be chosen because they are similar biologically to the target or representatives of a constellation of species of which the target is one. They also may be used to develop a predictive model to which the conservation target can be related. For substitutes to be appropriate, they should share the same key ecological or behavioral traits that make the target sensitive to environmental disturbance and the relationship between population vital rates and level of disturbance should match that of the target. These conditions are unlikely to pertain in most circumstances and the use of substitute species to predict endangered populations' responses to disturbance is questionable.*

Key Words: model systems, representative species, surrogates

El Uso de Especies Sustitutas en Biología de la Conservación

Resumen: *En biología de la conservación, los investigadores a menudo quieren estudiar las razones por las que una población en peligro está en declinación pero no lo pueden hacer directamente por razones logísticas o políticas. En lugar de eso, estudian a una especie que la sustituye con la esperanza de que proporcione luz sobre el problema de conservación. Aquí delineamos los supuestos subyacentes en este método. Los sustitutos pueden ser poblaciones o especies diferentes y pueden ser seleccionados porque son biológicamente similares a la especie blanco o representan a una constelación de especies de la que forma parte la especie blanco. También pueden ser utilizados para desarrollar un modelo predictivo con el cual puede ser relacionado el blanco de conservación. Para que los sustitutos sean adecuados deben compartir las mismas características ecológicas o conductuales que hacen que la especie blanco sea sensible a la perturbación ambiental y la relación entre tasas poblacionales vitales y el nivel de perturbación deben ser correspondientes. Es probable que estas condiciones no prevalezcan en la mayoría de las circunstancias y por lo tanto el uso de especies sustitutas para predecir las respuestas de poblaciones en peligro a la perturbación es cuestionable.*

Palabras Clave: sustitutos, especies representativas, sistemas modelo

Introduction

There is an increasing trend toward using surrogate systems to find solutions to conservation problems. Surrogate systems fall into two major categories: those that use the presence of a species to identify areas that should become the focus of conservation attention (e.g., Lambeck 1997; Simberloff 1998; Caro & O'Doherty 1999; Andelman & Fagan 2000; Zacharias & Roff 2001; Sanderson et al. 2002; Caro et al. 2004) and those that use the response of one species or population to an environmental disturbance to predict the response of another to a similar disturbance (e.g., Oatley et al. 1992; McComb et al. 2001). The second category often involves situations in

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which a researcher is unable to study a species or population of conservation concern because of (1) difficulty in locating and observing individuals of rare and often persecuted species, (2) potentially inadequate sample sizes (few individuals from a small population), (3) concerns about disrupting a small population when carrying out experiments, (4) difficulties in obtaining permission to work on rare species, (5) financial problems in carrying out research far from a home institution, or (6) scientific territoriality over work on small populations of charismatic species. In other situations, however, researchers also study common species to generate predictive ecological models of rare species.

Both strategies involve the use of substitute species, which we define as "species or populations that are studied on the assumption that they show how populations of conservation concern might respond to environmental disturbance." We evaluated the utility of conservation substitutes by identifying different types of substitutes that can be used in studying population responses to anthropogenic change, discussing the logic underlying the use of such substitutes and outlining criteria that must be met for studies of substitute species to prove useful in tackling conservation problems (Westoby 2002).

Choosing Substitute Species

The use of substitute species in conservation biology is a special case of the application of scientific model systems. In medicine, for example, mice are used as alternatives to humans because insights can be gained from subjecting mice to procedures that would not be either feasible or allowed on humans. The underlying assumption is that for certain aspects of biology (e.g., genetics, histology, physiology) the mouse is thought to be similar enough to humans to yield medical insights. Similarly, in aquatic ecotoxicology, laboratory studies focus on the fathead minnow (*Pimephales notatus*), the African clawed frog (*Xenopus laevis*), or the zooplankter *Cerodaphnia* because the physiological responses of these organisms are thought to be indicative of other organisms in aquatic systems. Although ecotoxicologists and the public may have little inherent interest in these species per se, it is thought that if pollutant concentrations negatively affect these species, they are also likely to affect other species of direct interest and, presumably, the ecosystem overall.

More formally, substitute species have been selected in one of three ways: (1) They are chosen on the basis of close genetic or ecological similarity (Fig. 1a). Here the response to disturbance is assumed to approximate closely the response of the target species to the same disturbance. For example, if the key trait is dispersal tendency and the species' response to habitat fragmentation

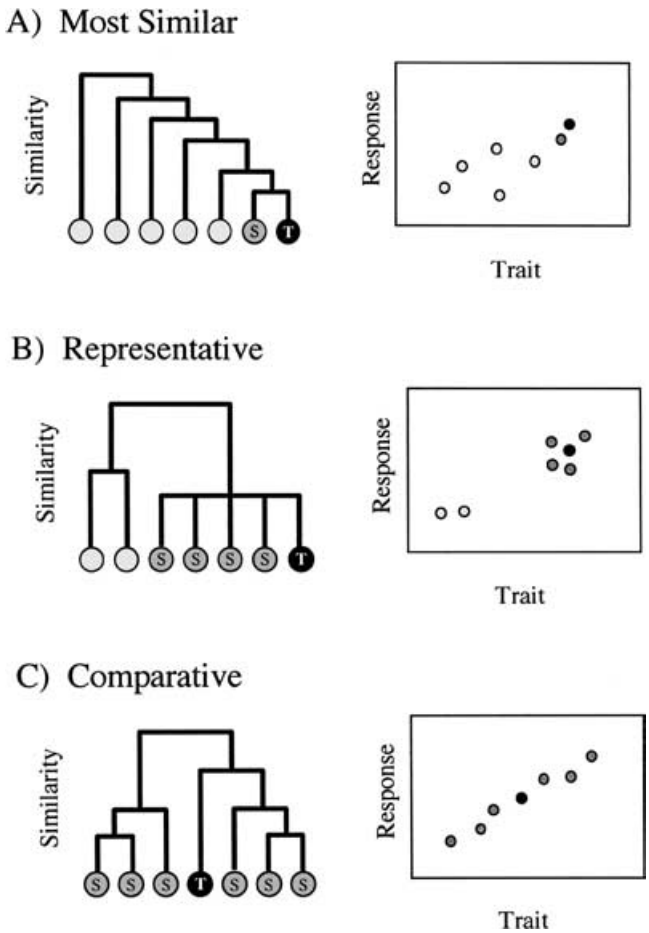

Figure 1. Schematic representation of possible substitute-species systems to link response (λ) to disturbance. Panels on the left indicate the degree of similarity between the target species of conservation concern (T circle) and possible substitute species (S circle). Similarity may be measured as phylogenetic, behavioral, and/or ecological. In (a) a substitute species (S) is chosen on the basis of being most similar to the target species. Even if the target species is specialized, one can predict its response based on knowledge of the traits exhibited by the substitute (second right dot, right panel). In (b) a group of species are sufficiently similar to each other and to the target species that any one of the group could serve as a representative substitute. Hence knowledge of the traits exhibited by any member of this group (to the right in the right panel) will be adequate to predict the response of the target species. In (c) the target species may be dissimilar from possible substitute species. A reliable relationship exists, however, between the trait and the response variable as determined by a comparative analysis of several other "substitute" species. The response of the target (center dot) can then be predicted from knowledge of the trait alone.

(Robinson 1992; Gehring & Swihart 2003), then this first type of substitute species would be a very closely related, ecologically similar species that exhibits similar dispersal tendencies to the target but whose population is still doing well because it has not yet been exposed to high levels of fragmentation. (2) The substitute is chosen because it is a member of a group of species, any of which could serve as a representative (Fig. 1b). These substitutes involve a set of species whose numbers are unlikely to have a population response identical to the target species and seem similar enough to the target that if they exhibit a consensus pattern it is likely to be close to the target's response (Dearborn et al. 2001; Weseloh et al. 2002). (3) Substitute species are chosen because they supply information that will help identify the shape of the response curve to differences in trait values (Fig. 1c). In this case, many of the species studied might not be similar to any particular target species. This is the "brick in the wall of science" idea, in which research findings slowly build a picture of how two variables are related to each other. Here, and in contrast to 1 and 2, substitute species are used to develop, test, and refine general theory often based on first principles. These species might be quite different from the target species, but the target follows the same relationship (i.e., falls on the same line) as the substitute species (Van Vuren 1998).

Underlying Logic of Substitute Species

In conservation, a common goal is to determine how a target species will be affected by some action, either a disturbance (having a negative effect) or a conservation effort (having a positive effect). Use of a substitute species presumes that it will respond to these actions in a similar manner, yet the assumptions underlying this expectation are rarely specified. To clarify these assumptions, we express the degree of similarity between substitute and target in a formal conceptual format. Conservation interest is often centered on the conditions that allow a target species to persist (i.e., when $\lambda \geq 1$, where λ is the population's finite growth rate rather than a physiological response as in ecotoxicology). In particular, one may be interested in the effects of an environmental stressor or disturbance, D (often anthropogenic), on population growth rate, $\lambda(D)$. A related metric of interest might be the population's persistence threshold, the level of disturbance, D^*, that results in borderline species persistence ($\lambda(D) = 1$). A disturbance level $> D^*$ results in population decline (Fig. 2a).

The most optimistic scenario is that the substitute and target species have similar $\lambda(D)$ functions (Fig. 2b). The substitute species might be doing well, whereas the target is declining simply because the target is exposed to greater stress than the substitute. In that case, the two should have similar persistence thresholds and, in general, under conditions when the substitute does well the target should do well. Conversely, when the substitute does poorly, so should the target (Fig. 2b). A plausible alternative, however, is when the target and substitute

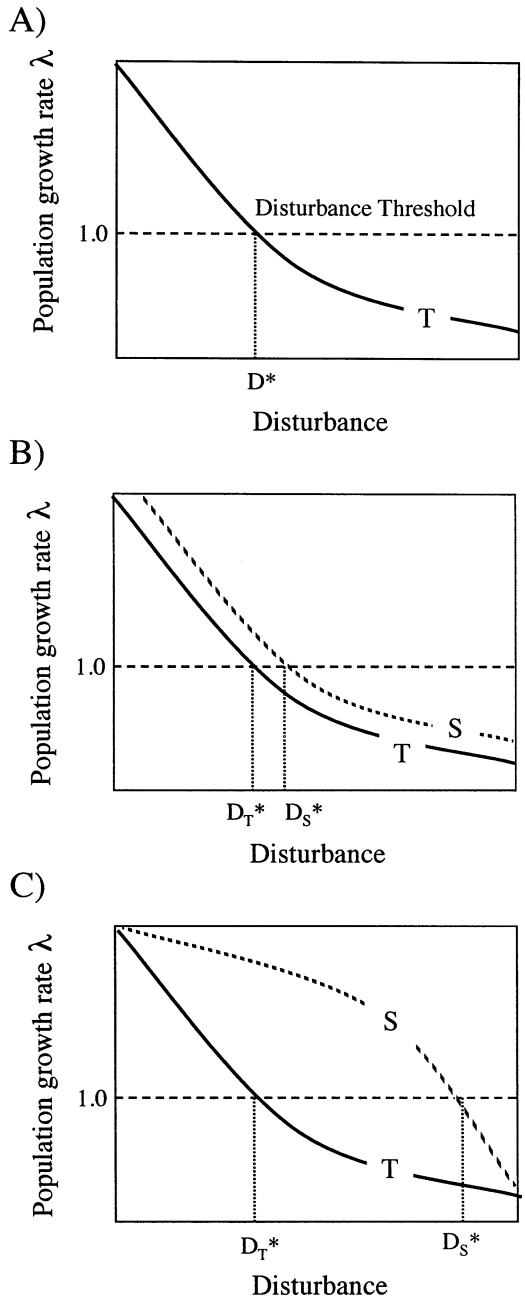

Figure 2. (a) Population growth rate (λ) plotted against increasing level of disturbance (D) for target species (T). In (b) the target species (T) and substitute species (S) have similar trajectories such that the level of disturbance that results in $\lambda = 1$ (a stable population growth rate) (termed D) is similar for T and S. In (c) S is relatively impervious to disturbance having a much higher D* than T.*

have different trajectories as disturbance increases, with the target faring poorly relative to the substitute (Fig. 2c). In that case, knowing more about $\lambda(D)$ and D^* for the substitute might be of little use and could even be misleading for managing the target.

Additionally, in many cases, in lieu of studying disturbance thresholds or demography directly, traits that are thought to influence demography and responses to disturbance are studied. In this situation, one requires at least three pieces of information to have confidence that study of a substitute species will yield useful predictions for the target (i.e., the scenario in Fig. 2b): (1) One needs to know the relationship between the level of disturbance (D) and a demographic response (ultimately λ), specifically, the disturbance threshold (D^*) below which a substitute population is no longer viable. (2) One needs to identify the key trait (X) or set of traits for the substitute that influences this threshold (i.e., we need to link a trait to the substitute's demographic response). (3) One needs to know the "value" of this trait possessed by the target and substitute if one is to predict the response for the target based on the substitute's trait values. So, our working hypothesis is that if one knows the relationship (1) between D and λ and specifically can identify the disturbance threshold (D^*) for the substitute species and (2) the relationship between the disturbance threshold (D^*) and a key trait (X) of the substitute, then (3) knowing only the value of this trait (X) for the target species one can reliably predict D^* for the target and is therefore justified in drawing inferences from a substitute species.

How Might Substitutes Fail to Predict the Target's Response?

When might the substitute gambit fail? First, and most obviously, the target may be under far greater disturbance than any candidate substitute species one might choose to study (e.g., rhinoceroses poached for their horns; Leader-Williams & Albon 1988). Second, a substitute species would be inadequate if there is no relationship between the disturbance threshold D^* and the key trait X across a group of species or populations. This might occur simply because the wrong trait was identified or because substitutes were studied only under good conditions (i.e., failure to determine accurately the shape of the D-λ curve over a sufficiently broad range of D). Third, even if there is a relationship between D^* and X for the substitute species, the target species may fall off the curve. There are at least two possible reasons for this: (1) The relationship between D^* and X no longer holds (perhaps because the target is additionally insulted by another factor or the target possesses such an unusual phenotype that the usual rules do not pertain (the reason why the target is in trouble in the first place). (2) A relationship between D^* and X does exist but is fundamentally different for the target species (Fig. 2c). For example, species of conservation concern may be subject to different patterns of density dependence because they exist as small populations, which might alter relationships between key traits for substitute and target disturbance thresholds.

Usefulness of Substitute Species in Addressing Conservation Questions

Can we ever be confident that a substitute species will provide a reliable indication of the expected response of a target species? The fact that the target is faring poorly but substitutes are doing well must mean either that potential substitutes have not yet been exposed to high levels of disturbance (e.g., Fig. 2b), or that the target is a member of a taxon that is much more sensitive to the disturbance (e.g., Fig. 2c). In the first case, study of a substitute species might prove useful assuming increased levels of disturbance would affect the target species in the same way. In the latter case, the target's poor ability to cope with stress might reflect the possibility that it falls far from the line for other substitutes. In that case, studying substitutes is not likely to yield useful insights for the target species.

Unfortunately, it seems plausible that species of conservation interest are indeed often fundamentally different from other species (Gaston 1994). After all, target species are the ones that are doing poorly, whereas other taxa continue to persist or even thrive despite human disturbance. The literature is replete with examples of species living in the same disturbed habitat showing differential sensitivities to human-induced landscape alteration (e.g., Marsh & Pearman 1997; Collinge 2000; Crooks 2002; Klein et al. 2002; Crooks et al. 2004). In these cases the focus of study should not be on a substitute species but on the specific limiting traits that make the target species particularly poor at coping with key stressors (Sih & Gleeson 1995). Promising approaches include the study of gene flow disrupting local adaptation (Storfer & Sih 1998), assessments of effects of lack of evolutionary history with a given stressor (Berger et al. 2001), or assessments of the possibility of sensory-based evolutionary traps (Schlaepfer et al. 2002).

In general, we suggest that three criteria must be met if we are to use substitute species with confidence. The relationship between levels of disturbance (D) and demographic vital rates (ideally λ) must be established for the substitute species. This is no minor feat, particularly because to quantify a demographic parameter (λ) considerable effort must be made to follow marked individuals over several years. Moreover, one needs these data over a broad-enough range of levels of D to develop a predictive relationship. The key trait (X) or traits affecting demographic viability in the substitute and target species must be identified. Again, this is no small task, and there are

numerous examples where researchers thought a particular factor was responsible, but it turned out to be quite another. For example, the use of nestboxes as a restoration tool cannot be generalized across ducks because patterns of territoriality differ, making species differentially sensitive to intraspecific brood parasitism (Eadie et al. 1998). The relationship between the trait value (X) and the disturbance threshold (D^*) must be established for the substitute species. One needs this information for several species or populations with differing values of X to develop a predictive relationship for D^*. Even assuming one can determine these values, there is still the possibility that the target may differ from the substitutes' relationship between D^* and X.

To us, these three hurdles seem almost insurmountable; thus, in most cases we suspect it is incautious to use substitute species, especially in a discipline such as conservation biology, where caution is the watchword (Caro & Eadie 2005). This leaves unanswered the question of what to do if one absolutely cannot study the target species. We suggest the following: (1) Identify the traits most likely to affect the demographic viability of the target species and find substitute species that share those traits. (2) Measure λ for the substitute species rather than some other reproductive parameter, and establish a relationship between D and λ for substitute species. This at least indicates how D could affect population viability in a general sense and determines whether a disturbance threshold (D^*) exists. (3) Study substitutes with a sufficient range of values of X so that one might establish a relationship between X and D^* (i.e., focus on a number of substitute species in the same research program). (4) Failing the above, efforts to determine whether X affects any demographic parameter could provide insight into how the target species would perform given its values of X. In all cases, researchers should make explicit their assumptions when observing a substitute species rather than trying to convince readers that the substitute is a good model for solving a conservation problem.

Conclusion

In contrast to the use of indicator species in ecotoxicology, where physiological responses of substitute and target to pollution are known or assumed to be similar, in conservation biology similar demographic responses of substitute and target species to anthropogenic change cannot be taken for granted. Because conservation decisions are important for society and researchers have a responsibility for making well-informed recommendations to management authorities and political institutions, it is appropriate to proceed with great caution. Our arguments indicate that the assumptions required to use substitute species in conservation biology are too onerous when applied to trying to predict population responses to anthropogenic disturbance. Where at all possible, we advocate making every possible effort to examine the target species directly before resorting to substitute species.

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