Contributed Paper

Use of Surrogates to Predict the Stressor Response of Imperiled Species

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Abstract: *Rare or narrowly distributed species may be threatened by stressors to which they have never been exposed or for which data are very limited. In such cases the species response cannot be predicted on the basis of directly measured data, but may be inferred from the response of one or more appropriate surrogate species. Here, I propose a practical way to use the stressor response of one or more surrogate species to develop a working hypothesis or model of the stressor response of the target species. The process has 4 steps: (1) identify one or more candidate surrogate species, (2) model the relationship between the stressor and the response variable of interest for the surrogate species, (3) adapt the stressor–response relationship from the surrogate species to a model for the target species, possibly using Bayesian methods, and (4) incorporate additional data as they become available and adjust the response model of the target species appropriately. I applied the approach to an endangered fish species, the amber darter (*Percina antesella*), which is potentially threatened by urbanization. I used a Bayesian approach to combine data from a surrogate species (the bronze darter [*Percina palmaris*]) with available data for the amber darter to produce a model of expected amber darter response. Although this approach requires difficult decisions on the part of the manager, especially in the selection of surrogate species, its value lies in the fact that all assumptions are clearly stated in the form of hypotheses, which may be scrutinized and tested. It therefore provides a rational basis for instituting management policy even in the face of considerable uncertainty.*

Keywords: amber darter, endangered species, management policy, *Percina antesella*, storm-water runoff, substitute species, surrogate species

Utilización de Sustitutos para Predecir la Respuesta de Especies en Peligro a Factores Estresantes

Resumen: *Las especies raras o de distribución restringida pueden estar amenazadas por factores estresantes a los que nunca han sido expuestos o para los cuales existen datos muy limitados. En tales casos, la respuesta de las especies no puede ser pronosticada sobre la base de datos medidos directamente, pero pueden ser inferidos de la respuesta de una o más especies sustitutas apropiadas. Aquí propongo una manera práctica de utilizar la respuesta a factores estresantes de una o mas especies sustitutas para desarrollar una hipótesis de trabajo o modelo la respuesta de la especie a factores estresantes. El proceso comprende cuatro pasos: (1) identificar uno o más candidatos a especie sustituta, (2) modelar la relación entre el factor estresante y la variable de respuesta de interés para la especie sustituta, (3) adaptar la relación factor estresante-respuesta de la especie sustituta a un modelo para la especie objetivo y (4) incorporar datos adicionales a medida que sean disponibles y ajustar el modelo de la respuesta de la especie objetivo. Apliqué el método a una especie de pez en peligro,* Percina antesella*, que potencialmente está amenazada por la urbanización. Utilice un enfoque bayesiano para combinar datos de una especie sustituta (*Percina palmaris*) con los de* P. antesella *para producir un modelo de la respuesta esperada. Aunque este enfoque requiere de decisiones difíciles por parte del manejador, especialmente la selección de la especie sustituta, su valor yace en el hecho de que todos los supuestos están claramente establecidos en forma de hipótesis, que pueden ser examinadas y probadas. Por lo tanto proporciona una base racional para el establecimiento de políticas de manejo aun en situaciones de considerable incertidumbre.*

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Palabras Clave: escorrentía de aguas pluviales, especie en peligro, especie sustituta, *Percina antesella*, política de manejo

Introduction

In the past decade the use of surrogate, substitute, indicator, and umbrella species in the practice of conservation biology has increased (reviewed by Caro & O'Doherty 1999; Carignan & Villard 2002) as has the volume of literature warning of the pitfalls of such practices (e.g., Andelman & Fagan 2000; Hitt & Frissell 2004; Favreau et al. 2006). The majority of this debate concerns the use of surrogates or umbrella species to identify conservation priorities. Nevertheless, surrogate species can also be used to predict the response of a rare or poorly studied target species to anthropogenic stressors (Wahlberg et al. 1996; Landres et al. 1988; Caro et al. 2005). (I use *surrogate species* in the same sense Caro et al. [2005] used *substitute species*.) This latter practice has been criticized as "incautious" (Caro et al. 2005) or "inappropriate" (Landres et al. 1988) because there are no guarantees that the target species will respond in the same manner as the surrogate.

Nevertheless, there are cases in which the response of a species to a potential stressor cannot be known from existing data, and suitable experiments cannot be conducted without jeopardizing survival of the species. This is especially true for narrowly endemic species, many of which are imperiled. For example, the amber darter (*Percina antesella*)—a small freshwater fish—only occurs in 2 rivers in the headwaters of the Coosa River system in the southeastern United States. Populations in both rivers are potentially threatened by increasing urbanization, but because of the limited distribution of the species, it has not yet been sufficiently exposed to the effects of urbanization to determine thresholds of response. A "natural experiment" in which the species is exposed to increased urbanization could threaten its survival. A potential solution is to examine the relationship between urban cover and a surrogate species that is related to the amber darter or that has similar habits but is more widely distributed so that it has been exposed to urbanization over part of its range. A working hypothesis of the stressor response of the amber darter can be built on this surrogate stressor response and provide a rational basis for managing urban-related stressors.

Motivated by the practical need to institute management policies for the amber darter and other imperiled fish species, I propose a way to use data from surrogate species to inform predictive models for the response of a target species to stressors. Use of a surrogate is appropriate only when it is infeasible to directly measure the response of the target species to the stressor (or when such data are very limited) and when urgent management action is required (Landres et al. 1988). A similar approach has been used previously to parameterize demographic and metapopulation models (e.g., Wahlberg et al. 1996; Schtickzelle et al. 2005) with data from surrogate species. My focus here is on relatively simple statistical models that correlate some indicator of population status, such as species occupancy, abundance, or population growth rate (lambda), with an anthropogenic stressor. This class of model may be the only option available for species with unknown or difficult-to-estimate demographic parameters. I describe the approach, apply it to the amber darter as an example, and discuss the conditions under which it might be effectively used for other species.

Approach

The general approach is to develop a statistical stressor–response relationship for a surrogate species and then to "transplant" this relationship into a model for the target species. This can be done in a 4-step process: (1) identify one or more candidate surrogate species, (2) model the relationship between the stressor and the response variable of interest for the surrogate species, (3) adapt the stressor–response relationship from the surrogate species to a model for the target species, and (4) incorporate additional data as they become available and adjust the response model of the target species.

Identify Candidate Surrogate Species

Although many criteria have been suggested for selecting surrogate species (Landres et al. 1988; Carignan & Villard 2002), 3 are most relevant in this context: probability that the species will respond to the stressor in the same way as the target species, availability of data, and sensitivity to the stressor. The ideal surrogate is one that responds to the stressor in precisely the same way as the target species (Caro et al. 2005). Because the response of the target species is unknown, however, in practice one needs to identify candidate surrogates on the basis of other characteristics that are likely to correlate with stressor response. These could be traits such as habitat use, physiology, or phylogeny. In addition, for a surrogate to be useful, there must be sufficient data to estimate the relationship with the stressor within a reasonably narrow confidence interval or the potential to collect such data. Finally, the surrogate species must show sensitivity to the stressor. This last requirement follows from the underlying assumption that the target species is potentially sensitive to the stressor, which drives the need for some management policy. Therefore, the precautionary principle suggests that if only 1 surrogate is used it should be one that shows considerable sensitivity to the stressor. Additional surrogates, if available, may be used to bracket the range of reasonable responses—that is, to provide alternative hypotheses of the response of the target species. Another approach to incorporating multiple surrogates is to average their responses (see step 3, below).

Model the Relationship between the Stressor and the Response Variable of Interest

The next step is to generate a model of the surrogate's relationship with the stressor. The response variable can be any indicator of population status that is of interest and measurable, although population growth rate is perhaps the optimal indicator when it is available (Caro et al. 2005). The modeling method can be any technique that produces a model that may be decomposed into individual parameter estimates. In most cases it is only the individual parameter estimate for the species response to the stressor that will be "transplanted" into the model for the target species. The rest of the target-species model is derived from empirical data so that the model accurately predicts the species distribution in the absence of the stressor on the basis of other relevant covariates (such as soil type or stream size). Then, in step 3, the transplanted parameter estimate for the stressor is added to this model to predict species response when the stressor is present. The need for an individual parameter estimate for the stressor precludes the use of modeling techniques such as neural networks (e.g., Joy & Death 2004) that cannot be decomposed into individual parameter estimates. Similarly, the use of interaction terms involving the stressor will generally be precluded. The only exception to these restrictions is the case in which the surrogate species is likely to behave so similarly to the target species that the entire predictive model may be transplanted. This might be the case, for example, if the surrogate and target are closely related species or different populations of the same species.

Adapt the Stressor–Response Relationship from the Surrogate Species to the Target Species

The ultimate goal of this process is to produce a model that adequately represents the current population status of the target species and incorporates its response to future increases in stressor levels on the basis of the response of the surrogate(s). There are several decisions to make in determining how to build this model. For simplicity, I first discuss the case in which there is only one surrogate species and then extend the discussion to multiple surrogates.

A key decision is how to combine data from the surrogate species with data (if any) from the target species. There are 3 options. First, one could develop a well-supported predictive model of the response variable (i.e., population status) of the target species that does not incorporate the stressor and then extend the model by adding the parameter estimate for the stressor variable derived from the surrogate-species model. This approach assumes that the target species will respond exactly the same way as the surrogate species.

Second, if some data on the target species response to the stressor are available, a Bayesian or empirical Bayesian approach can be used to combine data from the surrogate species with data from the target species (Link & Hahn 1996; Noon 2002; Linacre et al. 2004; McCarthy & Masters 2005). The estimate of the surrogate species parameter for the stressor variable may be treated as a "prior" (in the Bayesian sense) for the stressor variable in the target species model. Models for the target and surrogate species may be solved simultaneously. Again, only the parameter estimate for the stressor variable is shared among the 2 species models; parameter estimates for other predictor variables of the surrogate species do not affect the other predictor variables of the target species. An analogous approach may be used in a maximum-likelihood framework by treating the stressor variable as a shared parameter between both models and solving simultaneously.

Third, in the rare case in which it can be assumed that the model for the surrogate species is adequate for the target species (see step 2), the surrogate-species model may be used directly as a substitute for creating a model for the target species.

In all cases it is useful to evaluate the model performance by testing its ability to predict population status under current conditions. A poor-performing model should be improved, if possible, by adding or removing covariates. This type of post hoc tweaking is acceptable because at this stage the goal is not hypothesis testing, but the development of a good-fitting predictive model to serve as a hypothesis of response under future or hypothetical conditions.

There are 2 ways in which data from multiple surrogates may be used. The first is to use the multiple responses to place bounds on the potential response of the target species; these can be viewed as alternative hypotheses of species response. For purposes of management, it may be necessary to select one of these (such as the most sensitive) as the working hypothesis. The second approach is to average the surrogate responses, perhaps with Bayesian methods. This expresses the full range of uncertainty in the response of the target species in one model, although the mean of the resulting probability distribution may show considerably less sensitivity to the stressor than the most sensitive surrogate. Therefore, if this approach is used, it would be more conservative to base the working hypothesis and associated management action on a lower quantile of the resulting distribution (such as the 10% or 25% value) rather than on the mean.

Incorporate Additional Data as They Become Available and Adjust the Response Model

Ideally, additional data will take the form of observations of the target species in relation to the stressor, which can provide an actual test of the working hypothesis established from the surrogate species responses. This may come from field observations or laboratory studies. In cases in which the stressor is effectively managed, however, field observations may not yield new information because the stressor levels will not increase. If laboratory studies are not possible, some additional confidence may be gained by collecting more data on surrogates. Again, Bayesian methods may be useful in combining data from multiple sources.

Amber Darter Example

The amber darter is a small fish endemic to the Conasauga and Etowah Rivers in Georgia and Tennessee (U.S.A.). It is confined to reaches within the mainstem of the Conasauga River, the mainstem of the Etowah River, and the lower sections of a few major Etowah tributaries. The species is listed as endangered under the U.S. Endangered Species Act and is 1 of 3 species targeted for protection under a proposed habitat conservation plan (HCP) for the Etowah basin. Storm-water runoff from impervious surfaces within the rapidly urbanizing Etowah basin is believed to be a major threat to the species survival; management of runoff is a central component of the proposed HCP (Etowah HCP Advisory Committee 2007; Wenger et al. 2008*a*). Nevertheless, owing to its limited range, the response of the amber darter to indicators of urban effects cannot be inferred from present distribution patterns. Although the amber darter has been found at a few sites in the Etowah mainstem in the vicinity of the city of Canton, Georgia, it would be premature to conclude that the species is tolerant of urbanization on the basis of these few collections. Therefore, to set levels of storm-water control that are likely to be protective but not unnecessarily restrictive, the relationship between the amber darter and the stressor must be estimated with information from surrogate species.

Although urban runoff is a complex phenomenon (Walsh et al. 2005), its relationship to biota can be roughly estimated on the basis of effective impervious area (EIA) as an indicator. The EIA is the subset of impervious surfaces that is connected to streams by the conveyance network; this measure correlates better with species population status than total impervious area (Hatt et al. 2004; Walsh et al. 2004). Results of previous studies provide information on the relationship between presence and absence of fish species of the Etowah basin and EIA (Wenger et al. 2008*b*). These 5 species are potential surrogates for the amber darter in that they meet at least 1 of the 3 criteria—the availability of data. The next step is to identify one or more species that meet the other 2 criteria.

Identify Surrogate Species

Wenger et al. (2008*b*) examined the relationship of fish occurrence with EIA for 5 species: tricolor shiners (*Cyprinella trichroistia*), speckled madtoms (*Noturus leptacanthus*), Etowah darters (*Etheostoma etowahae*), Cherokee darters (*E. scotti*), and bronze darters (*Percina palmaris*). The bronze darter is congeneric with the amber darter and similar to the amber darter in foraging mode and habits and thus might respond to urbanization in a similar manner. The bronze darter and amber darter, however, are not especially close relatives. Phylogenetic relations among species of *Percina* are largely unresolved, but the 2 species are assigned provisionally to different subgenera (Near 2002). Nevertheless, only one other member of the amber darter's *Imostoma* clade (Page 1974; Near 2002) is known from the upper Coosa River and it is extremely rare. Of the species of *Percina* sympatric with the amber darter, the bronze darter is the most similar in habits and habitat used. In addition, modeling indicated that the bronze darter was sensitive to EIA, which satisfies the final criterion for a useful surrogate species. Thus, I chose the bronze darter as the primary surrogate and considered the responses of the other species alternative hypotheses of the amber darter's response.

Estimate the Response of the Surrogate to the Stressor

The response variable of interest was probability of presence (i.e., species occupancy), and the stressor was measured in units of EIA. I estimated the responses of the bronze darter and other species to EIA with hierarchical logistic regression with methods that account for imperfect detection probability. I used 357 samples collected between 1999 and 2003 from 252 sites in the Etowah basin. Details of the modeling are described in Wenger et al. (2008*b*). I selected the best-supported model for each species from multiple competing models. The best model for the bronze darter, including mean coefficient estimates, was

$$\begin{aligned}\text{logit (occurrence)} = {} & -2.68 + 3.85 * \text{area} - 0.12 * \text{area}^2 \\ & + 1.17 * \text{dlink} - 1.49 * \text{dlink}^2 \\ & + 0.38 * \text{elevation} \\ & + (-1.21 * \text{impounded}) \\ & - 7.25 * \text{EIA} + 0.44 * \text{slope},\end{aligned}$$

where logit is the logit transformation, area is watershed area, dlink is downstream link magnitude, impounded is the area in the tributary system impounded by dams, and slope is the mean slope of the tributary system. All parameters were normalized.

Adapt the Stressor–Response Relationship from the Surrogate Species to the Target Species

Because there were some data on the amber darter's distribution that could inform its relationship with EIA, I used a Bayesian approach to combine information from both species. I used the posterior parameter estimate for EIA from the best-supported bronze darter model as the prior for the EIA parameter estimate for the amber darter. I used diffuse (noninformative) priors for the parameters of the bronze darter model. The only other parameter in the amber darter model was watershed area, which was sufficient to describe the distribution of the species in large streams. The same data set of 357 collection records was used for both species, although amber darters were only observed in 50 collections at 13 of the sites, whereas there were 103 records at 60 sites for the bronze darter. The resulting amber darter model, including mean coefficient estimates, was

$$\text{logit (occurrence)} = -7.09 + 3.29 * \text{area} - 2.56 * \text{EIA}.$$

The response curve for the bronze darter indicated that the species occurrence probability approached zero at about 5% EIA, on the basis of the mean parameter estimate for EIA (Fig. 1a). The response curve for the amber darter indicated that occurrence probability approached zero at about 10% EIA (Fig. 1b). This difference reflected the influence of the data points for the amber darter itself, particularly the fact that some collections had been made in the vicinity of urban areas. The 90% credible interval for the amber darter EIA parameter was also quite broad. The response curve for the 5% value indicated that occurrence probably could approach zero at as little as 5% EIA, whereas the curve for the 95% value indicated that this threshold could be higher than 20% EIA.

I used 3-fold cross-validation to estimate performance of the amber darter model in predicting existing presence and absence records. The model correctly predicted amber darter presence and absence 97% of the time. This value was high because the species is confined to those sites within the data set with the largest drainage area, making it easy to correctly predict absence from all smaller streams. Because raw predictive performance measures are in general biased high for rare species (Manel et al. 2001), we also calculated the area under the curve (AUC) of the receiver–operator characteristic (ROC) plot, a measure of the ratio of true positives to false positives when the species occurrence decision threshold is varied between zero and one. The AUC of the ROC is considered a robust measure that is reportedly invariant to species prevalence (Manel et al. 2001; Olden et al. 2002). The AUC score was 0.99, which indicated very good predictive performance. Of course, this was a measure of the model's ability to predict the fish's distribution under current conditions and did not provide a measure of performance under future conditions.

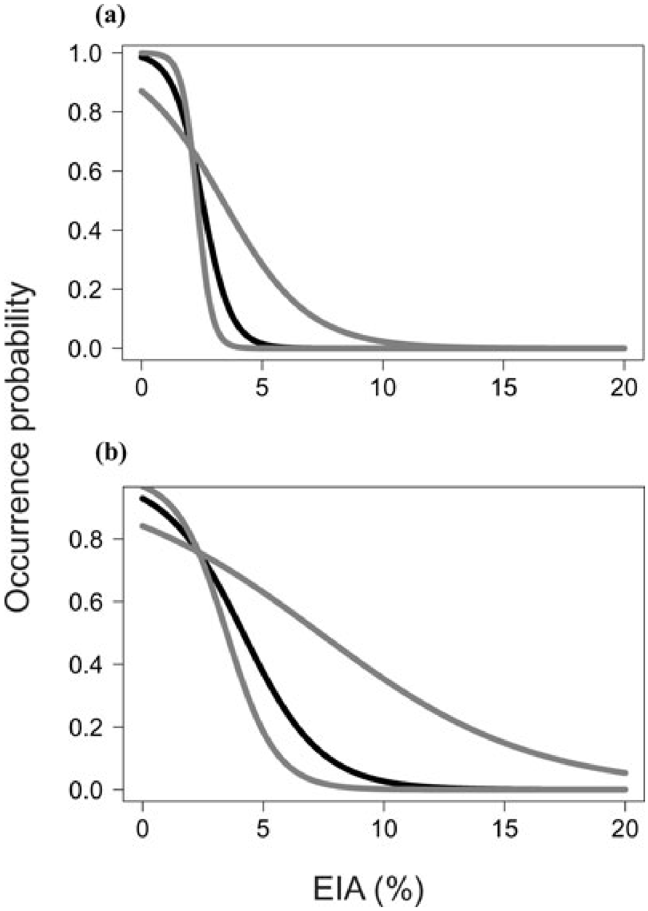

Figure 1. Modeled occurrence probability of the (a) bronze darter and (b) amber darter in response to increasing impervious cover. Black lines are the response curve for the mean parameter estimate for effective impervious area (EIA) and gray lines are the response curves for the 5 and 95% values for the parameter estimate for EIA.

The responses of the other 4 species provided alternative hypotheses for the amber darter. The most sensitive species was the tricolor shiner, which became very rare at EIA of 2% and above (Wenger et al. 2008*b*). The least sensitive species was the Cherokee darter, for which EIA was not a useful predictor of occurrence (although EIA was correlated with Cherokee darter abundance; Wenger & Freeman 2008).

Incorporate Additional Data and Adjust the Response Model

Under the Etowah Aquatic HCP, the estimated mean response of the amber darter to EIA is used to guide storm-water management policies that limit future EIA (Etowah HCP Advisory Committee 2007; Wenger et al. 2008*a*). As additional urbanization occurs under these policies, the response of the amber darter will be monitored and the resulting data incorporated into an updated model. Depending on the outcome, the storm-water policy may be adjusted by means of the adaptive management provisions of the HCP. Future studies that shed light on the mechanisms of the effects of storm water on fish species should also be considered as sources of data to be incorporated into the amber darter model.

Discussion

The approach to predicting the response of a data-poor species of conservation interest to increasing stressors builds on previous studies in which data from surrogate species were used to parameterize metapopulation models and demographic models (e.g., Wahlberg et al. 1996; Schtickzelle et al. 2005) and especially population viability analyses (PVA; Etterson & Bennett 2006). In previous applications, however, data on surrogate species were used to augment or fill information gaps in the target species data, or data on target species were used to validate predictions from a surrogate-species model. Here, I extended the use of surrogate data to cases in which a lack of data precludes the use of PVA and other demographic techniques and in which species are so narrowly distributed that they may not be exposed to the stressor of concern, such that model predictions may not be testable in the near future.

This approach is appropriate when there is a need for immediate management action because of an impending threat and data on the species of concern are insufficient to guide that action. The approach is probably most applicable to narrowly distributed endemic species that have not yet been exposed (or have had limited exposure) to a stressor that will likely negatively affect the organism. Nevertheless, if there is no impending threat, it is possible that management action may be deferred until additional data are collected, perhaps through experimental laboratory approaches. For example, if a species is thought to be directly threatened by a chemical toxin, it may be possible to rear some individuals in captivity in order to conduct exposure trials. Naturally, studies will be more challenging and time-consuming if threats are more complex or poorly understood, such as is the case with storm-water runoff from impervious surfaces. In such cases, management actions derived from surrogate-species models may be necessary for extended periods of time. The advantage of using this approach to guide management actions is that assumptions underlying the use of a surrogate-based model are clearly stated. The model for the target species is a working hypothesis subject to scrutiny and debate.

The principal challenge of the approach is that it requires some difficult choices on the part of the researcher, particularly in selection of the surrogate. There are many cautionary tales of the use of inappropriate surrogate species in conservation planning (e.g., Andelman & Fagan 2000; Hitt & Frissell 2004), and those warnings are well heeded in this context as well. A close analogy may be drawn with the use of surrogate species for estimating contaminant sensitivity to targets. In setting aquatic toxicity standards, it has long been the practice to use a few fish species (e.g., fathead minnow [*Pimephales promelas*]) as surrogates for all other species, although researchers point out that the probability of selecting the most sensitive species as surrogates is very small, suggesting that at least some species will be unprotected by these standards (Cairns 1986). Others recommend the use of safety factors in setting toxicity standards, especially in cases of species of conservation concern (Sappington et al. 2001; Besser et al. 2005). In the approach I present here, it is critical that the surrogate species be at least as sensitive to the stressor in question as the target species, or management policies will not be protective. This means that if possible, the stressor response of multiple species should be evaluated before selecting a surrogate or surrogates. A surrogate should not be selected a priori without estimating its sensitivity, unless there is excellent evidence that it will respond in the same way as the target (as in the case of use of a different population of the same species as the surrogate).

Landres et al. (1988) reviewed a wide range of criteria for selecting surrogate species: sensitivity, variability of response, specialist versus generalist, body size, residency status, and area requirement. They rejected all except sensitivity (which should be high), variability of response (which should be low), and residency status (which should be permanent, as opposed to migratory). Because their focus was on selecting species as indicators of habitat quality, rather than as surrogates for other species, they did not include the criterion that the surrogate species should respond similarly to the target. I substituted this latter requirement for the residency status requirement, which it will generally encompass. Otherwise, I am in agreement with Landres et al. (1988) that other criteria are relatively unimportant in selecting potential surrogates.

In some cases 2 of the criteria for selecting a surrogate may be in conflict: the species most closely related to the target (or the one most similar in habits) may not be the most sensitive. Which criterion takes precedence? There can be no hard-and-fast rule for this, and different investigators might make different decisions with the same data set. If only one surrogate is to be used, it must show at least some sensitivity to the stressor to be useful, so a closely related but highly tolerant species should generally be rejected in favor of a more distantly related but sensitive species. If there are some data available for the target species, this can also influence the decision.

In my example I based my decision not to use the highly sensitive tricolor shiner as a surrogate for the amber darter not only on phylogenetic relationships and habits but also on the fact that the scarce data on the amber darter showed occurrences in the vicinity of an urban area, which provided a piece of evidence that the species is not extremely sensitive to impervious cover. Thus, the use of an extremely sensitive, unrelated surrogate that differed greatly in habits from the target species did not seem well supported. The alternative approach is to average across multiple surrogates to obtain one broad distribution encompassing the range of possible responses. Nevertheless, this simply defers the hard work because someone must still decide whether the mean or some lower quantile represents the most appropriate working hypothesis on which to base management action. Whatever the method used, it is important to explain the logic for selection of the surrogate species so that other investigators can judge for themselves whether the choice is appropriate or not.

In my presentation of the approach and in my example, I alluded to the relationship between the stressor and the species under examination as correlative. In fact, correlation alone is insufficient; there must be at least a hypothesized causal link between the 2 (Landres et al. 1988). Furthermore, both the surrogate and target species should be linked to the stressor by the same hypothesized causal pathways. This should be shown via conceptual models that describe the hypothesized relationship between the stressor and the species population parameter of interest, including intermediate mechanistic steps to the extent that they can be described (Noon 2002). A good understanding of these relationships is also important for identifying appropriate management options. Further discussion is beyond the scope of this paper, but Noon (2002) provides an overview of how the use of surrogate species (or "indicator species") fits into the larger picture of ecosystem management and monitoring.

I emphasized the use of Bayesian statistics for combining data from multiple sources. Bayesian techniques are increasingly being used by ecologists, although this is often because they can handle complex model structures (Clark 2005), not because of a need to incorporate prior information or to combine multiple data sets. Thus, most current modeling applications use "noninformative" priors. Nevertheless, one of the real strengths of the Bayesian approach is its ability to combine data from multiple sources. McCarthy and Masters (2005) describe 2 examples in which Bayesian methods were used to combine multiple data sets that resulted in increased precision of parameter estimates and reduced need for additional data collection. The strengths of the Bayesian methods are particularly well suited to the approach I outlined here, which will often involve combining data from multiple surrogates or from one or more surrogates and a target species. Bayesian methods also allow considerable flexibility. For example, it is possible to weight data from different species according to the probability that they are useful surrogates, perhaps on the basis of phylogenetic distance from the target species.

My approach to the use of surrogate species differs somewhat from that suggested by Caro et al. (2005). They suggest that to use a surrogate species, it is necessary to identify a trait or set of traits that explains the response of a surrogate to the stressor. The response relationship can then be mapped onto the target species on the basis of the "value" of the trait. I agree that this level of mechanistic understanding is ideal and is a worthy goal, but I also agree with Caro et al. (2005) that the hurdles associated with achieving this understanding will be "almost insurmountable" in practice. In my limited experience, simply identifying traits responsible for a species' sensitivity is no mean feat. Nevertheless, in the cases where this is feasible, it is advisable to follow the methods suggested by Caro et al. (2005) and use the approach outlined here only as a fallback plan.

In determining whether to use this approach or an alternative, it may be helpful to structure the decision as a series of questions, as follows:

1. Is the species under imminent threat from stressors? If not, it may be prudent to defer action and in the interim to collect additional data to inform the species response to stressors. If the species is under imminent threat, move on to question 2.
2. Are there data from the species itself that may be used to create a predictive model of stressor response? If so, there is no need to use a surrogate. If not, or if the data are limited, move on to question 3.
3. Is it possible to use the approach recommended by Caro et al. (2005)? If so, this may be a more robust method of incorporating data from a surrogate species. If not, move on to question 4.
4. Are there data on potential surrogate species that may be used for the approach outlined in this paper? If so, then the approach I outlined may prove useful. If not, then collecting such data should be a high priority. In the interim the stressor will need to be managed on the basis of an arbitrary (but explicitly stated) assumption about species response. Taking no action also inherently reflects an arbitrary assumption: that the species is not sensitive to the stressor.

Use of a systematic, transparent process such as this in developing a working hypothesis to guide management for imperiled species should lead to defensible management decisions, even when data are in short supply.

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Literature Cited

Andelman, S. J., and W. F. Fagan. 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences of the United States of America **97:**5954–5959.

Besser, J. M., N. Wang, F. J. Dwyer, F. L. Mayer, and C. G. Ingersoll. 2005. Assessing contaminant sensitivity of endangered and threatened aquatic species: part II. Chronic toxicity of copper and pentachlorophenol to two endangered species and two surrogate species. Archives of Environmental Contamination and Toxicology **48:**155–165.

Cairns, J. J. 1986. The myth of the most sensitive species. BioScience **36:**670–672.

Carignan, V., and M.-A. Villard. 2002. Selecting indicator species to monitor ecological integrity: a review. Environmental Monitoring and Assessment **78:**45–61.

Caro, T., J. Eadie, and A. Sih. 2005. Use of substitute species in conservation biology. Conservation Biology **19:**1821–1826.

Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. Conservation Biology **13:**805–814.

Clark, J. S. 2005. Why environmental scientists are becoming Bayesians. Ecology Letters **8:**2–14.

Etowah HCP Advisory Committee. 2007. Etowah aquatic habitat conservation plan. University of Georgia River Basin Center, Athens. Available from http://www.etowahhcp.org (accessed February 2008).

Etterson, M. A., and R. S. Bennett. 2006. On the use of published demographic data for population-level risk assessment in birds. Human and Ecological Risk Assessment **12:**1074–1093.

Favreau, J. M., C. A. Drew, G. R. Hess, M. J. Rubino, F. H. Koch, and K. A. Eschelbach. 2006. Recommendations for assessing the effectiveness of surrogate species approaches. Biodiversity and Conservation **15:**3949–3969.

Hatt, B. E., T. D. Fletcher, C. J. Walsh, and C. M. Taylor. 2004. The influence of urban density and drainage infrastructure on the concentrations and loads of pollutants in small streams. Environmental Management **34:**112–124.

Hitt, N. P., and C. A. Frissell. 2004. A case study of surrogate species in aquatic conservation planning. Aquatic Conservation: Marine and Freshwater Ecosystems **14:**625–633.

Joy, M. K., and R. G. Death. 2004. Predictive modelling and spatial mapping of freshwater fish and decapod assemblages using GIS and neural networks. Freshwater Biology **49:**1036–1052.

Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology **2:**316–328.

Linacre, N. A., A. Stewart-Oaten, M. A. Burgman, and P. K. Ades. 2004. Incorporating collateral data in conservation biology. Conservation Biology **18:**768–774.

Link, W. A., and D. C. Hahn. 1996. Empirical Bayes estimation of proportions with application to cowbird parasitism rates. Ecology **77:**2528–2537.

Manel, S., H. C. Williams, and S. J. Ormerod. 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. Journal of Applied Ecology **38:**921–931.

McCarthy, M. A., and P. Masters. 2005. Profiting from prior information in Bayesian analyses of ecological data. Journal of Applied Ecology **42:**1012–1019.

Near, T. J. 2002. Phylogenetic relationships of *Percina* (Percidae : Etheostomatinae). Copeia 2002:1–14.

Noon, B. R. 2002. Conceptual issues in monitoring ecological resources. Pages 27–71 in D. E. Busch and J. C. Trexler, editors. Monitoring ecosystems: interdisciplinary approaches for evaluating ecoregional initiatives. Island Press, Washington, D.C.

Olden, J. D., D. A. Jackson, and P. P. Peres-Neto. 2002. Predictive models of fish species distributions: a note on proper validation and chance predictions. Transactions of the American Fisheries Society **131:**329–336.

Page, L. M. 1974. Subgenera of *Percina* (Percidae-Etheostomatini). Copeia 1974:66–86.

Sappington, L. C., F. L. Mayer, F. J. Dwyer, D. R. Buckler, J. R. Jones, and M. R. Ellersieck. 2001. Contaminant sensitivity of threatened and endangered fishes compared to standard surrogate species. Environmental Toxicology and Chemistry **20:**2869–2876.

Schtickzelle, N., M. F. WallisDeVries, and M. Baguette. 2005. Using surrogate data in population viability analysis: the case of the critically endangered cranberry fritillary butterfly. Oikos **109:**89–100.

Wahlberg, N., A. Moilanen, and I. Hanski. 1996. Predicting the occurrence of endangered species in fragmented landscapes. Science **273:**1536–1538.

Walsh, C. J., P. J. Papas, D. Crowther, P. Sim, and J. Yoo. 2004. Stormwater drainage pipes as a threat to a stream-dwelling amphipod of conservation significance, *Austrogammarus australis*, in South-eastern Australia. Biodiversity and Conservation **13:**781–793.

Walsh, C. J., A. H. Roy, J. W. Feminella, P. D. Cottingham, and P. M. Groffman. 2005. The urban stream syndrome: current knowledge and the search for a cure. Journal of the North American Benthological Society **24:**706–723.

Wenger, S. J., and M. C. Freeman. 2008. Estimating species occurrence, abundance and detection probability using zero-inflated distributions. Ecology. In press.

Wenger, S. J., T. L. Carter, L. A. Fowler, and R. A. Vick. 2008*a*. Runoff limits: an ecologically-based stormwater management program. Stormwater **9:**45–58.

Wenger, S. J., J. T. Peterson, M. C. Freeman, B. J. Freeman, and D. D. Homans. 2008*b*. Stream fish occurrence in response to impervious cover, historic land use and hydrogeomorphic factors. Canadian Journal of Fisheries and Aquatic Sciences **65:**1250–1264.