

The Effort–Outcomes Relationship in Applied Ecology: Evaluation and Implications

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Knowing the outcome(s) of management efforts in applied ecology is topical and useful. The effort–outcomes principle states that there is a cause-and-effect relationship between the desired outcomes of management and the effort applied (the inputs) but with diminishing returns. A question addressed by this relationship is the following: How much management effort is enough to achieve a desired outcome? We evaluate the relationship—namely, how it is described or estimated—give empirical examples, and outline a novel and explicit conceptual framework that connects management efforts to outcomes. We conclude that the relationship has been described three ways previously: in stylized graphs, from computer algorithms, and in observational studies. We recommend a fourth way employing manipulative experiments carried out as part of an adaptive management program and designed explicitly to estimate the relationship's parameters.

Keywords: applied ecology, biodiversity conservation, diminishing returns, effort–outcomes relationship, pest control

Management in applied ecology aims to achieve an outcome(s) and uses scarce resources to do so. Applied ecology extends over activities such as biodiversity conservation, sustainable harvest, and pest control. It encompasses aims, methods, programs, policies, and legislation across a range of spatial and temporal scales. The desired outcomes in biodiversity conservation are typically increased abundance and distribution, reflecting International Union for Conservation of Nature (IUCN) conservation criteria (IUCN 2016); in sustainable harvesting, the aim is to allow an ongoing harvest with no long-term decline in abundance of the harvested species; and in pest control, the aim is to increase the abundance of the species affected by the pests. To link and guide management over this broad range of aims, a set of 25 prescriptive and empirical principles has been proposed (Hone et al. 2015). One of the three empirical principles, the effort–outcomes principle, states that there is a cause-and-effect relationship between the desired outcomes of management and the effort applied (the inputs) but with diminishing returns. The concept encapsulated in this core principle is implicit in almost all ecological management and easily taken for granted, but it is reported infrequently and has not been evaluated critically. In this article, we identify examples of the relationship, propose a simple unifying form for it, recognize some intermediate stages, and evaluate its utility.

It is generally expected that desired outcomes will increase with the resources allocated, although this has rarely been demonstrated (Leader-Williams and Albon 1988). For example, the authors of a worldwide review of vertebrate conservation efforts and outcomes stated, “We have no data on the relationship between expenditure on biodiversity and conservation success” (Hoffman et al. 2010, p. 1509). Some benefits of expenditure were demonstrated but a relationship was not. An ability to estimate the effects of different levels of effort will inform difficult decisions about the cost-efficient allocation of resources.

Knowledge of the form of the effort–outcomes relationship could assist in deciding management priorities (figure 5 in Murdoch et al. 2007) and lower the cost of achieving a management target (figure 2 in Cattarino et al. 2016). Conservation, harvest, and pest-control programs involve expenditure and are usually subject to review, sometimes at the political level (e.g., in Australia, through committees of the parliament's Senate). Nongovernmental agencies also face scrutiny by funders, stakeholders, and critics. An ability to provide sound estimates not only of the extent to which defined aims have been achieved but also of what would have been achieved if a larger or smaller budget had been approved would be highly valued by program planners and managers and their reviewers. Requests for additional funding would be much easier to justify and defend with a quantified and evidence-based relationship, ideally one expressed

as an equation with empirically derived parameters. The honest alternative is to answer, “We don’t know,” which is certainly unhelpful. In short, the routine testing and publication of management results would be helpful (Sutherland et al. 2013).

The effort–outcomes relationship has been described in a variety of studies, although often with a different name: It has been labelled variously the input–output relationship (Conway 1981), benefit functions (Arponen et al. 2005), the species–investment curve (Murdoch et al. 2007, Wilson et al. 2007), utility functions (Carwardine et al. 2009), the investment–outcome relationship (Walsh et al. 2012), the action–response curve (Adams et al. 2014), the species–response curve (Cattarino et al. 2016), and the site–persistence relationship (Di Fonzo et al. 2016). These are all equivalent relationships employing a measure of effort (in either monetary or nonmonetary units) on the x-axis (independent variable) and an outcome or response (at the population, species or community level) on the y-axis (dependent variable). The focus here is on management for which there is a single desired outcome; we recognize that managers are sometimes faced with more complex scenarios involving more than one type of effort and desired outcome (Runge et al. 2013), but we do not extend our evaluation beyond the simple case.

This article has three parts. First, we present a unifying statement of the relationship, relate it to similar concepts in economics, and identify a four-level structure that emphasizes its basis in ecological processes and assists consideration of specific cases. Second, drawing on previous developments of the concept, we describe and evaluate three different ways the relationship has been estimated and describe a fourth and more useful way. The latter estimates the relationship’s parameters. Third, we present empirical evidence for the relationship. Such a unifying and comprehensive evaluation of the effort–outcomes relationship appears not to have been published previously.

Methods

We searched the scientific literature in a two-stage process to find published examples of the effort–outcomes relationship. Initially, we used the Web of Science to search for relevant scientific publications using phrases of interest, namely “effort–outcome relationship in applied ecology,” “effort–outcome relationship in conservation,” “species–investment curve in conservation,” “investment–outcome relationship in conservation,” “action–response curve in conservation,” “species–response curve in conservation,” “benefit functions in conservation,” “utility functions in conservation,” and “site–persistence relationships in conservation.” That search yielded seven publications with at least one such phrase, which we considered insufficient. In the second stage, we used published examples of the relationships to search backward in time for publications that were cited therein. We also searched forward in time from those known publications to publications that cited known earlier publications on the topic. The paucity of results in the first stage of searching can

be attributed to the absence of use of the keyword phrases in the publications. The years 1988 to 2015 were used as years for searching.

The effort–outcomes relationship and its intermediate stages

As the name implies, the relationship expresses the amount of the desired outcome (M) obtained from a specified amount of management effort (E). It is fundamentally a quantitative cause-and-effect relationship. Both effort and outcome can be expressed either monetarily or in nonmonetary ways, and as a specific example of the latter, effort may be the number of nest boxes provided for a bird species and the outcome the abundance of the birds.

We assume that the outcome variable should increase as the effort expended is increased. The effort–outcome relationship will generally include an initial approximately linear region (figure 1, line A), in which an increase in effort produces a proportionate increase in the desired outcome. The relationship may have a sigmoidal shape (figure 1, line B) because of interactions within and between species in response to management efforts. There could also be a phase of no response until a threshold level of effort (E_T) occurs (figure 1, line C). In all cases, at high levels of effort, there will be diminishing returns—that is, the amount of additional outcome achieved for each extra unit of effort is reduced (figure 1). Diminishing returns is a fundamental principle in economics (Gans et al. 2009) and has been reported (Grantham et al. 2008) or demonstrated (Helmstedt et al. 2016) in the evaluation of conservation programs and in pest control (Hone 2013). The progressive reduction in the additional outcomes may occur through a variety of mechanisms, such as because managers initially apply effort in easily accessible locations or because target species gradually become more wary and harder to remove or translocate.

We propose that economic analyses—such as cost-effectiveness analysis, in which the outcomes are not expressed in monetary terms (Laycock et al. 2009), and cost–benefit analysis, in which both effort and outcomes have monetary units (Hone 1994)—have the effort–outcomes relationship as an implicit foundation. In cost-effectiveness analysis, the ratio of costs ($E =$ effort) to outcomes (M), $E:M$, is to be determined. The effort–outcomes relationship recognizes that such a ratio is not constant but varies with the level of effort. The ratio $E:M$ can be inverted from $E:M$ to $M:E$, to consider outcomes (M) with multiple levels of effort (E). If used for cost–benefit analysis, the relationship does not, by itself, provide an optimal solution; rather, it provides an important part in estimating benefits of different levels of effort.

The effort–outcomes relationship is envisaged as arising through ecological processes, especially demographic and trophic, linking four levels of variables (figure 2), a scheme similar to that of figure 1a and 1b in Walsh and colleagues (2012). Quantities at level 1 are measures of management effort (E) such as staff hours or funds expended and may

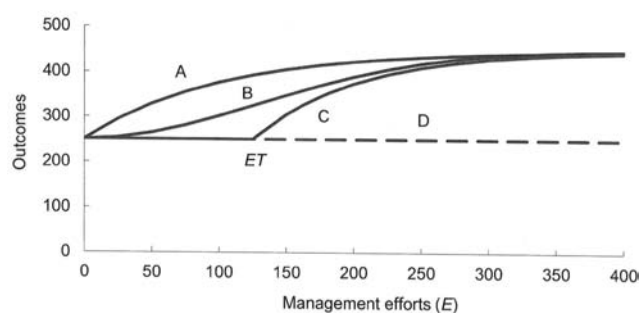


Figure 1. Hypothesized empirical relationships between the level of outcomes in applied ecology and the level of management effort (arbitrary units). The intercept on the y-axis represents the outcome with no management. The axes must be quantitative and could be measured in monetary terms. The forms of the relationships are positive concave-down (A), sigmoidal (B), and concave-down with a threshold (ET) level of effort (C). The horizontal dashed line (D) shows no relationship between outcomes and management efforts.

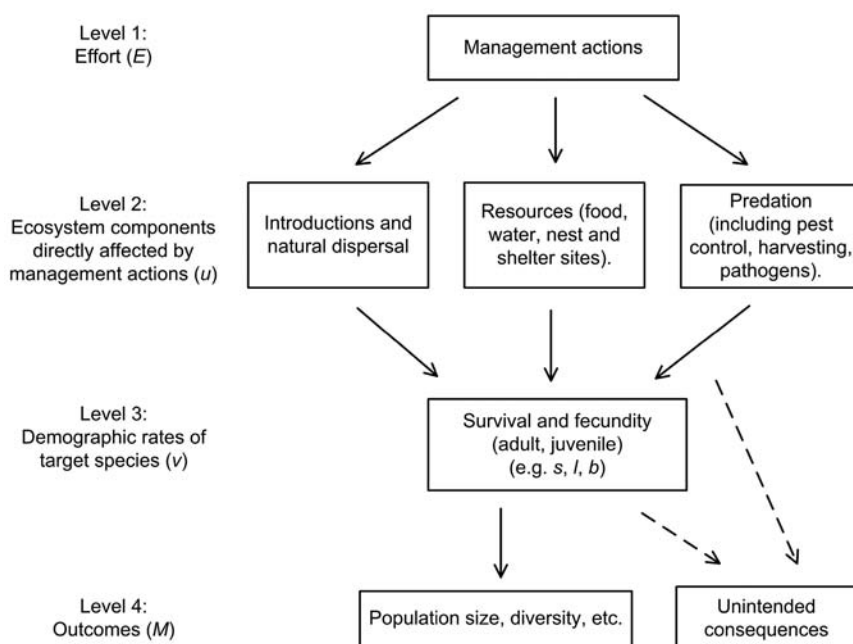


Figure 2. A schematic representation of the cause-and-effect relationships at the population level connecting management efforts (E , level 1), natural trophic features and interactions (u , level 2), demographic rates (v , level 3), and management outcomes (abundance, growth rates, diversity; M , level 4). Demographic rates are adult (s) and juvenile (l) survival and fecundity (b). The demographic rates determine abundance and growth rates and are determined by trophic effects of resources, predators, and pathogens, as well as their interactions, which themselves are influenced by management efforts (E). Harvest and pest-control removals (culls) directly influence survival rates. Introductions for conservation and natural dispersal directly influence abundance. The four relationship levels identified here are also used in supplemental table S1. The arrows show the main directions in which the interactions operate with feedback effects, such as compensatory mortality, not illustrated but possibly occurring.

involve deploying breeding sites, supplementary feeding, traps, poisons or sterilization agents. The trophic features, including resources such as food and breeding sites, and trophic interactions at level 2 are influenced by management efforts. Trophic features and interactions lead to changes within a population, especially demographic rates (the level 3 variables). These altered demographic rates then lead to changes in abundance, population growth rates or other desired outcomes (M) at level 4 (figure 2). In the case of management of a community the outcomes will be expressed as the number of species, species protected (e.g., diversity or species richness) or some related measure. Management of pests may alter pest abundance, but the latter is a level-2 quantity: The measure of biodiversity or agricultural production affected adversely by the pests is the ultimate (level 4) measure of outcome.

There are empirical examples of effort–outcomes relationships (table 1), but more of the intermediate steps (supplemental table S1). We consider the lists illustrative and not exhaustive, because of the difficulty of searching the literature, as we described earlier. Examples of the intermediate steps are the relationship between breeding success in malleefowl (*Leipoa ocellata*) and red fox (*Vulpes vulpes*) control efforts in southern Australia (Walsh et al. 2012). Breeding success is a demographic rate (figure 2, level 3), so the relationship is not an effort–outcome relationship. Similarly, the positive relationship between the probability of finding an invasive weed species and search effort (Moore JL et al. 2011) describes an important intermediate step in weed management but does not relate the benefits of weed control to control effort. We note that management may also produce unintended consequences (figure 2), which can be undesirable (Adriaansen et al. 2016) or beneficial (Norbury et al. 2015).

Evaluating ways of describing the effort–outcomes relationship

We now describe and evaluate ways in which the effort–outcomes relationship has been reported and studied.

Stylized graphs. The most basic representation of the relationship is as simple qualitative relationships, illustrated by stylized or schematic graphs (figure 15.1 in Conway 1981, figure 1 in Arponen et al. 2005, figure 1 in Carwardine et al. 2009, figure 3a, 3c in Adams et al. 2014, figure 1b in Cattarino et al. 2016). Some studies provided equations describing

Table 1. Empirical examples of effort–outcomes relationships in applied ecology.

Relationship	Species	Sources
Change in abundance and antipoacher efforts	African elephant, black rhinoceros	Leader-Williams and Albon (1988)
Vegetative cover and number of guards	Plants in tropical parks	Bruner et al. (2001)
Species status and costs	Endangered species	Miller et al. (2002), Male and Bean (2005), Gibbs and Currie (2012)
Trends in abundance and special protection areas	European birds	Donald et al. (2007)
Attainment of conservation targets and costs	Multiple species	Laycock et al. (2009)
Abundance of native birds and years of pest control	Native podocarp forest birds	Innes et al. (2010)
Proportion of herds with no detected bTB and possum control efforts	Cattle, deer, brushtail possums and <i>Mycobacterium bovis</i>	Hone (2013)

Note: The relationships are estimated between management outcomes (level 4 in figure 2) and management efforts (level 1 in figure 2). In each relationship, the dependent variable is stated first. The list is illustrative and is not exhaustive.

the curves (Arponen et al. 2005, Joseph et al. 2009, Cattarino et al. 2016) but do not estimate the relationship's parameters. Such stylized graphs provide a conceptual framework to guide management decision-making. Other examples of such stylized graphs are the generic relationships in fisheries management between yield, profit, and fishing effort, which can be used to estimate the optimal fishing effort (figure 1 in Hilborn 2007), and potential changes in the Australian economy over time with and without climate-change abatement (figure 1.4 in Garnaut 2008). Stylized graphs are useful because they show explicitly the assumptions about the direction, shape, and thresholds in the effort–outcomes relationship. The stylized graphs can show linear or curved relationships, some with diminishing returns (Arponen et al. 2005, Carwardine et al. 2009, Adams et al. 2014, Cattarino et al. 2016) at high levels of management effort. Some examples (Arponen et al. 2005, Carwardine et al. 2009, Adams et al. 2014, Cattarino et al. 2016) are formulated so that the outcome is zero when effort is zero, others so that some outcome above zero occurs even with no effort (Conway 1981, figure 3 in Di Fonzo et al. 2016). Surprisingly, none of the stylized graphs include ineffective management, which is represented by a horizontal line showing the same outcome for each level of effort (figure 1, line D).

Computer algorithms. The second way in which the relationship has frequently been presented is as an output from a computer algorithm. Such outputs can show positive curved relationships with diminishing returns (figures 2 to 5 in Grantham et al. 2008, figure 6 in Yokomizo et al. 2009, figure 2 in Gibbs and Currie 2012, figures 1 and 2 in Helmstedt et al. 2016, figure 2 in Di Fonzo et al. 2016) or simply positive trends (figures 5 and 6 in McCarthy et al. 2008). Results can also take the form of a negative relationship; for example, the probability of going extinct (figure 2 in McDonald-Madden et al. 2008) or the number of species lost (gone extinct) decreases as funding increases (figure 2 in Carwardine et al. 2012). However, those results could also

be re-expressed positively by redefining the outcomes as species extant (not lost).

Computer algorithms can be useful to evaluate a greater range of effort levels than have been, or could reasonably be, achieved in actual field management. Models may use expert judgement to weight communities, species, or threatened-species status (Joseph et al. 2009). Expert judgement can be biased, but these human frailties can be reduced (Speirs-Bridge et al. 2010). The model outputs can also be regarded as hypotheses for field evaluation in observational or experimental studies. The computer algorithms typically do not have statistical analyses of relationships, such as regression and correlation. These analyses are prospective or predictive in nature.

Observations. The third manner in which the effort–outcome relationship has been expressed is an output of statistical analyses, mainly regression and correlation of empirical results from observational field studies. These analyses are retrospective in nature in contrast to the analyses of computer algorithms. Observational studies can evaluate the assumptions of stylized graphs and computer algorithms and models. Such analyses require a range of levels of effort. However, some observational studies have only compared outcomes with and without effort, such as some positive effect of funding on endangered species trends or status (Ferraro et al. 2007) but no effect of the existence of recovery plans (Bottrill et al. 2011). Examples involving a range of effort levels include positive trends in the abundance of African elephants (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*; figure 2a) in relation to higher levels of antipoacher efforts (Leader-Williams and Albon 1988), as well as positive changes in the status of endangered species with higher levels of funding (table 1; Miller et al. 2002, Male and Bean 2005, Gibbs and Currie 2012). Greater freedom of livestock herds from bovine tuberculosis occurred with higher levels of expenditure on brush-tailed possum (*Trichosurus vulpecula*)

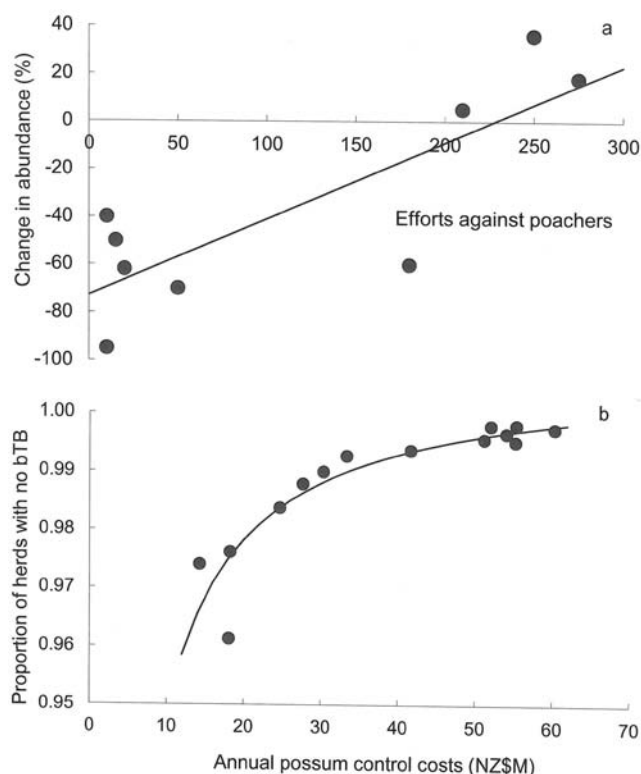


Figure 3. Empirical examples of the effort–outcomes relationship in applied ecology. (a) The relationship across nine African countries between the change in abundance of black rhinoceros over the years 1980 to 1984 and efforts against poachers. The solid line is the fitted linear regression. Redrawn from Leader-Williams and Albon (figure 4 in 1988). (b) The diminishing-marginal-returns relationship between the proportion of cattle and farmed deer herds with no detected bovine tuberculosis (bTB) and annual costs of brushtail-possum control in New Zealand. The solid line is the fitted regression. Redrawn from figure 4 in Hone (2013).

control in New Zealand (figure 2b, table 1). The disease is endemic in possums, which are an introduced pest. The underlying theory with equations was described (Hone 2013 and references therein). This primarily agricultural example has relevance to biodiversity conservation because possums have significant negative biodiversity impacts (figures 3, 5, and 8 in Norbury et al. 2015), so possum control is an example with beneficial unintended consequences.

An example from community ecology is provided by Bruner and colleagues (2001), who reported that the effectiveness of tropical conservation parks, as was assessed by vegetative cover, was positively and significantly correlated with the number of guards allocated to protect biodiversity per square kilometre of park (table 1). In another example, a significant positive relationship between effectiveness of conservation efforts (assessed as the percentage attainment of prior targets) and costs, when animal (vertebrate and

invertebrate) and plant species were weighted by utility, was reported for the UK Biodiversity Action Plan (Laycock et al. 2009).

For both black rhinoceros and elephant populations, the results were used to estimate threshold levels of antipoaching effort, for each of about \$230 per square kilometre, needed to achieve at least stable (annual finite population growth rate $\lambda \geq 1.0$) populations (Leader-Williams and Albon 1988). This illustrates the real utility of such empirical relationships. Only linear relationships were reported in this study, but in the longer term, such linear relationships are unrealistic because each population has a maximum annual growth rate and ecological factors would limit abundance. The relationship is expected to then shift downward. The rhinoceros and elephant relationships occurred for species subject to illegal economic exploitation. In the analysis for both rhinoceros and elephants, the importance of correlated variables, such as income and governance, could be examined, but such analyses were beyond our review. The tuberculosis–possum study evaluated linear and curved relationships (Hone 2013) with much stronger support for the latter, as was assessed by Akaike weights, showing clear diminishing returns at high levels of annual costs.

The observational studies of the effort–outcomes relationship typically reported statistically significant relationships, with the proportion of variation (R^2) explained ranging from a high of 83% in the livestock disease outcome (Hone 2013) to 68% for black rhinoceros trends and a much lower 32% for African elephant trends (Leader-Williams and Albon 1988). One study reported that only a low (13%) proportion of the variation in the outcome measure (recovery progress) was accounted for by funding, taxon, threats, and recovery potential (Male and Bean 2005), and funding, along with taxon and years listed, accounted for only 8% of the variation in the status of endangered species (Gibbs and Currie 2012). An earlier study questioned whether endangered species recovered because of the funding or the funding increased because of the endangered species status (Simon et al. 1995). Such a question about a cause-and-effect relationship can be answered by experiments, although we recognize that sometimes they may not be feasible economically or justifiable ethically. In such cases, the results of observational studies should be used and interpreted as such and not interpreted as being from manipulative experiments.

Manipulative experiments. A fourth way to describe an effort–outcome relationship is through the results of experiments that include multiple levels of management effort. However, we found no examples of a field experiment with multiple levels of management effort that estimated the outcomes. Several experimental studies have compared outcomes of management effort versus no effort (Ferraro et al. 2007, Bottrill et al. 2011) but did not evaluate multiple levels of effort (table 2).

Table 2. Examples of field experiments in applied ecology that could have estimated the effort–outcomes relationship or a relationship intermediate between efforts and outcomes.

Study and source	Design used	Alternative design
Effects on sheep production of rabbit abundance (Fleming et al. 2002)	Four levels of rabbit abundance, four replicates, total 16	Eight levels of rabbit abundance, two replicates, total 16
Effects on bTB incidence in cattle of proactive badger control (Donnelly et al. 2006)	Two levels of badger control, 10 replicates, total 20	Eight levels of badger control, two replicates, total 16
Effects on wildlife of dingo control (Brook et al. 2012)	Two levels of dingo control, nine replicates, total 18	Nine levels of dingo control, two replicates, total 18
Effects on wildlife of dingo control (Allen et al. 2013)	Two levels of dingo control, six replicates, total 12	Six levels of dingo control, two replicates, total 12
Effects on wildlife of dingo control (Colman et al. 2014)	Two levels of dingo control, seven replicates, total 14	Seven levels of dingo control, two replicates, total 14

Note: The principal design features used—such as levels of experimental treatments, number of treatment replicates, and total sites—are described. Alternative designs that would estimate regression parameters of the effort–outcomes relationship more effectively are recommended. Abbreviation: bTB, bovine tuberculosis.

We argue that explicit recognition of the effort–outcomes relationship has specific implications for the design of experiments to evaluate management activities. Instead of the more usual two-level experiment comparing outcomes with and without management with a large number of treatment replicates of each, it would be more useful to use several levels of management effort (including zero) and have fewer replicates for each. The focus then changes from answering the question “is there an effect of management?” to “how much management is enough to achieve a desired outcome?” Therefore, the appropriate analysis will change from one for detecting differences (such as ANOVA) to one for detecting a relationship (such as regression).

We suggest that generating such a relationship is an integral component of adaptive management. Knowledge of the shape of an effort–outcomes relationship could assist in deciding management priorities (Murdoch et al. 2007), in facilitating faster returns on investments (Pullin et al. 2009), in determining optimal targets for maximizing species persistence under limited funding (Di Fonzo et al. 2016), and in lowering costs of achieving a management target (Cattarino et al. 2016). Such knowledge was described as a key technical requirement for planning effective and efficient management (Adams et al. 2014).

In designing experiments to estimate a response relationship, additional levels of effort (the treatments) can be substituted for replicates of each level (Dillon 1968 pp. 104–105, Moore DRJ and Caux 1997), although some degree of replication should be maintained (Cottingham et al. 2005). If, as we propose, the effort–outcomes relationship is curved downward at high levels of effort (figure 1), then as many as six levels of management efforts will be needed to estimate the regression parameters. The number of levels should be determined from a pilot study to estimate variance between and within treatments or after consultation with a statistician. We propose alternative designs of this type for a variety of published studies (table 2). A pragmatic view may be that such experiments are too expensive, but

some of the studies listed in table 2 cost millions of dollars, so the issue is not whether money is available but how to allocate it to achieve cost-effective and efficient experimental design that will produce parameter estimates of utility to management.

Conclusions

Recognition and estimation of the relationship between effort expended and desired outcomes have benefits for management decision-making in all branches of applied ecology. A four-level structure, with explicit recognition of intermediate variables and the management and ecological processes connecting them, clarifies interpretation of specific cases. The relationship can be represented in four ways, in order of increasing rigor: as a stylized graph, by computer algorithms, through observational studies, and through experimental studies. There is empirical support for the relationship: The evidence ranges from strong to weak and more often relates to one or more intermediate stages rather than the full relationship. Aspects of the relationship have been reported previously in a range of forms and under a variety of names, but we propose that it should be regarded as a central principle of applied ecology, drawn on in all management planning and implementation. Future studies are strongly encouraged (a) to use manipulative experiments incorporating multiple effort levels to estimate the relationship’s parameters and (b) to practice adaptive management by applying the results as they become available. It is recommended that future studies on this topic use the phrase “effort–outcomes relationship” as a keyword to facilitate other researchers and managers finding associated publications.

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Supplemental material

Supplementary data are available at *BIOSCI* online.

References cited

- Adams VM, Alvarez-Romero JG, Carwardine J, Cattarino L, Hermoso V, Kennard MJ, Linke S, Pressey RL, Stoeckl N. 2014. Planning across freshwater and terrestrial realms: Cobenefits and tradeoffs between conservation actions. *Conservation Letters* 7: 425–440.
- Adriaansen C, Woodman JD, Deveson E, Drake VA. 2016. The Australian plague locust—risk and response. Pages 67–86 in Shroder JF, Sivanpillai R, eds. *Biological and Environmental Hazards, Risks, and Disasters*. Elsevier.
- Allen BL, Allen LR, Engeman RM, Leung LK-P. 2013. Intraguild relationships between sympatric predators exposed to lethal control: Predator manipulation experiments. *Frontiers in Zoology* 10 (art. 39).
- Arponen A, Heikkinen RK, Thomas CD, Moilanen A. 2005. The value of biodiversity in reserve selection: Representation, species weighting, and benefit functions. *Conservation Biology* 19: 2009–2014.
- Bottrill MC, Walsh JC, Watson JEM, Joseph LN, Ortega-Argueta A, Possingham HP. 2011. Does recovery planning improve the status of threatened species? *Biological Conservation* 144: 1595–1601.
- Brook LA, Johnson CJ, Ritchie EG. 2012. Effects of predator control on behaviour of an apex predator and indirect consequences for mesopredator suppression. *Journal of Applied Ecology* 49: 1278–1286.
- Bruner AG, Gullison RE, Rice RE, da Fonseca GAB. 2001. Effectiveness of parks in protecting tropical biodiversity. *Science* 291: 125–128.
- Carwardine J, Klein CJ, Wilson KA, Pressey RL, Possingham HP. 2009. Hitting the target and missing the point: Target-based conservation planning in context. *Conservation Letters* 2: 3–10.
- Carwardine J, O'Connor T, Legge S, Mackey B, Possingham HP, Martin TG. 2012. Prioritizing threat management for biodiversity conservation. *Conservation Letters* 5: 196–204.
- Cattarino L, Hermoso V, Bradford LW, Carwardine J, Wilson KA, Kennard MJ, Linke S. 2016. Accounting for continuous species-responses to management effort enhances cost-effectiveness of conservation decisions. *Biological Conservation* 197: 116–123.
- Colman NJ, Gordon CE, Crowther MS, Letnic M. 2014. Lethal control of an apex predator has unintended cascading effects on forest mammal assemblages. *Proceedings of the Royal Society London B* 281 (art. 210133094).
- Conway G. 1981. Man versus pests. Pages 356–386 in May RM, ed. *Theoretical Ecology. Principles and Applications*, 2nd ed. Blackwell.
- Cottingham KI, Lennon JT, Brown BL. 2005. Knowing when to draw the line: Designing more informative ecological experiments. *Frontiers in Ecology and Environment* 3: 145–152.
- Di Fonzo MMI, Possingham HP, Probert WJM, Bennett JR, Joseph LN, Tulloch AIT, O'Connor S, Densem J, Maloney RF. 2016. Evaluating trade-offs between target persistence levels and numbers of species conserved. *Conservation Letters* 9: 51–57.
- Dillon JL. 1968. *The Analysis of Response in Crop and Livestock Production*. Pergamon Press.
- Donald PF, Sanderson FJ, Burfield IJ, Bierman SM, Gregory RD, Waliczky Z. 2007. International conservation policy delivers benefits for birds in Europe. *Science* 317: 810–813.
- Donnelly CA, et al. 2006. Positive and negative effects of widespread badger culling on tuberculosis in cattle. *Nature* 439: 843–846.
- Ferraro PJ, McIntosh C, Ospina M. 2007. The effectiveness of the US Endangered Species Act: An econometric analysis using matching methods. *Journal of Environmental Economics and Management* 54: 245–261.
- Fleming PJS, Croft JD, Nicol HI. 2002. The impact of rabbits on a grazing system in eastern New South Wales. 2. Sheep production. *Australian Journal of Experimental Agriculture* 42: 917–923.
- Gans J, King S, Stonecash R, Mankiw NG. 2009. *Principles of Economics*, 4th ed. Cengage Learning.
- Garnaut R. 2008. *The Garnaut Climate Change Review*. Cambridge University Press.
- Gibbs KE, Currie DJ. 2012. Protecting endangered species: Do the main legislative tools work? *PLOS ONE* 7 (art. e35730).
- Grantham HS, Moilanen A, Wilson KA, Pressey RL, Rebelo TG, Possingham HP. 2008. Diminishing returns on investment for biodiversity data in conservation planning. *Conservation Letters* 1: 190–198.
- Helmstedt KJ, Shaw JD, Bode M, Terauds A, Springer K, Robinson SA, Possingham HP. 2016. Prioritizing eradication actions on islands: It's not all or nothing. *Journal of Applied Ecology* 53: 733–741.
- Hilborn R. 2007. Defining success in fisheries and conflicts in objectives. *Marine Policy* 31: 153–158.
- Hoffman M, et al. 2010. The impact of conservation on the status of the world's vertebrates. *Science* 330: 1503–1509.
- Hone J. 1994. *Analysis of Vertebrate Pest Control*. Cambridge University Press.
- . 2013. Diminishing returns in bovine tuberculosis control. *Epidemiology and Infection* 141: 1382–1389.
- Hone J, Drake VA, Krebs CJ. 2015. Prescriptive and empirical principles of applied ecology. *Environmental Reviews* 23: 170–176.
- Innes J, Kelly D, Overton JMcC, Gillies C. 2010. Predation and other factors currently limiting New Zealand forest birds. *New Zealand Journal of Ecology* 34: 86–114.
- [IUCN] International Union for Conservation of Nature. 2016. IUCN Red List 2016.2. (10 October 2016; www.iucnredlist.org)
- Joseph LN, Maloney RF, Possingham HP. 2009. Optimal allocation of resources among threatened species: A project prioritization protocol. *Conservation Biology* 23: 328–338.
- Laycock H, Moran D, Smart J, White P. 2009. Evaluating the cost-effectiveness of conservation: The UK Biodiversity Action Plan. *Biological Conservation* 142: 3120–3127.
- Leader-Williams N, Albon SD. 1988. Allocation of resources for conservation. *Nature* 336: 533–535.
- Male TD, Bean MJ. 2005. Measuring progress in US endangered species conservation. *Ecology Letters* 8: 986–992.
- McCarthy MA, Thompson CJ, Garnett ST. 2008. Optimal investment in conservation of species. *Journal of Applied Ecology* 45: 1428–1435.
- McDonald-Madden E, Baxter PW, Possingham HP. 2008. Making robust decisions for conservation with restricted money and knowledge. *Journal of Applied Ecology* 45: 1630–1638.
- Miller JK, Scott JM, Miller CR, Waits LP. 2002. The Endangered Species Act: Dollars and sense? *BioScience* 52: 163–168.
- Moore DRJ, Caux PY. 1997. Estimating low toxic effects. *Environmental Toxicology and Chemistry* 16: 794–801.
- Moore JL, Hauser CE, Bear JL, Williams NSG, McCarthy MA. 2011. Estimating detection-effort curves for plants using search experiments. *Ecological Applications* 21: 601–607.
- Murdoch W, Polasky S, Wilson KA, Possingham HP, Karieva P, Shaw R. 2007. Maximizing return on investment in conservation. *Biological Conservation* 139: 375–388.
- Norbury GL, Pech RP, Byrom AE, Innes J. 2015. Density-impact functions for terrestrial vertebrate pests and indigenous biota: Guidelines for conservation managers. *Biological Conservation* 191: 409–420.
- Pullin AS, Knight TM, Watkinson AR. 2009. Linking reductionist science and holistic policy using systematic reviews: Unpacking environmental policy questions to construct an evidence-based framework. *Journal of Applied Ecology* 46: 970–975.
- Runge MC, Grand JB, Mitchell MS. 2013. Structured decision making. Pages 51–72 in Krausman PR, Cain JW III, eds *Wildlife Conservation and Management: Contemporary Principles and Practices*. John Hopkins University Press.
- Simon BM, Leff CS, Doerksen H. 1995. Allocating scarce resources for endangered species recovery. *Journal of Policy Analysis and Management* 14: 415–432.

- Speirs-Bridge A, Fidler F, McBride M, Flander L, Cumming G, Burgman M. 2010. Reducing overconfidence in the interval judgments of experts. *Risk Analysis* 30: 512–523.
- Sutherland WJ, et al. 2013. Conservation practice could benefit from routine testing and publication of management outcomes. *Conservation Evidence* 10: 1–3.
- Walsh JC, Wilson KA, Benshemesh J, Possingham HP. 2012. Unexpected outcomes of invasive predator control: The importance of evaluating conservation management actions. *Animal Conservation* 15: 319–328.
- Wilson KA, et al. 2007. Conserving biodiversity efficiently: What to do, where and when. *PLOS Biology* 5: 1850–1861.
- Yokomizo H, Possingham HP, Thomas MB, Buckley YM. 2009. Managing the impact of invasive species: The value of knowing the density–impact curve. *Ecological Applications* 19: 376–386.

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