

Unexpected outcomes of invasive predator control: the importance of evaluating conservation management actions

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Abstract

Decisions regarding the implementation of conservation management actions should be based on the effectiveness of past investments. However, because of limited evaluation of existing data, actions may be prescribed without evidence of producing a beneficial conservation outcome. We analysed empirical data, collected over 23 years across southern Australia, on the impact of fox baiting on malleefowl to determine its effectiveness. We employed data from extensive monitoring surveys to evaluate the observed relationships between investment in fox control, fox baiting intensity, fox presence and two alternative measures of the malleefowl's response: the number of breeding pairs and population growth. This study is the first to quantify the return on investment from fox control in a conservation context. We discovered there is limited quantitative evidence for a benefit of fox baiting on malleefowl, despite it being the main management action implemented for this nationally threatened, well-studied and iconic species. We found that fox baiting did not significantly decrease the presence of foxes and fox presence was positively correlated with malleefowl conservation. Malleefowl breeding population size increased with investment in baiting, although this relationship depended on the number of years the site had been baited. Nonetheless, most sites had a negative relationship between investment and breeding population. In contrast, malleefowl population growth did not benefit from baiting, suggesting that fox baiting is generally not a cost-effective management action for the conservation of this species. This study provides a powerful example of why management decisions should be based on evidence, rather than ecological intuition. Even though the malleefowl is one of the best-monitored species of conservation concern in Australia, we are still uncertain how to cost-effectively manage this species. We emphasize the urgent need to assess what data we have and determine which species and what actions are most in need of evaluation.

Introduction

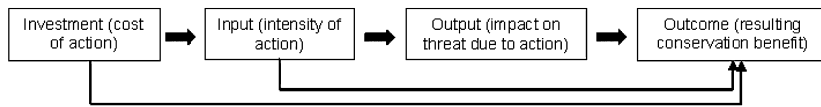
The continuing global decline of biodiversity (Butchart *et al.*, 2010) necessitates active management of threatened species. Given that funding for conservation is limited (James, Gaston & Balmford, 2001; Balmford *et al.*, 2003), it is essential to invest in effective and efficient management actions to ensure that conservation outcomes are maximized and limited resources are spent wisely (Wilson *et al.*, 2007; Underwood *et al.*, 2008).

A key part of prioritizing investments is an understanding of how the target species or the environment will respond to a management action (Murdoch *et al.*, 2007). The return on investment is the increase in benefit with investment divided by the cost of investment. This can be modelled using the relationship between the level of investment and the result-

ing conservation outcome, i.e. the observed benefit. Such information can allow conservation managers to determine the marginal benefits obtained from investing in a management action. Using this investment–outcome relationship, we can then predict whether prescribed actions will be effective at achieving the defined conservation objective, gauge whether the cost of implementing the actions falls within the budget allocated for the project, compare the cost-effectiveness of different management actions, and prioritize these actions to gain the greatest conservation outcome for a fixed budget or achieve a specified objective for the lowest cost; all of which are essential components in the conservation resource allocation process (Mace, Possingham & Leader-Williams, 2006).

Often, however, the relationship between the level of investment and the conservation outcome is unknown

(a) General management



(b) Fox control

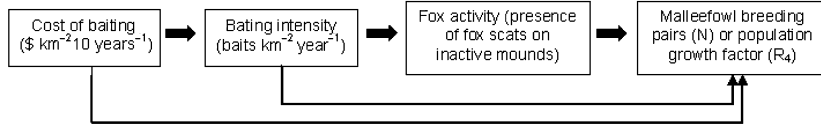


Figure 1 Stages of the management process, for (a) a general case study, and (b) fox control for malleefowl conservation. The relationships between each step should be quantified in order to calculate return on investment relationships.

(Sutherland *et al.*, 2004) because of limited monitoring and evaluation, poor documentation and accessibility of data, and limited transfer of knowledge between scientists and practitioners (Pullin *et al.*, 2004). As a result, management decisions are often based on qualitative anecdotal information or management practices that have been implemented in the past (Pullin & Knight, 2005). There are several examples of studies where management actions have been tested and evaluated for their effectiveness using evidence (for example Smith *et al.*, 2010; St Clair *et al.*, 2011), but few have incorporated management costs (Naidoo *et al.*, 2006) or developed return on investment relationships (but see Montgomery, Brown & Adams, 1994; Wilson *et al.*, 2007; Busch & Cullen, 2009; Duca *et al.*, 2009). When the effectiveness of a management action is estimated or assumed, there is no guarantee that investment in that action will achieve the conservation objective cost-effectively.

To adequately assess the effectiveness of a management action, it is important to quantify the relationships between the investment in an action, the intensity of the intervention (referred to herein as the input), the impact on the threatening process (referred to herein as the output) and the conservation outcome (Fig. 1a). This ensures that the management action is having the desired impact on the targeted threat, as well as the targeted outcome. Quantifying the relationships between the different stages of the management process using evidence is almost inconceivable for most conservation problems given the incomplete state of monitoring, evaluation and data management in most projects (Cook, Hockings & Carter, 2010). To show how the return on investment of a management action can be evaluated using evidence and incorporating the intermediate steps, input and output, we use malleefowl *Leipoa ocellata* as a case study. This species has been managed and monitored across its entire southern distribution in Australia for over 23 years.

The malleefowl is an endemic Australian bird, living in semi-arid mallee habitat (Benshemesh, 2007). Malleefowl are ground-dwelling megapodes that incubate their eggs using external heat in large mounds, which they build from sand and decaying leaf litter (Frith, 1959). This species is listed as vulnerable under the Australian Environment Protection and Biodiversity Conservation Act 1999 and IUCN Red List (2009). Multiple threats are associated with the

decline of this species' distribution, including habitat loss and fragmentation, predation by the introduced European red fox *Vulpes vulpes*, frequent fires and grazing competition with introduced and native herbivores (Benshemesh, Barker & MacFarlane, 2007).

Fox baiting is currently the main management action used for malleefowl conservation (Benshemesh, 2007), despite the lack of empirical evidence of how effective fox baiting is at increasing malleefowl abundance. In addition to the fox baiting implemented for conservation, fox baiting often occurs on agricultural properties surrounding malleefowl habitat, with potential indirect benefits to this threatened species. Of all exotic pest species in Australia, the European red fox is one of the greatest causes of loss in agriculture (Bomford & Hart, 2002; Reddiex *et al.*, 2006) and has severe ecological impacts on native wildlife (Saunders, Gentle & Dickman, 2010). One study concluded that captive bred malleefowl chicks, when released into the wild, survived longer in areas with intense fox baiting compared with sites where fox control was not conducted (Priddel & Wheeler, 1997). However, this study only measured short-term survival rates and by the end of the 20-month trial, most chicks in the baited and non-baited areas had died as a result of fox predation. The widespread use of fox control for malleefowl conservation is an indication that fox baiting is assumed to be effective at increasing malleefowl recruitment into the adult breeding population, despite previous reasoning (Frith, 1962) and analyses (Benshemesh *et al.*, 2007) suggesting that foxes may actually have little overall impact on the stability of malleefowl populations.

In this study we evaluate whether fox baiting is effective at maintaining or increasing malleefowl populations. We use empirical data to quantify the return on investment between fox baiting and the resulting conservation outcome by modelling the response of malleefowl to previous fox control regimes, while incorporating environmental factors that might influence this relationship. We also model the relationships observed between investment in fox control, fox presence and the malleefowl conservation outcome, to improve our understanding on the intermediate steps of the management process and to assess the value of collecting empirical data on inputs and outputs in determining the impact on malleefowl conservation outcomes. Even though extensive research has been conducted on fox baiting in

Australia, this study is the first to quantify the return on investment in fox control in a conservation context (McLeod, Saunders & Kabat, 2008).

Materials and methods

The malleefowl dataset

The empirical data used for this analysis were collected from a variety of sources, including direct observations from annual malleefowl monitoring surveys, information on management actions from Australian state government officials and anecdotal evidence. Much of this information was collated into a single database (Benshemesh *et al.*, 2007) and is hereafter referred to as the malleefowl dataset (see Supporting Information Appendix S1).

The malleefowl dataset is comparatively large and long term for an Australian threatened species (Garnett & Crowley, 2000), consisting of data for 64 monitoring sites established in remnant habitat across southern Australia over 23 years. The dataset contains information on the intensities of fox baiting implemented in most years at each site each year (providing a measure of management input), relative measures of fox presence (a measure of management output) and the number of malleefowl breeding pairs (a measure of conservation outcome) (Fig. 1b). The malleefowl dataset also contains environmental covariates, which were included when modelling the relationships to account for differences between each site (Table 1).

Measures of investment, input, output, and outcomes of fox baiting

The intensity of fox baiting (the measure of management input) was calculated using the number of baits laid $\text{km}^{-2} \text{year}^{-1}$, averaged over 100 km^2 at each site (Benshemesh *et al.*, 2007). The relationship between investment and input was a direct linear conversion of the average fox baiting intensity at each malleefowl monitoring site to the cost of baiting at that intensity. We developed the return on investment curves budgeting for a 10 year baiting program, to

ensure ongoing management. We calculated the net present value (or endowed cost) of ground baiting over ten years to be \$58.31 per 10 baits, assuming that one bait was laid each year for a decade, while accounting for inflation and discounting (Appendix S1). We then estimated the endowed investment in fox baiting for each site over a 10 year baiting program, by multiplying this net present cost of 10 baits (\$58.31) by the number of baits laid $\text{km}^{-2} \text{year}^{-1}$ at each site. This measure of investment in fox baiting had a unit of $\$ \text{km}^{-2} 10 \text{ years}^{-1}$.

We used the proportion of inactive malleefowl mounds that had fox scats present each year at each site as a surrogate measure of fox presence – the dependent output variable (Benshemesh *et al.*, 2007). To quantify the conservation outcome for malleefowl, we used the number of malleefowl breeding pairs (i.e. effective breeding population size) and the population growth factor. The effective breeding population size (N_{ij}) was measured by the number of active malleefowl mounds across each year, i , at a monitoring site, j . An active mound was defined as a nest with incubating eggs during the current breeding season and reflected the presence of a breeding pair of adult malleefowl. We calculated the malleefowl population growth factor (R_{ij}) for each site-year combination using discrete-time density-independent geometric growth, $R_{ij} = N_{ij+4}/N_{ij}$. The four year time interval allows for a time lag in the impact of management on chick, juvenile and adult survival and includes recruitment rates into the breeding population, as the age of sexual maturity ranges from 2 to 4 years old (Benshemesh, 2007).

Modelling the relationships between management steps

To quantify the return on investment relationship, we used two different methods and our two alternative measures of malleefowl conservation outcome. First, we modelled the relationships between the intermediate steps of the management process. Specifically, we tested whether fox baiting was effective at controlling foxes, by modelling the relationship between fox baiting investment and fox presence across sites, accounting for environmental covariates. We modelled the relationship between investment and output, rather than the intermediate investment–input and input–output relationships, as baiting investment and intensity were directly linked. Then, we determined the output–outcome relationships between fox presence and the two measures of conservation outcome for the malleefowl. The final step of the first method involved algebraic substitution to combine these models to obtain two overall investment–outcome functions. Second, we used empirical data of investment in fox baiting and the malleefowl outcome measures to directly model the investment–outcome relationships.

We evaluated each relationship using linear mixed effects models to account for the dataset's hierarchical structure, i.e. multiple measures across years, i , within monitoring site, j , within natural resource management (NRM) region, k . We included relevant environmental covariates in each relationship (see Table 1 and Appendix S1). We selected the

Table 1 Variables and environmental covariates used in the relationships for each site, j , across years, i

Symbol	Variables
I_{ij}	Investment in fox baiting ($\$ \text{ km}^{-2} 10 \text{ years}^{-1}$)
B_{ij}	Fox baiting intensity (baits $\text{km}^{-2} \text{ year}^{-1}$)
F_{ij}	Fox presence (proportion of inactive mounds with fox scats)
N_{ij}	Number of active malleefowl mounds
R_{ij}	Malleefowl population growth factor
G_{ij}	Number of years fox baiting occurred at a site prior to year i
H_{ij}	May–September rainfall (mm)
J_{ij}	Time since fire occurred in the habitat patch (years)
K_j	Area of monitoring site (km^2)
L_j	Habitat patch size (km^2)
M_j	Average proportion of surrounding land cleared (estimated at radii of 2, 5 and 10km from a site's centre)

most parsimonious models that best fit the data, following the model selection protocol described in Zuur *et al.* (2009) (see Supporting Information Appendix S1). All analyses were conducted in the statistical programme R (version 2.4.1) (R Development Core Team, 2008), using the nlme package (Pinheiro & Bates, 2000).

Results

The relationship between investment in fox baiting and fox presence

We found that higher investment in fox baiting reduced fox presence on inactive malleefowl mounds, although this relationship was not statistically significant (Fig. 2; Table 2). Fox presence and predation threat to malleefowl varied greatly among non-baited monitoring sites, with fox scats present on 0–72% of inactive malleefowl mounds. The effect of fox baiting on fox presence differed at each site and NRM region, as these were included in the best-fit model as random effect variables, generating a separate intercept for each of the 65 sites (intercepts – min = 0.097, mean = 0.104, max = 0.109, σ = 0.013) and four NRM regions (min = 0.083, mean = 0.104, max = 0.134, σ = 0.028). The number of years since baiting began at a site (hereafter referred to as baited years) was the only covariate that significantly contributed to the variation in the investment–output relationship. Fox presence was higher in areas where

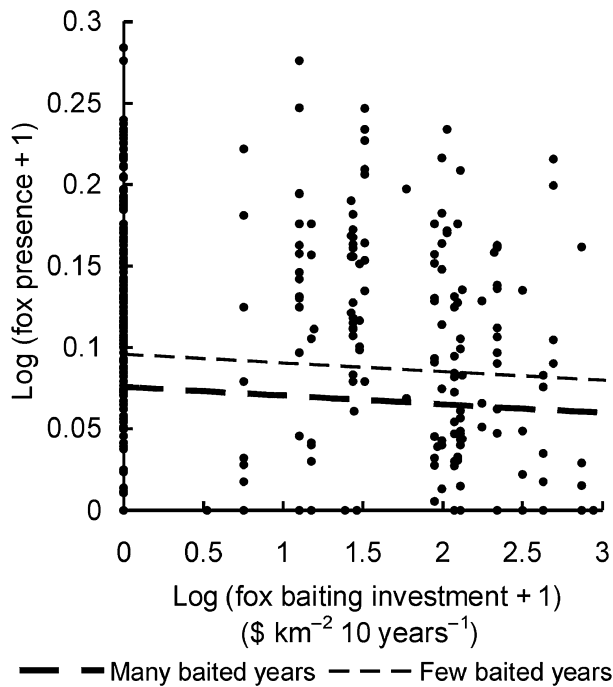


Figure 2 The best-fit investment–output relationship between the investment in fox baiting and the corresponding fox presence, including the effect of the number of baited years, the significant environmental covariate.

Table 2 The best-fit relationships between (a) the intermediate steps of the management process, that is investment in fox control, fox presence (output) and the two malleefowl conservation outcomes – number of breeding pairs (N) and population growth factor (R_d) (Figs 2 & 3); and (b) the overall investment–outcome relationships between investment and both malleefowl outcomes fitted using empirical data (Fig. 4)

Relationship	Equation	β_0	β_1	β_2	β_3	β_4	β_5	β_6	Res. SD* SE†	ϕ	n (B)	n (NB)
(a) Intermediate steps												
Investment – Output	$\log F_{ijk} = \beta_0 + \beta_1 \log I_{ijk} + \beta_2 \log G_{ijk} + v_{0k} + u_{0ijk} + \epsilon_{0ijk}$	0.104	-0.005	-0.027					0.063*	0.588	215	268
Output – Outcome (N)	$\log N_{ij} = \beta_0 + \beta_1 \log F_{ij} + \beta_2 \log G_{ij} + \beta_3 \log H_{ij} + \beta_4 J_{ij} + \beta_5 \log L_j + \beta_6 (\log F_{ij}^* J_{ij}) + u_{0ij} + \epsilon_{0ij}$	-0.612	1.044	-0.124	0.666	0.007	-0.208		0.236*	0.363	178	149
Output – Outcome (R_d)	$\log R_{dij} = \beta_0 + \beta_1 \log F_{ij} + \beta_2 \log G_{ij} + \beta_3 \log M_j + \epsilon_{0ij}$	0.038	0.824	0.079	0.491				0.181†	NA	82	107
(b) Overall return on investment functions												
Investment – Outcome (N)	$\log N_{dij} = \beta_0 + \beta_1 \log I_j + \beta_2 \log G_j + \beta_3 \log H_j + \beta_4 \log L_j + \beta_5 (\log I_j^* \log G_j) + u_{0j} + \epsilon_{0j}$	-0.413	0.106	0.027	0.668	-0.211	-0.204		0.231*	0.332	178	149
Investment – Outcome (R_d)	$\log R_{dij} = \beta_0 + \beta_1 \log I_j + \beta_2 \log F_j + \beta_3 \log L_j + \epsilon_{0ij}$	0.327	-0.012	0.817	-0.086				0.181†	NA	82	107

Symbols for variables and environmental covariates are shown in Table 1. The unexplained variance is represented in the model by ϵ_{0ijk} , while v_{0k} and u_{0ijk} show the deviations from the mean intercept for each individual Natural Resource Management region (k) and site (i), when included as random effects in the model. The residual standard deviations (Res. SD) and residual standard errors (Res. SE) are presented for the mixed effects models (*) and linear models (†), respectively. A continuous autoregressive correlation structure was used in most models to account for the correlation between multiple years within a site, shown by the correlation co-efficient (ϕ). The sample sizes (n) represent the number of site-year data points used to model each relationship during baiting (B) and non-baited (NB) periods. Significant coefficients in the best-fit relationships ($P < 0.05$) are shown in bold.

fox baiting had recently begun, compared with sites that had been baited for longer.

The relationship between fox presence and malleefowl breeding numbers or population growth factor

Surprisingly, we found a significant positive relationship between fox presence and the number of active malleefowl mounds (Table 2). The relationship was influenced by the number of baited years, rainfall during winter months, the years since a fire and habitat patch size, where the effective breeding population was greater in sites with fewer baited years, high rainfall, more years since a fire, or in smaller habitat patches (Fig. 3a). However, based on a significant negative interaction between fox presence and years since fire, in recently burnt sites, the number of malleefowl breeding pairs was higher if the fox presence is low (Supporting Information Appendix S2). In contrast, for sites that were burnt over 35 years ago, the malleefowl outcome improved as fox presence increased. Site was included as a random effect in the best-fit model and each monitoring site was modelled with a different intercept (min = -1.051, mean = -0.612, max = -0.167, $\sigma = 0.210$).

We found a similar counter-intuitive relationship between fox presence and the population growth factor, where malleefowl growth increased significantly at sites with a higher proportion of fox scats on malleefowl mounds (Table 2). The significant environmental covariates remaining in the best-fit model included the number of baited years and the proportion of cleared land surrounding the monitoring site, suggesting that malleefowl population growth factors were higher when baiting had occurred for a longer period of time and in heavily cleared land (Fig. 3b).

The relationship between investment in fox baiting and malleefowl breeding numbers or population growth factor

We found a significant positive relationship between investment in baiting and malleefowl breeding population using empirical data (Table 2). The influential environmental covariates in this investment–outcome model included the number of baited years (as an interaction with investment), winter rainfall and habitat patch size. Regardless of the level of investment in fox control, monitoring sites that that were in small habitat patches, with high rainfall had larger breeding populations of malleefowl (Fig. 4a). Despite the positive trend of this overall model, 70% of the sites with enough data to estimate a relationship per site ($n = 22$) had negative relationships between investment and outcome. This is explained by the negative interaction between investment and the covariate baited years. We found that when a site had been baited for only 1 or 2 years, the number of breeding pairs increased with investment in fox baiting, yet as baiting continued for 3 or more years (when all other environmental covariates are kept constant at an average

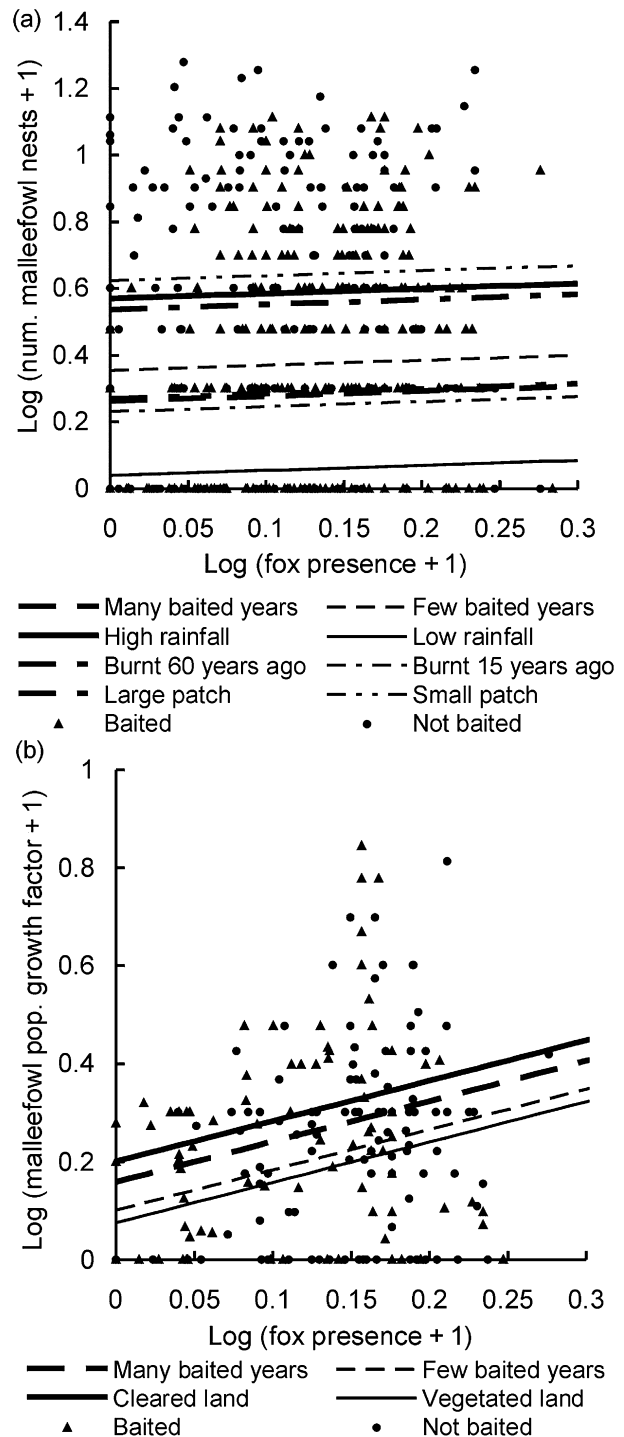


Figure 3 The best-fit models for the output–outcome relationships between the fox presence and (a) the number of malleefowl breeding pairs, and (b) the population growth factor. Significant environmental covariates in the best-fit models are shown, including the number of baited years, winter rainfall, years since a fire and habitat patch size (a) and the number of baited years and the proportion of cleared land surrounding the monitoring site (b). Note, the interaction between fox presence and the years since a fire is not illustrated in (a), but is shown in Supporting Information Appendix S2a.

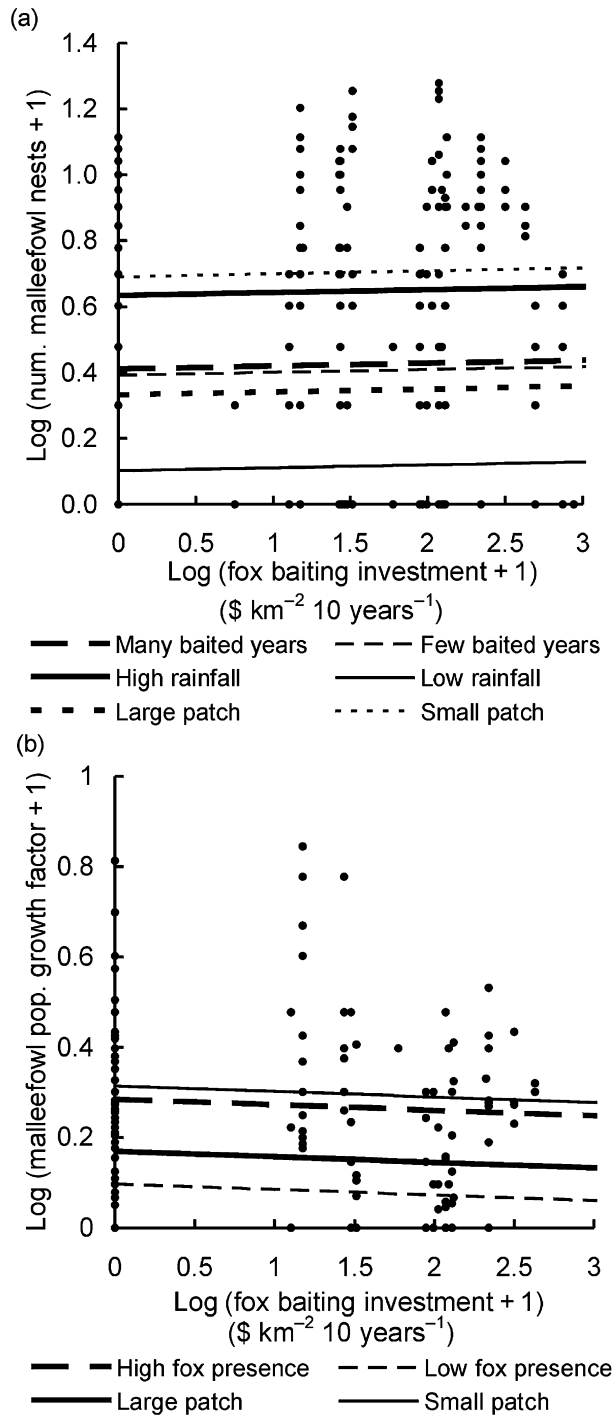


Figure 4 The best-fit investment–outcome relationships modelled directly using empirical data, between investment in fox control for a 10-year period and (a) the number of breeding malleefowl pairs, and (b) the malleefowl population growth factor. The influences of significant environmental covariates in the best fit models are shown, that is number of baited years, winter rainfall and habitat patch size (a) and fox presence and habitat patch size (b). Note, the interaction between baited years and investment in baiting is not illustrated in (a), but is shown in Supporting Information Appendix S2b.

value), further investment was correlated with a decline in the malleefowl breeding population (Supporting Information Appendix S2). Accordingly, the best-fit overall model included a random effect parameter for the intercept of each site (min = -0.851, mean = -0.413, max = 0.044, $\sigma = 0.222$).

The best-fit investment–outcome model showed no significant relationship between investment in fox control and the malleefowl growth factor (Fig. 4b). The influential environmental covariates in this investment–outcome model included fox presence and habitat patch size when modelling the population growth factor. Population growth factor was higher in sites located within small habitat patches and with higher fox presence (Fig. 4b). Site was not included as a random effect in the overall best-fit model between investment and population growth factor (Table 2).

The investment–outcome function developed by substituting models from the intermediate steps of the management process suggested that an increase in the investment in fox control would result in slight decreases in corresponding malleefowl breeding pairs and growth factor of this threatened species (Fig. 5; Supporting Information Appendix S3). However, as the parameter estimates for the explanatory variable and covariates were calculated based on substitution from models between investment–output and output–outcome relationships, the statistical significance of these results were uncertain.

Discussion

Even though fox baiting is effective for the conservation of native medium-sized mammal species (Dexter & Murray, 2009; Saunders *et al.*, 2010), we found that fox baiting was only a cost-effective management strategy for malleefowl in some circumstances, depending on the number of years a site had been baited. However, in most situations, malleefowl conservation did not effectively benefit from fox baiting at current levels of investment. The long-term effectiveness of fox baiting for malleefowl has been questioned previously (Benshemesh *et al.*, 2007), yet widespread fox baiting continues in many malleefowl habitats across Australia. Our study thus emphasizes the importance of evaluating and quantifying the returns from conservation investment using empirical data and demonstrates how the combination of decision making tools and evidence-based conservation can aid in achieving better conservation outcomes (Segan *et al.*, 2011).

Contrary to the perception that foxes are a major threat to malleefowl based on evidence of chick predation (Priddel & Wheeler, 1997; Priddel, Wheeler & Copley, 2007), both measures of malleefowl conservation outcome responded positively to higher levels of fox presence. This relationship, however, was reversed in the first few years after a fire, when the burnt habitat was unsuitable for malleefowl to breed because of lack of leaf litter, and when they may have been more vulnerable to predation (Benshemesh, 1992). Apart from periods after fire disturbance, foxes may not pose a significant threat to malleefowl populations, regardless of their effects through predation (Frith, 1962; Benshemesh

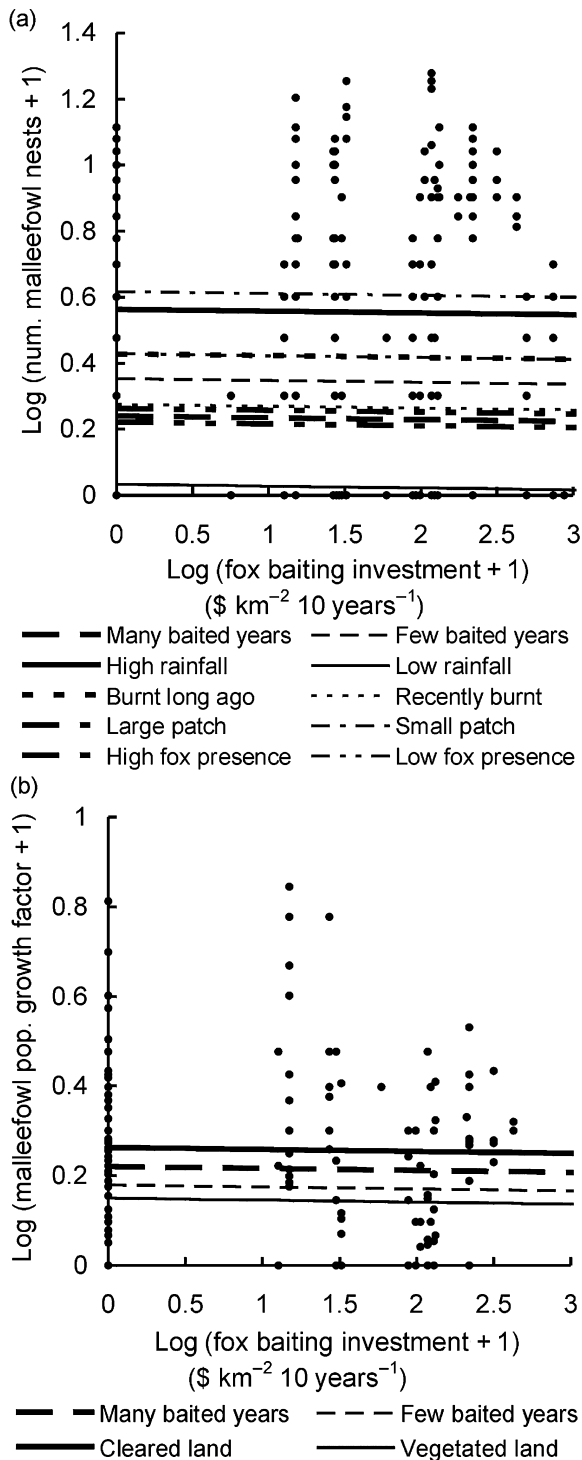


Figure 5 The investment–outcome relationships constructed using the substitution approach, between investment in fox baiting and (a) the number of malleefowl breeding pairs, and (b) the malleefowl population growth factor. The environmental covariates included in the substituted models were the number of baited years, winter rainfall, years since fire, habitat patch size and fox presence (a), and the number of baited years and the proportion of cleared land surrounding the monitoring site (b).

et al., 2007). The unexpected outcomes between fox presence and malleefowl outcomes reinforce the importance of analysing and synthesizing existing data on changes in population or abundance for the threatened species or ecosystem of interest, rather than measuring the level of threat reduction achieved or actions implemented, assuming follow-on conservation benefits (Kapos *et al.*, 2009).

We incorporated the effect of environmental characteristics in our relationships, rather than assuming that all sites were equal in their probability of management success, the severity of the threat, the ease and cost of implementing management, and their predicted response. While the negative trend between malleefowl breeding pairs and habitat patch size is unexpected, it is understandable because small reserves usually occur in more fertile country as less productive land is rarely cleared (Benshemesh *et al.*, 2007), and the surrounding cleared areas usually consist of croplands, which provide additional food sources for malleefowl during summer or drought periods (Harlen & Priddel, 1996).

Another interesting example of how a covariate influences the investment–outcome (malleefowl breeding pairs) relationship was the significant interaction between the number of baited years and investment in fox baiting. This suggests that the greatest return on investment may be achieved in the first year of baiting, subsequently decreasing with longer baiting regimes. This finding is contrary to what is recommended for fox baiting regimes, where ongoing annual or biannual baiting is prescribed to maintain low fox numbers (Saunders & McLeod, 2007). These contradicting results highlight the need for further experimental studies to confidently understand the drivers of the relationships between fox baiting, fox presence and malleefowl conservation outcomes and to account for unknown sources of variation.

Before managers use this study as evidence to cease potentially unsuccessful fox baiting in malleefowl habitat, there are several reasons for why our conclusions should be treated with caution. Primarily, our results are based on correlative models from a non-randomized uncontrolled dataset. This makes it difficult to account for unknown biases in fox management and malleefowl conservation across sites. In particular, higher investment in fox control may occur in sites with greater fox presence, thereby creating a feedback loop between dependent and independent variables – an issue known as endogeneity (Shadish, Cook & Campbell, 2002). For example, if baiting intensity was influenced by fox presence, any negative effect that fox control had on fox presence may be diminished. A reduction of the observed effectiveness of fox baiting would have flow-on impacts to the investment–outcome relationships developed using the substitution approach. This could result in potentially stronger negative relationships between investment in fox baiting and malleefowl outcome.

While endogeneity may potentially bias the results of our study, there is little evidence to suggest that fox baiting intensity was influenced by fox presence. Most land managers who conducted the fox control around malleefowl sites

did not routinely monitor fox presence or had access to the malleefowl dataset. Also, once baiting began at a site, its intensity usually remained constant over time, despite changes to fox presence. Even so, it is important to be aware of possible biases resulting from *ad hoc* use of the malleefowl dataset when interpreting the conclusions of this study. As recommended by several reviews on fox baiting in Australia (Reddiex & Forsyth, 2004; Saunders & McLeod, 2007), planned experimental designs to directly test for the difference in conservation outcomes between baited and non-baited sites, or baited and non-baited periods within sites, are needed for many threatened native species. Such an analysis would provide more reliable conclusions about the causal relationships between fox management and malleefowl conservation outcomes.

Another reason for not detecting solid evidence for the benefits of fox baiting for malleefowl is that the current average baiting intensity across malleefowl monitoring sites in this analysis (1.96 baits km⁻² year⁻¹) was well below the recommended fox baiting intensity for wildlife conservation; 5–10 baits km⁻² twice a year (Thomson & Algar, 2000; Saunders & McLeod, 2007). It is possible that an increase in the baiting intensity may deliver statistically significant positive malleefowl conservation outcomes. Alternatively, the positive association between malleefowl and foxes may indicate that both species respond independently to an unmeasured environmental covariate, such as primary productivity or soil fertility, masking any benefits fox baiting may have on malleefowl breeding numbers or growth factor. However, it is also possible that the benefits of fox baiting are obscured by the impact of unmanaged threats such as frequent and extensive fire, increased grazing pressure from exotic herbivores or extinction debt as a result of past land clearing and habitat degradation.

Given that fox baiting is the most common management action for malleefowl across Australia, there are several implications for this species' management in light of the results of this cost-effectiveness analysis. Despite the comparatively extensive malleefowl dataset, data on any management action other than fox baiting were inadequate for analysis. To ensure the future success of malleefowl conservation, the effectiveness of alternative management actions, such as reduction of grazing pressure by competing herbivores and prescribed burning, need also be evaluated. With data on multiple management actions, it would be possible to quantify their respective outcomes for malleefowl and prioritize which subpopulations should receive investment (McDonald-Madden, Baxter & Possingham, 2008; Joseph, Maloney & Possingham, 2009; Evans, Possingham & Wilson, 2011). Yet, even with one of Australia's most studied and managed threatened species, such a task as using empirical data is not yet possible.

For resource allocation between multiple threats to occur, a formal experimental design would be required to test the effectiveness of different management actions and their interactions. The malleefowl has a relatively large dataset, ongoing community support and public interest, funding opportunities, and several motivated, dedicated

leaders, making it an ideal species for an adaptive management programme (Walters, 2007; Benshemesh, 2008). Such a programme would enable a suitable experimental design to be developed and implemented with the advantage of greater explanatory power. However, adaptive management is often difficult to continue over a long period, making it less feasible for the majority of other threatened species (McCarthy & Possingham, 2007). Regardless of the design of future studies, the analysis of existing data, such as in the current study, provides valuable insights to help refine hypotheses, inform management decisions and provide a basis for more effective evidence-based conservation.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Methods – additional information.

Appendix S2. Graphical representation of the interactions between environmental covariates in the best-fit models, shown in Table 2. (a) The relationship between fox presence and the number of malleefowl breeding pairs, showing the interaction between fox presence and the years since a fire (ysf) occurred in the monitoring site. (b) The relationship between investment in fox baiting and the number of malleefowl breeding pairs, showing the interaction between investment in baiting and the number of baited years. All other environmental covariates in the best-fit models were kept constant at average values.

Appendix S3. Investment–outcome relationships derived from best-fit models between the intermediate steps of the management process in Table 2, using the substitution approach (Fig. 5).

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