BIRDS IN THE SKY, FISH IN THE SEA, MONEY IN THE BANK: QUANTITATIVE METHODS FOR EFFECTIVE CONSERVATION

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Abstract

My approach in this thesis was to explore how to wring more information out of existing data to reduce uncertainty, improve decision-making and hope to generate better conservation outcomes. I explore and develop a range of quantitative tools to this end. I look at three key areas: dealing with uncertainty, structuring decision making, and improving the use of existing information. I consider these concepts over three thematic case studies: monitoring the abundance of three vulture species in Cambodia, trading-off the costs and benefits of releasing information publicly when a new species or population is discovered, and comparing use of optimisation and project prioritisation protocols to allocate funding to species conservation efforts. In the first case-study, I develop new Bayesian hierarchical model to estimate vulture abundance, and compare the inferences available from this approach with less specialised approaches previously used. In the second case-study I develop a decision-making framework to allow decision-makers to explicitly trade-off costs and benefits, and apply the method to data collected from informants who have made these types of decisions themselves. In the final section, I explore whether additional information can improve optimisation to allocate funding, and compare performance in terms of expected avoided extinctions of the optimisation approach with a project prioritisation protocol. I find that there is indeed much more we can learn from the information we have. But this is not a free lunch – work needs to be done to uncover opportunities, and technical skills are often needed to make best use of them, and assumptions must often be made to draw conclusions.

Declaration

This is to certify that:

i) this thesis only comprises of my original work towards the PhD, except where indicated in the Preface,

ii) due acknowledgment has been made in the text to all other materials used,

iii) the thesis is fewer than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.

Gerard Edward Ryan

May 2021

Preface

Each chapter in this thesis consists of research conducted and lead by myself, in consultation with my supervisors Michael McCarthy and Emily Nicholson, as well as other researchers. Specifically, chapters one and two included collaborators from the organisations involved in the collection of the data that I used: Jonathan Eames, Thomas Gray, Robin Loveridge, and Sum Phearun. Chapters three and four were conducted in consultation with Christopher Baker. Chapter five was conducted in consultation with Stephen Garnett. In all cases, my collaborators discussed the work and provided comments and suggestions essential to the chapter. Otherwise, all analyses and writing consists of my own work.

Acknowledgements

First and foremost, acknowledgement to my supervisors Mick McCarthy and Em Nicholson — thank you to Pluto and back for all the years of support, mentorship, and patience. Many thanks to my wonderful collaborators in this work, Tom Gray, Robin Loveridge, Si Mahood, Sum Phearun, Jon Eames, Chris Baker, and Stephen Garnett. Thanks to the two anonymous examiners who provided helpful comments on improving this thesis. Thanks to the many people I owe for thoughts and input on this work and technical support, including Jose Lahoz-Monfort, Libby Rumpff, Will Morris, John Baumgartner, Jian Yen, Nick Golding and Casey Visintin. Thanks so much to the wider Quantitative Ecology Group for such a fabulous research culture and to the good close friends I have made, most of whom started with me, and most of whom have already long-finished – you are wonderful. Finally to my lovely family – thank you, I love you, and you can have me back now.

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Introduction

Humanity are beset by environmental problems from the modest to the severe, from the local to the global (Society for Conservation Biology 2019). Many measures of the global environment trend towards undesirable states (Almond et al. 2020; IUCN 2020a), suggesting that our various abilities to address the wide range of problems appears to be limited. In some cases we have not the knowledge or the ability to avert the last stages of crisis (e.g. Turvey et al. 2007). In many other cases, problems may be tractable, but the means at our collective disposal is not made available (Woinarski et al. 2017). Often, means is not available because of our collective balancing of our resources on a range of other needs and wants such as healthcare, food, clothing, or housing. As a result, global spending on conservation of the natural world has routinely found to be well below levels necessary to prevent ongoing degradation (McCarthy et al. 2012; Wintle et al. 2019). While it is essential that to sustain a healthy global environment conservation scientists must advocate more resources are directed to protecting and restoring nature, scientists must also aim to make the best use of information that we already have to improve our decision-making for conservation and thus outcomes.

Although historically much conservation management is done based on little data and high reliance on managers' experience (Cook et al. 2010), structured and quantitative approaches to decision making have been an area of much innovation in conservation (e.g., Bottrill et al. 2008; Wilson et al. 2009; Gregory et al. 2012b). In this thesis, I explore the use of quantitative methods to improve conservation outcomes. In particular I look at three key areas: dealing with uncertainty, structuring decision making, and improving the use of existing information. Uncertainty clouds many scientific disciplines, and is recognised as important in conservation and environmental science (Burgman 2005), where there may be a wide range of sources of uncertainty and poorly known environmental

systems. There may be uncertainty about what the best decision is, and the best decision may depend on the decision-maker's attitude to uncertainty (Pratt 1964; Kahnemann & Tversky 1979; Canessa et al. 2016). Structuring decision-making processes enable decision-makers to work through complex problems, deal with uncertainty, and make the trade-offs necessary in environmental management (Gregory et al. 2012a). In addition the use of more information may be expected to reduce uncertainty, and therefore improve decision-making. While the collection of new data may be expensive and not always justified (Canessa et al. 2015; Morris 2017), existing data that are either formalised or consisting of expert opinion, represent a potential 'free-lunch', in that there may appear to be little downside in utilising additional information where possible.

I consider these concepts over three thematic case studies. In the first section in chapters one and two, I explore a case study where monitoring vultures in Cambodia and I develop new estimate abundance from the existing monitoring data. The data were historically collected as a means of monitoring the national populations of the three resident vulture species, which are all critically endangered (IUCN 2020b): the White-rumped Vulture, *Gyps bengalensis*, the Slender-billed Vulture, *Gyps tenuirostris*, and the Red-headed Vulture, *Sarcogyps calvus* (Clements et al. 2013). In the early part of the 21st century, vulture populations in Asia declined rapidly due largely to the use of diclofenac in the treatment of sick cattle, which subsequently died and were consumed by vultures (Swan et al. 2006; Pain et al. 2008). The provision of safe food, in the form of carcasses of animals known not to have been treated with diclofenac, has become a common conservation measure in response to this (Clements et al. 2013; Loveridge et al. 2019). The Cambodian vulture monitoring data consist of counts of individuals observed at carcasses provided by conservation programmes both regularly at some sites, and simultaneously across all sites for the purposes of a national 'census'. The inability for such data to deal with imperfect detection, i.e., the probability that not all individuals in the population may be detected (Kéry & Schmidt 2008), means that the direct us of

counts for monitoring will likely underestimate the true population size, and may be biased in ways that are unknown, potentially leading to misleading conclusions informing conservation management. In chapter one, I develop a new statistical method – a 'simultaneous count model' — to estimate abundance from populations where individuals are unmarked, and counts are conducted simultaneously. I use simulation to test the performance and properties of the model, and then apply the method to the three Cambodian populations of vultures. The method uses hierarchical Bayesian methods to model imperfect detection, and although this approach only requires the simple count data, the analysis of it is technically specialised and likely to be beyond the skillset of many conservation monitoring programmes. In the second chapter I therefore compare the utility of this new method against using simpler methods to explore the status of the populations, the minimum number alive method, which uses the maximum count to infer a minimum population size, and fitting a generalised linear model to count data, to explore general trends. Both of these methods require less-specialised statistical knowledge and can be applied much more easily than the simultaneous count model approach. In this chapter I compare the relative demands of these three analysis approaches in terms of data and skill, with the inferential powers they convey.

In the second section of this thesis, in chapters three and four, I explore a conservation decision-making problem: what information should be publicly released when a species is newly discovered or re-discovered. For example, the first known salamander species from Laos — the Lao newt *Laotriton laoensis* — was discovered by scientists in 1998 and dutifully described in 2002 in a scientific journal (Stuart & Papenfuss 2002). The species is evolutionarily distinctive (Dubois & Raffaëlli 2009; Phimmachak et al. 2012), and highly attractive, with tan-striped dorsal ridges and bright orange ventral spots on a dark black body (Stuart & Papenfuss 2002). Such a discovery is scientifically interesting, and the discovery of an attractive new species in a little-known part of the world is of general interest to the global public. While the species appears to have previously

existed largely unmolested, and its “advertisement” in a scientific journal led to demand for collection of the species for the international pet trade (Stuart 2006; Stuart et al. 2014), and the species is now considered Endangered due to the population declining because of this illegal harvest (IUCN 2020b). It is clear from this example that there are dangers of publicising information about species that may be threatened when information is known about them. This risk is also true for newly discovered populations of species known to be of high commercial value, like rhinos (Meijaard & Nijman 2014). However the alternative, not making such information available, can have implications ranging from reduced public engagement or financing of conservation, to inhibition of scientific or management activity through lack of available information. Solutions to this problem have called for restriction of publishing under certain circumstances focusing on reducing risk to species, and range from rudimentary descriptions of trade-off scenarios (Lindenmayer & Scheele 2017), to basic decision frameworks (Meijaard & Nijman 2014), and complex decision trees (Tulloch et al. 2018). A difficulty with these existing frameworks is that they do not provide decision-makers the opportunity to consider their own unique circumstances, and make trade-offs under their own specific risk attitude. In addition, these frameworks also do not generally incorporate the possibility that information may become public against the will of decision-makers anyway. In chapter three, I develop a framework to trade off the potential costs and benefits to the species, while also considering this possibility that information may leak anyway. In chapter four, I extend this framework, and apply it to a range of real-world decision scenarios, based on data collected from interviews with decision-makers involved with the discovery and publicity (or not) of new species or new populations. I explore the role of uncertainty in influencing the optimal decision, and demonstrate approaches to account for uncertainty and risk attitude for decision-making. The intent of these chapters is to provide decision-makers with a framework that can be used with existing information to guide these trade-offs for future decisions about what information to release regarding the discovery of new species.

In the final section of the thesis, the fifth chapter, I explore how we can use existing information about species to allocate conservation funding more efficiently. The efficient allocation of 'stuff' in conservation (funds, land) has been a wide and fruitful area of research and application over the last 15 years with a range of approaches to spatially prioritizing landscapes for a range of goals (Moilanen et al. 2009), and the development of protocols to efficiently allocate funding to conservation project portfolios (Joseph et al. 2009; Carwardine et al. 2014). Many of these tools use computational tools like simulated annealing (e.g., Marxan (Watts et al. 2009)), or step-wise selection heuristics to allocate resources in a way that is more efficient that many other approaches, but may not be the strictly optimal result. Previous work by Mc Carthy and colleagues (McCarthy et al. 2008) has demonstrated that optimisation approaches can be applied to efficiently allocate funding to threatened species to theoretically maximise the conservation outcomes for a range of goals, e.g. minimising the number of threatened species or extinctions. The work of McCarthy and colleagues looked exclusively at efficiency based on species' IUCN Red List status (McCarthy et al. 2008). In chapter 5 I first extend this work to explore the importance of a range of other biological and management factors in the efficiency of allocating investments, to determine whether this use of a broader range of existing information could be used to improve the optimization and thus improve conservation outcomes. In the second part of this chapter, I explore whether allocation of funding following a numerical optimization can provide greater conservation outcomes than using a project prioritisation protocol approach.

Overall the aim of this thesis is to develop and explore the use of quantitative methods to improve decision-making processes in conservation, and therefore achieve better conservation outcomes. I consider how we may reduce uncertainty in chapters 1, 2, 4, and through estimating detection rates for vultures, accounting for the range of possible costs and benefits in species discoveries. I provide structure around decision-making processes in chapters 3, 4, and 5, through developing and solving

formalised objective functions for publicity decisions and funding allocation problems. And throughout all chapters, I explore how the additional use of existing data may be used to improve conservation outcomes.

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Chapter One: Simultaneous-count models to estimate abundance from counts of unmarked individuals with imperfect detection

This chapter is the basis for the article:

Ryan, G.E., Nicholson, E., Eames, J.C., Gray, T.N., Loveridge, R., Mahood, S.P., Sum, P. and McCarthy, M.A., 2019. Simultaneous-count models to estimate abundance from counts of unmarked individuals with imperfect detection. Conservation Biology, 33(3), pp.697-708.

Introduction:

Abundance is a fundamental measure in ecology and environmental management. Detecting all individuals in a population is usually impossible when monitoring (Dice 1941), so estimates of abundance must account for imperfect detection (MacKenzie et al. 2005). Counts of individuals can provide an index of abundance if the probability of detection does not vary in time or space, or if variation in detection is accounted for, allowing population dynamics to be inferred by repeating counts in space or time (Link & Sauer 1998). However, if detection varies in unknown ways, or if absolute abundance is the parameter of interest, then counts alone will not be informative (Anderson 2001; MacKenzie et al. 2005; Archaux et al. 2012). Knowing *a priori* whether the probability of detection varies is usually not possible (Guillera-Arroita et al. 2014), but a variety statistical methods exist that account for imperfect detection when estimating abundance, generally using the number of individuals seen in combination with some additional information, such as distance of sighting, double-observation, markings, removals, or some combination of these (e.g., Borchers et al. 1998; Nichols et al. 2000; Buckland et al. 2007; Amundson et al. 2014). Getting such additional information in the field however can be difficult, expensive, or compromise animal welfare, so methods have flourished to use counts of sightings from unmarked animals as well as

supplemented data, such as mark-resight (McClintock et al. 2009), or exclusively, such as N-mixture models (Royle 2004a; fig. 1.1a).

Simple counts remain common in monitoring practice, despite the limitations of inference when imperfect detection is ignored and the range of available methods to estimate abundance (Kellner & Swihart 2014; Stephens et al. 2015). In particular, some surveys aim to census entire populations by conducting counts by different observers simultaneously at multiple locations (as distinct from double-observer counts, which occur simultaneously at the same location). Examples include breeding-ground counts of geese (Mitchell 2015), roost counts of ibises (Wright et al. 2012), cockatoos (Williams et al. 2016), and jackdaws (Blanco et al. 2014), cave counts of seals (Martínez-Jauregui et al. 2012), and camp or fly-out counts of bats (Westcott et al. 2015). Simultaneous counts are sometimes used in monitoring programmes to produce a minimum population estimate, to prevent double-counting of individuals, or reduce non-detections (e.g., Clements et al. 2013). The utility of this monitoring depends on an assumption either that a constant proportion or the population is detected, or that simultaneous counts act as complete censuses, i.e. all individuals in the population are counted.

There are two existing alternatives for analysing simultaneous count data to estimate abundance that while accounting for detection. First, a simple binomial model considers the entire population as just two groups — detected and undetected (fig. 1.1a), and models the observation process overall sites together. With repeated surveys, information on the variation in the number of individuals detected could be used to estimate detection probabilities and abundance. Here we term this a “binomial simultaneous-count model” approach. If counts are simultaneous, and the overall population is closed to recruitment, mortality and migration within survey periods, and all individuals in the population have the potential to be detected over the course of sampling, this abundance and detection are analytically simple to estimate. However although simple, we know of

no studies using this particular approach, and it does lose information on variation in detection and abundance among sites that may be of interest in some studies. A more complex approach is a binomial N-mixture model, which considers the observation process each site, where individuals at that site are either detected or not detected (fig. 1.1b). Although useful for counts of unmarked individuals, they will not apply well in all circumstances. Binomial N-mixture models allow abundance at each site to vary with some distribution, typically Poisson (Royle 2004a) or negative-binomial (Martin et al. 2005). Accounting for further variation in abundance or variation in detection among sites requires estimation of covariates, and so it may not be possible to account for such variation where covariates are unknown, or there are too few sites to estimate their coefficients. If the area of sites in binomial N-mixture models is poorly defined, it is impossible to accurately extrapolate density at sites to absolute abundance. If individuals are mobile and may occur at a number of sites on different occasions within a sampling period, the assumption of closure is not met, and estimates will be unreliable. Thus binomial N-mixture models do not make use of the information that counts are simultaneous.

We develop a "multinomial simultaneous-count model" approach similar to the binomial N-mixture model intended to apply specifically to simultaneous counts (fig. 1.1c, table 1.1). We model an observation process over the entire population of interest. The multinomial simultaneous-count model (fig. 1.1c) considers that on each sampling occasion an individual present in the population is either detected at no more than one site, or remains undetected , consisting of k+1 groups, where k is the number of surveyed sites and each individual occurs in exactly one of these groups. Although more complex than the binomial simultaneous-count model, it allows estimation of site level detection processes as well as population abundance.

We differentiate the "simultaneous-count model approach" from N-mixture model approaches, for several key reasons (table 1.1). Firstly, the intent: binomial N-mixture models are intended to

estimate site-specific abundance (or density), and estimate this over many sites, whereas simultaneous-count models are intended to estimate the abundance of an entire population over those sites. Secondly, binomial N-mixture models apply the observation process at each site separately, whereas the simultaneous-count model approach consider observations in a single process over all sites. And thirdly, although the binomial simultaneous-count model and binomial N-mixture model are the same if applied to a single site, the binomial simultaneous-count model is not a mixture model, because there is no mixing distribution, only a single estimate of *N*. The simultaneous-count model approach assumes that the area surveyed represents the entire population of interest, that the whole population is closed during survey periods, and that individuals are not double-counted, which is likely to be true when surveys are simultaneous. The advantages of this simultaneous-count model approach over an N-mixture model approach are that the probability of detection at individual sites can vary without the need for estimable covariates, estimates of abundance are not sensitive to having a well-defined survey area, and there is no assumption that the population at a site is closed within the survey period (table 1.1). To our knowledge such an approach has not been described or tested in wildlife monitoring before, though could be applicable to other situations with similar survey designs where unmarked individuals are counted simultaneously over a population.

Table 1.1. Comparison of simultaneous-count model approach and N-mixture model approach.

	Simultaneous-count model approach		**N-mixture model approach**	
Detection model	**Binomial**	**Multinomial**	**Binomial**	**Multinomial**
Modelling of observation process level	All sites (summed together)	All sites	Single site	Single site

Data	Simultaneous counts	Simultaneous counts	Counts	Counts & other data, e.g. encounter history
Estimates	Total population size	Total population size	Site abundance/ density	Site abundance/ density
Estimate detection probability at each site	No	Yes	Yes, unique with covariates	Yes, unique with covariates
Scale of closure required	Population	Population	Site	Site
Can accommodate variation in detection/abundance among sites	Yes	Yes	With inclusion of covariates	With inclusion of covariates
Robust to poorly defined site area	Yes	Yes	No	No

Here we describe multinomial and binomial simultaneous-count models (SCMs), evaluate their performance via simulation, compare the multinomial and binomial models, and apply the multinomial model to a motivating case study of counts of three critically endangered vulture species in Cambodia: Red-headed Vulture *Sarcogyps calvus*, Slender-billed Vulture *Gyps tenuirostris*, and White-rumped Vulture *Gyps bengalensis* (BirdLife International 2014). These vulture populations are globally significant, geographically disjunct from other populations of the same species and so

geographically closed, and the binomial N-mixture model approach cannot be easily applied because there are few monitoring sites, the populations are dispersed unevenly in the landscape with no known covariates to account for this, and individuals are known to move among sites between sampling occasions (Clements et al. 2013).

Materials and methods:

Simultaneous-count models for abundance

Consider a closed population for some brief survey period: there is no migration, recruitment, or mortality, and the population is bounded in a distinct geographic area. The population is surveyed simultaneously at *k* sites on multiple occasions within the period of closure. At each site *i*, on occasion *t*, some number of individuals, $y_{i,t}$ is counted, producing a series of counts $y_{1:k,\,t}$. On each occasion, each individual in the population is either detected at no more than one site, or not detected, resulting in *k*+1 groupings into which each individual may occur (fig. 1.1b). The total population abundance of individuals that could be detected, *N,* is the sum of all the individuals detected at all *k* sites, plus the number of individuals not detected at any site, $y_{k+1,t}$ (which is unknown), so $N = \sum_{i=1}^{k+1} y_{i,t}$.

If the probability that in a given sampling occasion an individual is detected at site *i* is π_i, for sites 1:*k*, and the probability an individual is not detected at any of the sites is π_{k+1}, then $\sum_{i=1}^{k+1} \pi_i = 1$, because the individual must be somewhere.

Counts of individuals detected and not detected, $y_{1:k+1,t}$ have a multinomial distribution from a population of *N* and with probabilities of π_1 to π_{k+1}:

$y_{1:k+1,t} \sim multinomial(N, \pi_{1:k+1})$ eqn. 1

The likelihood for this is:

$$L(N, \pi_1, \pi_2, \dots, \pi_{k+1} | y_1, y_2, \dots, y_{k+1}) = N! \prod_1^{k+1} \frac{{\pi_i}^{y_i}}{y_i!}$$ eqn. 2

Which, when we separate the elements corresponding to the undetected population equals

$$L(N, \pi_1, \pi_2, \dots, \pi_{k+1} | y_1, y_2, \dots, y_{k+1}) = \frac{N!(1-\sum_1^k \pi_i)^{(N-\sum_1^k y_i)}}{(N-\sum_1^k y_i)!} \prod_1^k \frac{{\pi_i}^{y_i}}{y_i!} \qquad \text{eqn. 3}$$

If we consider the binomial equivalent of this, where observations from all surveyed sites are treated as a single site,

$$\sum_1^k y_i \sim binomial\left(N, \sum_1^k \pi_i\right) \qquad \text{eqn. 4}$$

Then the likelihood is:

$$L\left(N, \sum_1^k \pi_i, \pi_{k+1} | \sum_1^k y_i, y_{k+1}\right) = \frac{N!(1-\sum_1^k \pi_i)^{(N-\sum_1^k y_i)}}{(N-\sum_1^k y_i)!} \times \frac{(\sum_1^k \pi_i)^{(\sum_1^k y_i)}}{(\sum_1^k y_i)!} \qquad \text{eqn. 5}$$

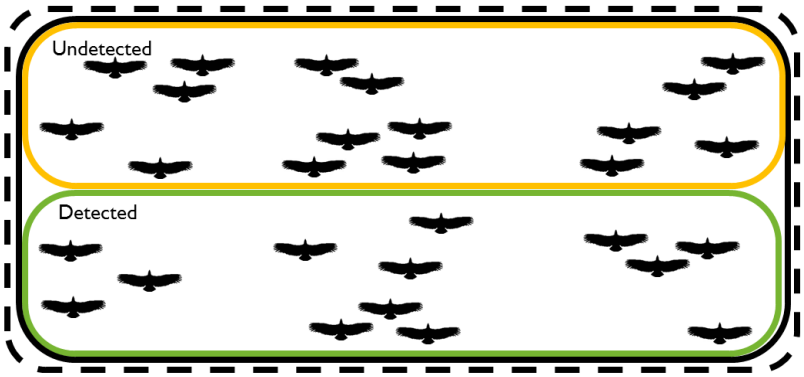
Although equations three and five are not equivalent, the elements of the likelihood including *N* are identical, and so the likelihoods with respect to *N* are exactly proportional to each other. Therefore, both binomial and multinomial formulations of the model should generate the same maximum likelihood and Bayesian estimates of *N*.

Note that π_i represents the probability that an individual is detected at site *i* on a given sampling occasion, not the probability that it occurs there. Individuals present at a site but not detected will be incorporated into probability π_{k+1}. So π_i could be considered as the product of the probability that an individual occurs at site *i* on a given occasion, and the probability that the individual is detected given that it occurs there.

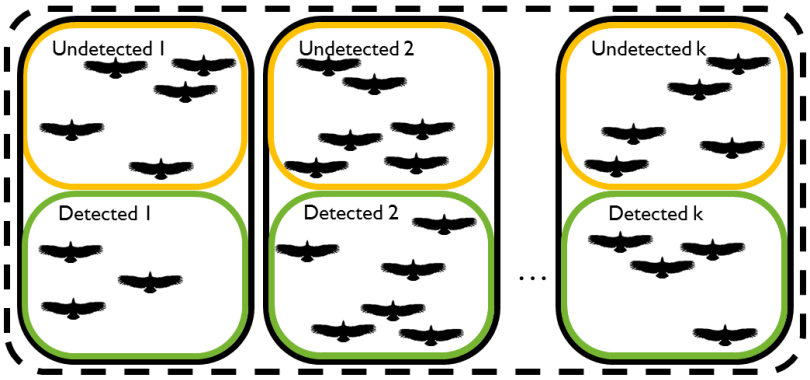
The simultaneous-count model assumes that individuals are not double-counted, and that the population is closed during sampling. Closure can be relaxed to estimate an open (changing) population such as through a robust design framework consisting of a mix of periods of population closure with repeated surveys, interspersed by 'open' periods, where N may vary.

Figure 1.1 provides a graphical contrast of the simultaneous-count models and the binomial N-mixture model, while Table 1.1 compares these as well as multinomial N-mixture models. The SCM

detection process and abundance estimates operate at the population level, while in N-mixture models, the detection process and abundance estimates operate at a single site level with the a multinomial process in multinomial N-mixture models resulting from additional information such as removals, double-observer counts, or encounter histories (e.g., Royle 2004b; Kéry & Royle 2010, 2016).



(a)



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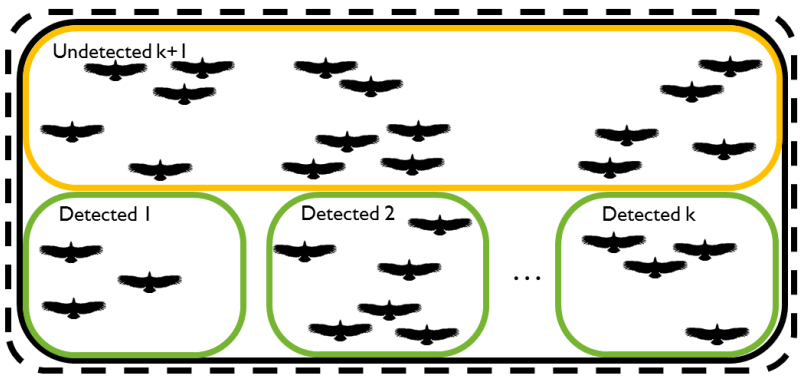


(c)

Figure 1.1. Our population of interest is enclosed in the dotted line, our observation process is modelled within the black line, and some individuals are detected (green) or not detected (yellow). If we survey over k sites, we may consider (a) a binomial simultaneous-count model process where individuals are either detected or not, (b) a binomial N-mixture model where observation operates at each site, or (c) a multinomial simultaneous-count model process where individuals in the population are either detected in one of the *k* sites, or undetected.

Simulations

We conducted simulation experiments to test how well the simultaneous-count models estimated known values. Sets of simulations explored specific parameters of interest. In each set we vary the parameter, and repeat simulations over orthogonal combinations of detection probability, and number of sampling occasions and sites for both multinomial and binomial simultaneous-count models (table 1.2). We typically simulated an initial population, N_0, of 1000 individuals, sampling on two to sixty-four occasions, and the net probability of detection — the probability an individual was detected anywhere — of 0.1, 0.5, or 0.9 (table 1.2). Net probability of detection, *p'*, is the sum of the probabilities that an individual is detected at each site: $p' = \sum_1^k \pi_i = 1 - \pi_{k+1}$, and equals *p* in the binomial models. We split *p'* evenly among sites such that $\pi_1 = \ \pi_2 = \cdots = \pi_k = \frac{p'}{k}$. For example if *p'* = 0.5 and there are two sites, the probability an individual will be detected at one of those sites is $\pi_1 = \ \pi_2 = \frac{0.5}{2} = 0.25$. We conducted five sets of simulations; the main aims and details are described below, and the full combination of parameters are listed in Table 1.2:

1. **Binomial models**: this set aimed to establish that the model we had specified was consistent with sampling at a single site, i.e., when they should be identical.
2. **Number of sites:** compared how the simultaneous-count models performed with differing numbers of sites: one, two, three, five, seven, or nine.

3. **Growth rate:** examined a robust-design open population specification of the simultaneous-count models to changes in abundance. We specified an exponential population growth rate R, where $R = N_{t+1}/N_t$, and $N_t = N_0 \times R^t$. We simulated surveying populations at one, three, or seven sites, over two, four or eight years, with two, four, or eight sampling occasions per year, and exponential growth rates, R, of 0.9, 0.98, 1, 1.02, and 1.1.
4. **Population size:** examined performance of the models with populations of 10, 100, 1000, or 10 000 individuals, in one, three or seven sites, and we did not truncate the hyper-prior for N, λ (see *Analysis*, below).
5. **Spread of observed population:** compared when the probability of detection was even among sites, as our other simulations, and when the probability of detection differed among sites. Where probabilities of detection differed, half of the net probability of detection was assigned to a single site, and the remainder spread evenly among the other sites, so that $\pi_1 = \frac{p\prime}{2}$, and $\pi_2 = \cdots = \pi_k = \frac{p\prime}{2(k-1)}$.

Table 1.2. Experimental design for simulation studies, showing fully crossed parameter sets for each group of simulations.

Simulation set	**1. Binomial models**	**2. Sites**	**3. Growth rate**	**4. Population size**	**5. Spread of observed population**
Open or closed population	Closed	Closed	Open	Closed	Closed
Sampling occasions (per year)	2, 4, 8, 16, 32, 64	2, 4, 8, 16, 32, 64	2, 4, 8	2, 4, 8, 16, 32, 64	2, 4, 8, 16, 32, 64

Net probability of detection (*p'*)	0.1, 0.5, 0.9	0.1, 0.5, 0.9	0.1, 0.5, 0.9	0.1, 0.5, 0.9	0.1, 0.5, 0.9; split evenly and unevenly among sites
Population size (N_0)	1,000	1,000	1,000	10; 100; 1,000; 10,000	1,000
Number of Sites	1	1, 2, 3, 5, 7, 9	1, 3, 7	1, 3, 7	3, 7
Population growth rate (*R*)	–	–	0.9, 0.98, 1, 1.02, 1.1	–	–
Years	1	1	2, 4, 8	1	1

Analysis

We specify the models in a Bayesian framework using JAGS 4.3.0 (Plummer 2003, 2017). Priors for $\pi_{1:k+1}$ are drawn from a Dirichlet distribution, and priors for N are drawn from a Poisson distribution, so: $\pi_{1:k+1} \sim Dirichlet(\alpha_{1:k+1})$, and $N \sim Poisson(\lambda)$, and $y_{1:k+1,t} \sim multinomial(N, \pi_{1:k+1})$ or $y_{1:k,t} \sim binomial(N, p)$ in the multinomial and binomial models respectively. A Poisson distribution was used as the prior for a discrete N, though other prior distributions are certainly possible. We set weak priors for λ (10^{-6}, 10^{-6}), and improve model convergence, we truncated our prior distribution for λ at 5,000 (except set four, see above). Priors for α were such that each $\alpha_{1:k} = \frac{1}{k}$, and $\alpha_{k+1} = 1$. Thus, equal prior weight is given to the probability of detection and non-detection, and is equivalent in both multinomial and binomial models with the same data.

New data were randomly generated for each simulation, and we ran 100 simulations for each combination of parameters.

The standard specified distributions in major MCMC software like WinBUGS, OpenBUGS, and JAGS do not allow multinomial likelihoods with missing values—in this case the number of individuals not detected, $y_{k+1,t}$. Although conceptually we could model the detection process in the multinomial SCM as a binomial for detection and non-detection, with a multinomial process for occurrence at each site, because the number of individuals detected each occasion varies this is not possible. Hence, we specify the multinomial model using the 'ones trick' (Spiegelhalter et al. 2003). The 'ones trick' allows the estimation of a likelihood from a distribution not specified within the software, where the likelihood is written in full.

Models were fit in JAGS with three chains, 100,000 iterations, 50,000 burn-in, and up to 3 updates if not converged initially. Convergence was confirmed *post hoc* with Gelman-Rubin statistics (Gelman & Rubin 1992; Brooks & Gelman 1998), where all r-hat values were <1.1, or those simulation fits were discarded. All analyses were conducted in R 3.x (R Core Team 2017). Code to replicate the entire analysis, as well as results summary files are available in Supporting Information 1: https://github.com/geryan/simultaneous_count_models.

Case study: Cambodian vulture populations

The motivation for developing the SCM was to estimate the abundance of the Cambodian populations of three critically endangered vultures; the Red-headed Vulture, Slender-billed Vulture, and White-rumped Vulture. In North-Eastern Cambodia where these populations occur, carcasses are provided at 'vulture restaurants' both to prevent poisoning and to supplement food because local wild ungulate populations are small (Loveridge et al. in press). To monitor the population, restaurants are surveyed simultaneously at all major sites on two occasions each year, two weeks apart in June, outside of the breeding season. These counts provide a lower limit on the population estimate, and are described further by Clements and colleagues (2013) and Loveridge and colleagues (in press). Here we consider count data from these simultaneous restaurants from 2006–2014 at six major sites where data are available for all years: Chhaep Wildlife Sanctuary, Prey Siem Pang Kang Lech Wildlife Sanctuary, Phnom Prich Wildlife Sanctuary, Lomphat Wildlife Sanctuary, Srepok Wildlife Sanctuary, and at the Sesan River (Loveridge et al. in press; Clements et al. 2013). Several other sites were included in a small number of years (Loveridge et al. in press), but as most occasions yielded very few or no birds, we exclude them to simplify analyses. This is not likely to substantially affect the results; any birds present at these excluded sites will be estimated in the unobserved population, and we assume detection rate is not affected by birds being attracted to excluded sites. Telemetry studies show that individuals stay within the study area and move among sites (Clements et al. 2013). This suggests that the key assumptions of our model are met: that the area surveyed represents the entire population of interest, that individuals are not double-counted, and that the population is closed between sampling occasions within the same year, but also that a binomial N-mixture model may not be appropriate.

We use the multinomial SCM to model two possible population trajectories: constant abundance, or exponential growth, fit as in our simulations. We also consider changes in probability of detection.

We expect birds may be 'trap-happy' as they stay near a carcass after feeding and the time between sampling occasions is short, so we may expect more vultures to appear at the second occasion each year. Therefore, we model either constant probability of detection, or where detection varies between the two occasions within each year, but is constant over years. Detection was varied by the same factor, over all sites, *v*, such that if the probability of detection at any site *i* on occasion *t* in year *y* is $\pi_{i,t,y}$, then $\pi_{i,t+1,y} = v \times \pi_{i,t,y}$. The probability an individual is not detected varies by a factor of μ, such that where there are *k* sites then:

$$v = \frac{1 - \mu \times \pi_{k+1,t,y}}{1 - \pi_{k+1,t,y}}$$

We expected that abundance would change over time, and that detection would be higher in the second sampling occasion than the first. Here we compare model fits using Deviance Information Criterion (DIC) as a simple and convenient method to illustrate this case study, though alternative model comparison methods are available and may better suit other applications (Tenan et al. 2014).

Results

Simulations

For a single site population, binomial and multinomial simultaneous-count models were equally accurate in estimating population size and probability of detection (fig. 1.2a. and b). Both models also performed similarly in capturing the true population value within the 95% credible interval. A large number of sampling occasions were necessary to achieve accurate estimates for both models, probably stemming from the prior that detection and non-detection were equally likely.

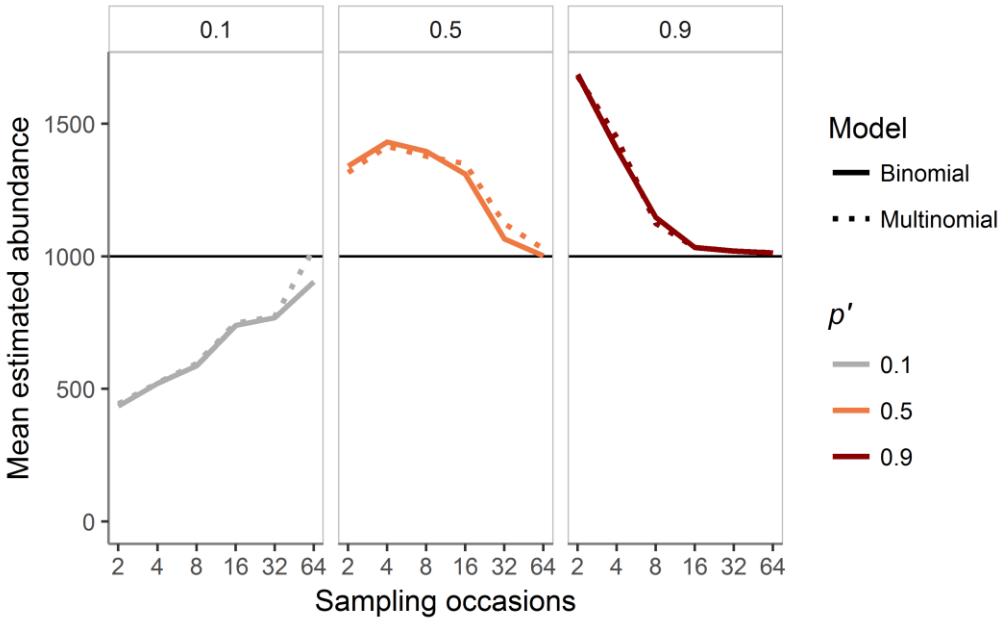
With larger numbers of sites, again both models performed similarly in estimating abundance and detection rates, regardless of the number of sites (fig. 1.3a and b). In some areas the multinomial SCM was overconfident so that many 95% credible intervals do contain the true value. Overconfidence was more likely in simulations with more sites, low probability of detection, and

more sampling occasions fig. 1.3c., suggesting the model may struggle with little information and become biased

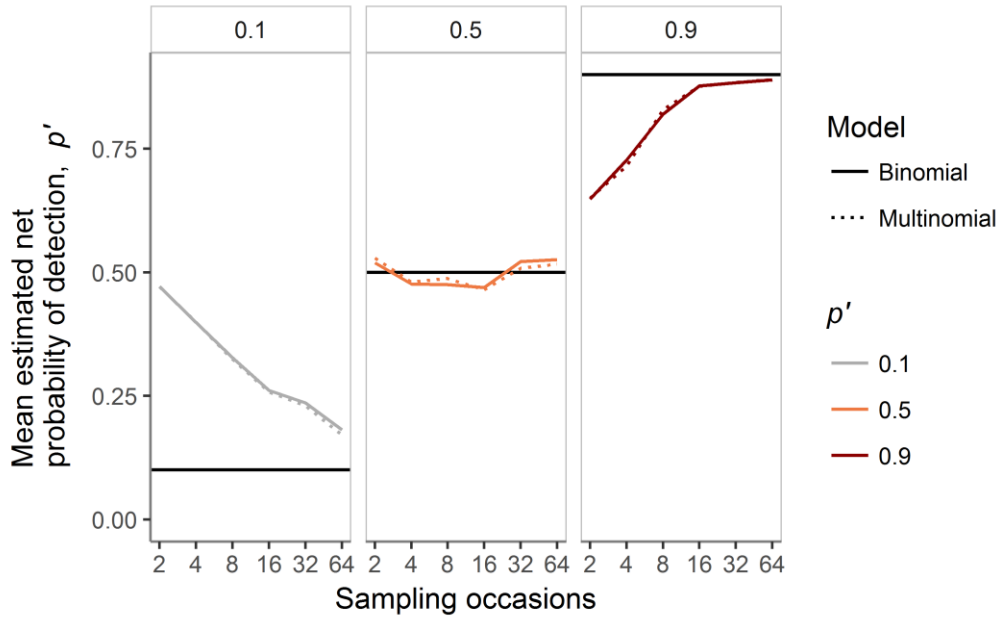
In an open population, estimates of growth rate were accurate and unbiased, fig. 1.4, though estimates of abundance and probability of detection when abundance changed over time were similarly accurate to when abundance was constant.

The pattern of results was similar again with different population sizes except for the largest population included, 10,000 (fig. 1.5). Estimates when population was 10,000 did not appear to get closer to the true abundance with increasing effort, and appear to be overconfident with many failing to capture the true value. We expect that this is caused by an inappropriate prior, which was the same regardless of the true population size, rather than an inherent failing of the model. This pattern occurred for both the multinomial and binomial models.

Whether the observed population was spread evenly or unevenly = among sites did not affect performance (fig. 1.6.); results for uneven splits were equally accurate to even.



(a)



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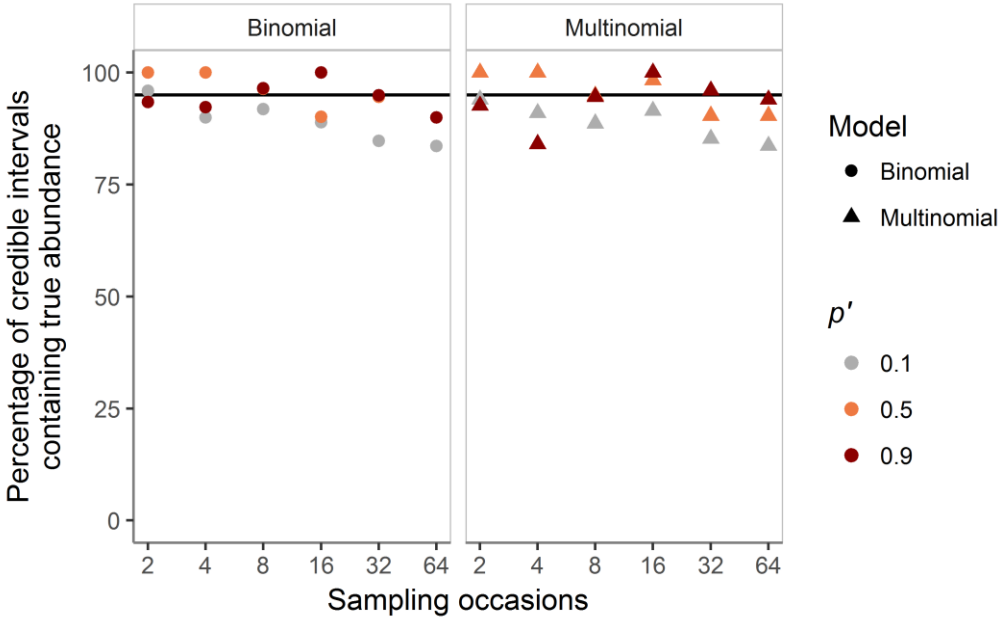
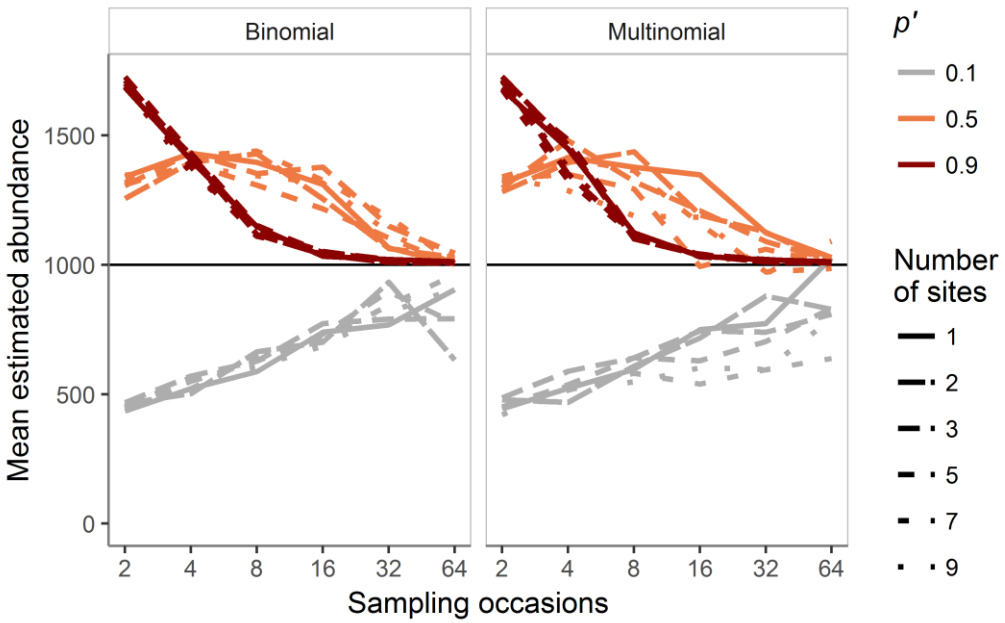


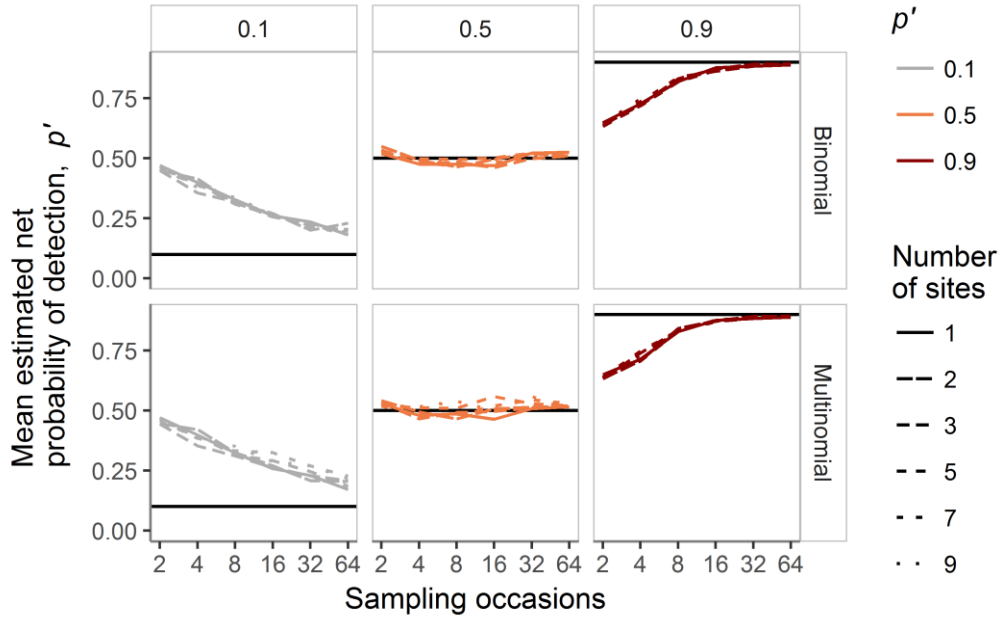
(c)

Figure 1.2. Simulations comparing the binomial and multinomial simultaneous-count model and estimates with a single site. Mean estimates of (a) abundance, and (b) probability of detection, for the two models (line-type), and combinations of number of sampling occasions (x-axis) and probability of detection (colour and panel). (c) Percentage of 95% credible intervals for estimate of

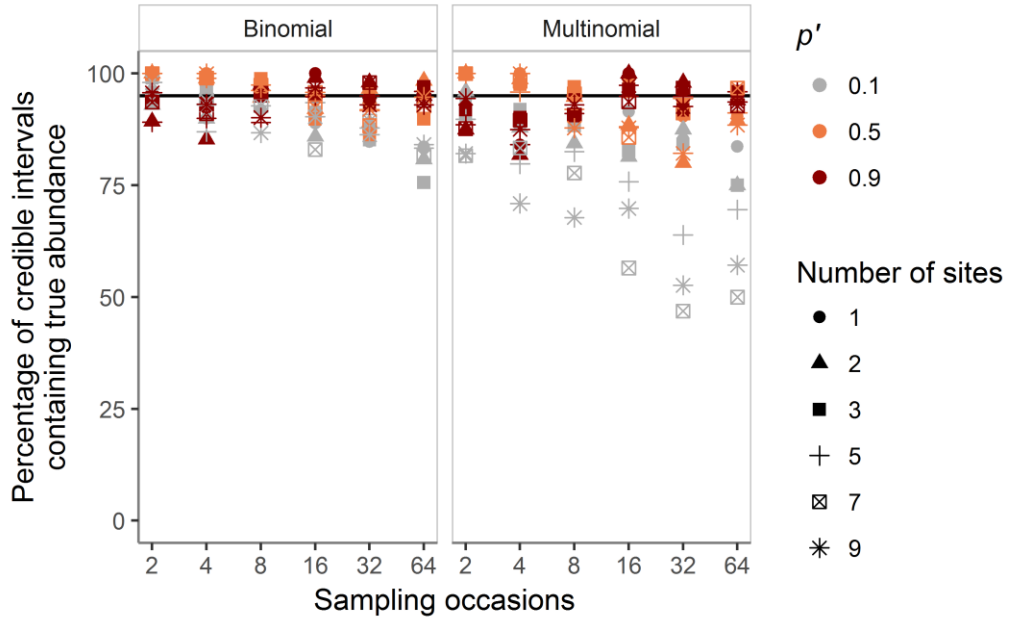
abundance that included the true value. Black horizontal lines represent the true values of (a) abundance and (b) probability of detection, and (c) 95%.


Binomial
Multinomial
Mean estimated abundance
1500
1000
500
0
2
4
8
16
32
64
Sampling occasions
p′
0.1
0.5
0.9
Number of sites
1
2
3
5
7
9

(a)

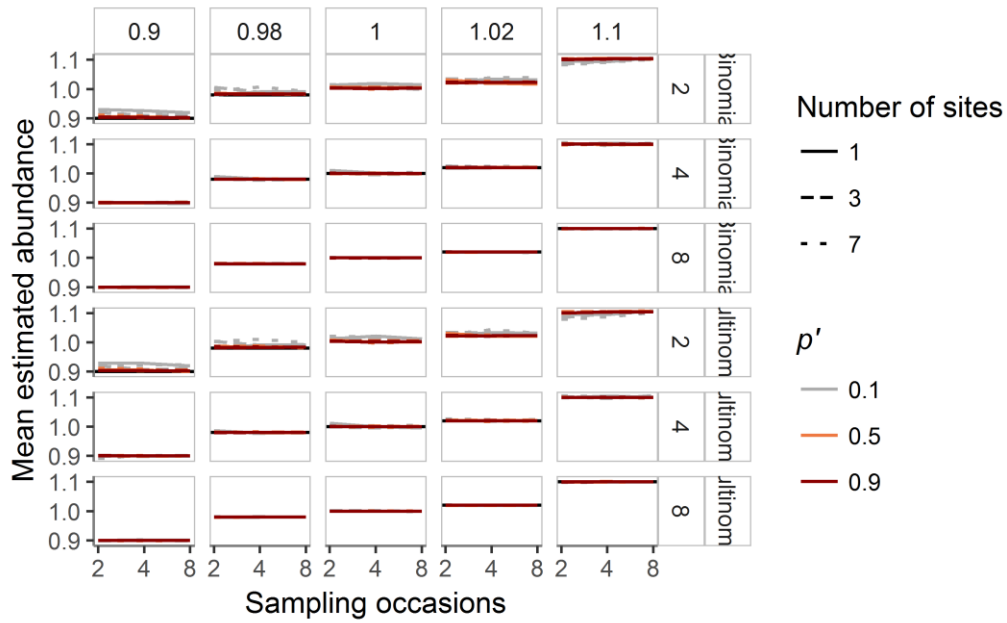

0.1
0.5
0.9
Binomial
Multinomial
Mean estimated net probability of detection, p′
0.75
0.50
0.25
0.00
2
4
8
16
32
64
Sampling occasions
p′
0.1
0.5
0.9
Number of sites
1
2
3
5
7
9

(b)

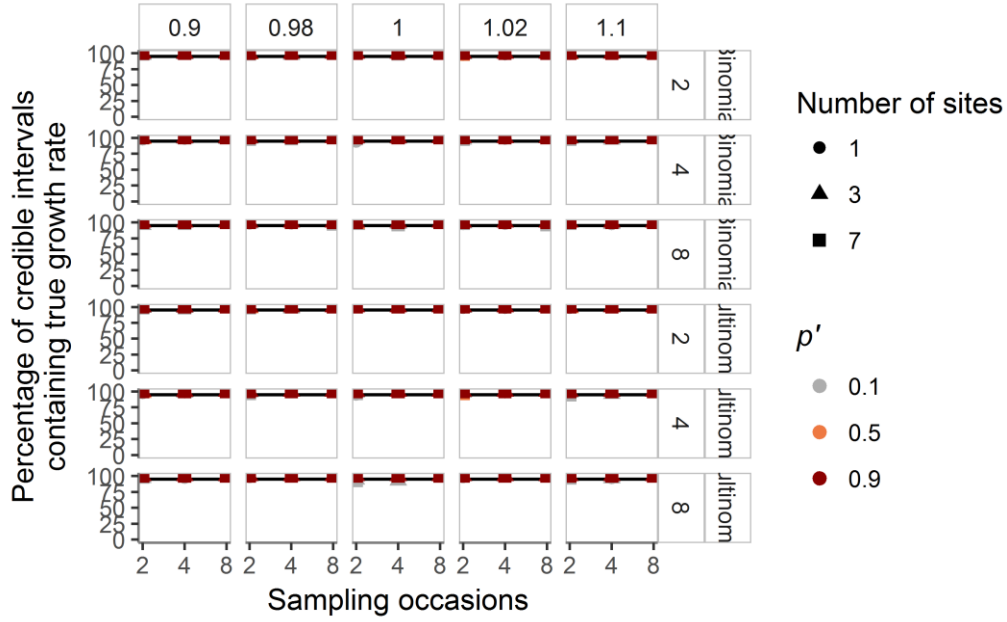


(c)

Figure 1.3. Simulations comparing estimates from the binomial and multinomial simultaneous-count model with a different numbers of sites. Mean estimates of (a) abundance, and (b) probability of detection, for combinations of number of sites (line-type), number of sampling occasions and probability of detection (colour, and vertical panel in b). (c) Percentage of 95% credible intervals for estimate of abundance that included the true value. Black horizontal lines represent the true values of (a) abundance and (b) probability of detection, and (c) 95%.



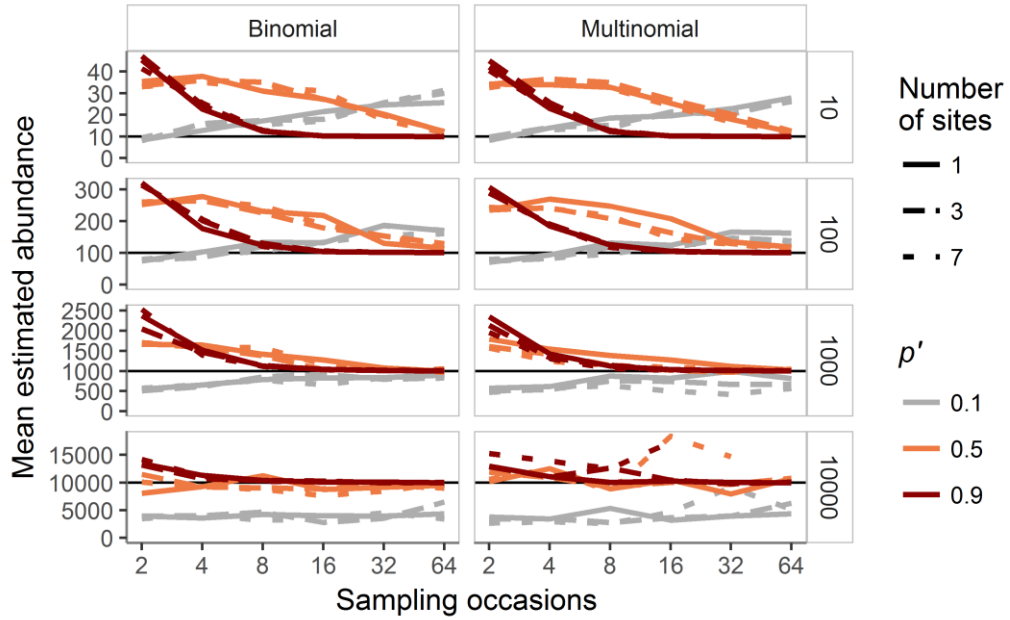
(a)



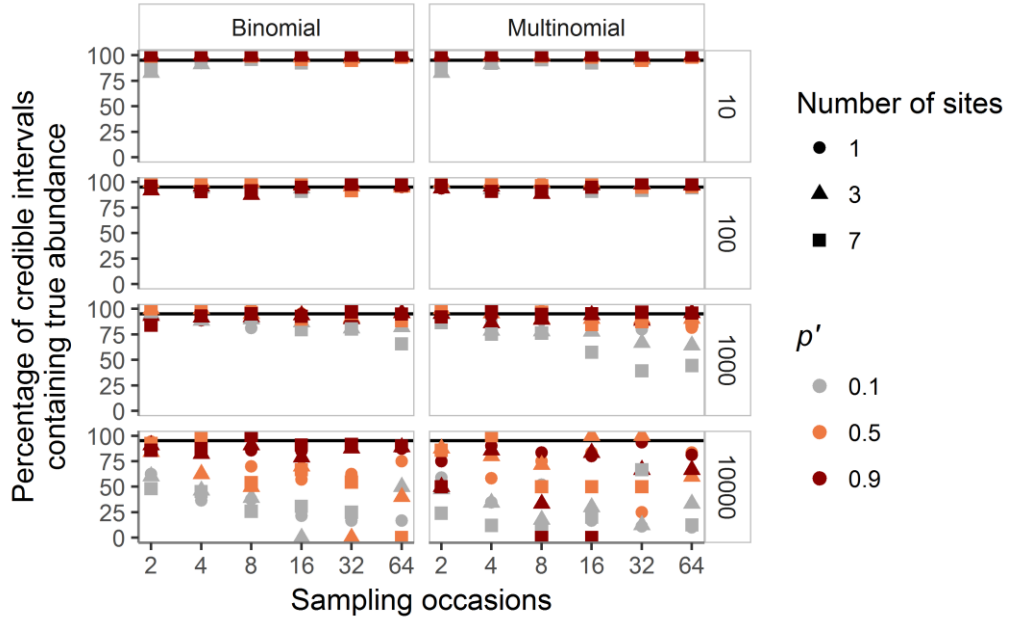
(b)

Figure 1.4. Simulations comparing estimates from the binomial and multinomial simultaneous-count model with different growth rates. (a) Mean estimates of growth for combinations of number of sampling occasions per year (x-axis), number of sites (shape), net probability of detection (colour), years (vertical panel), and growth rate (horizontal panel). (b) Percentage of 95% credible intervals for

estimate of growth rate that included the true value. Black horizontal lines represent (a) the true values of growth rate, and (b) 95%.

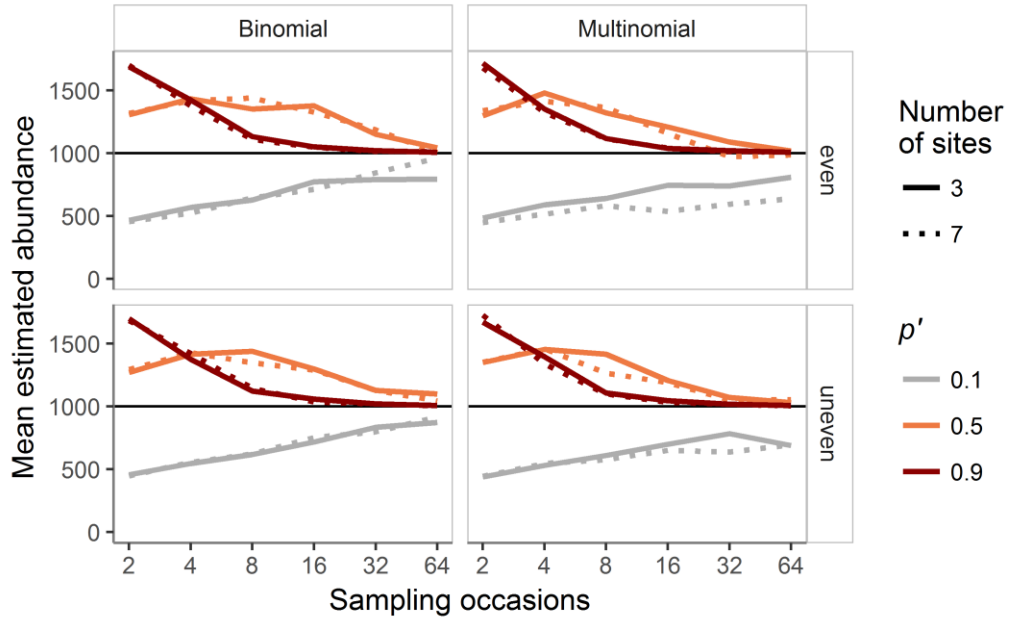


(a)

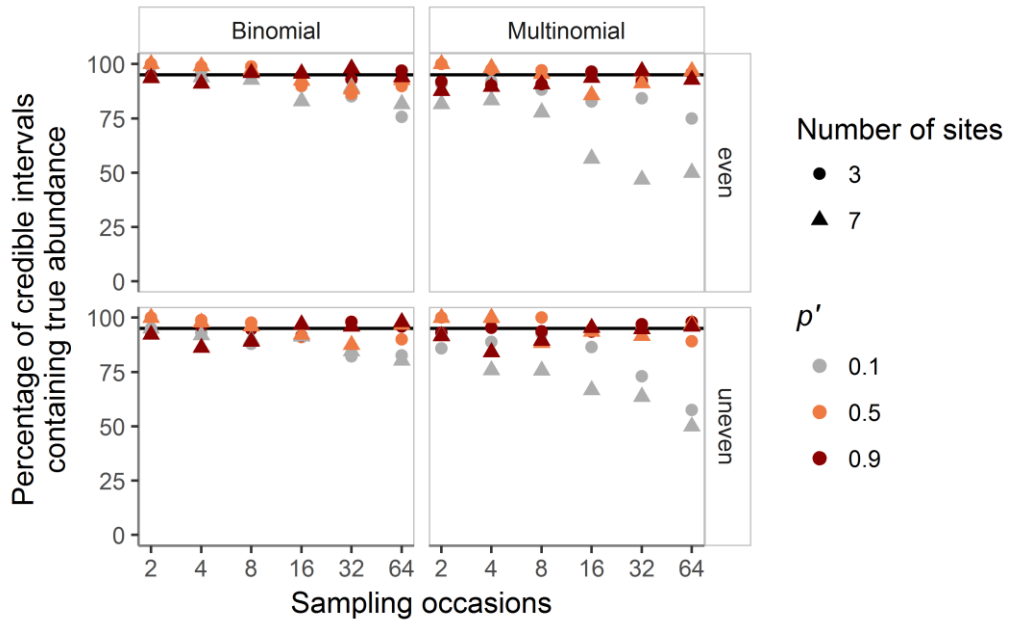


(b)

Figure 1.5. Simulations comparing estimates from the binomial and multinomial simultaneous-count model with different sized populations (horizontal panel). (a) Mean estimates of abundance, for combinations of number of sampling occasions per year, and probability of detection (colour). (b) Percentage of 95% credible intervals for estimate of growth rate that included the true value. Black horizontal lines represent (a) the true values of growth rate, and (b) 95%.



(a)



(b)

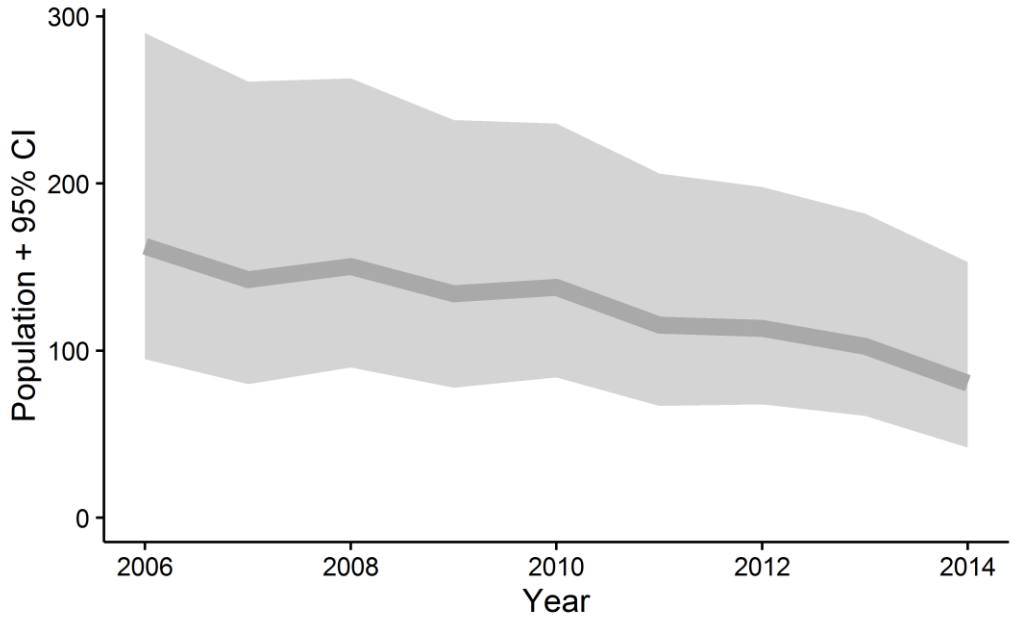
Figure 1.6. Simulations comparing estimates from the binomial and multinomial simultaneous-count mode where the number of individuals detected is spread evenly among sites, or unevenly. (a) Mean estimates of abundance, and (b) Percentage of 95% credible intervals for estimate of abundance

that contained the true value. Black horizontal lines represent (a) the true value of abundance, and (c) 95%.

Vulture population estimates

The top model for Red-headed Vulture was an exponentially changing population with constant probabilities of detection, while the top model for both Slender-billed and White-rumped Vulture was the exponential population trend and detection varying with sampling occasion (Supporting Information 4). We report here only the top supported models. For Slender-billed and White-rumped Vulture, the top models were clearly best supported, while for Red-headed Vulture, the top model with constant detection was only slightly better supported that the model where detection varied between sampling occasions. In the top model for Red-headed Vulture, the estimate of change in probability of detection, *v*, was close to one and had credible intervals bounding one, suggesting little support for variation in probability of detection.

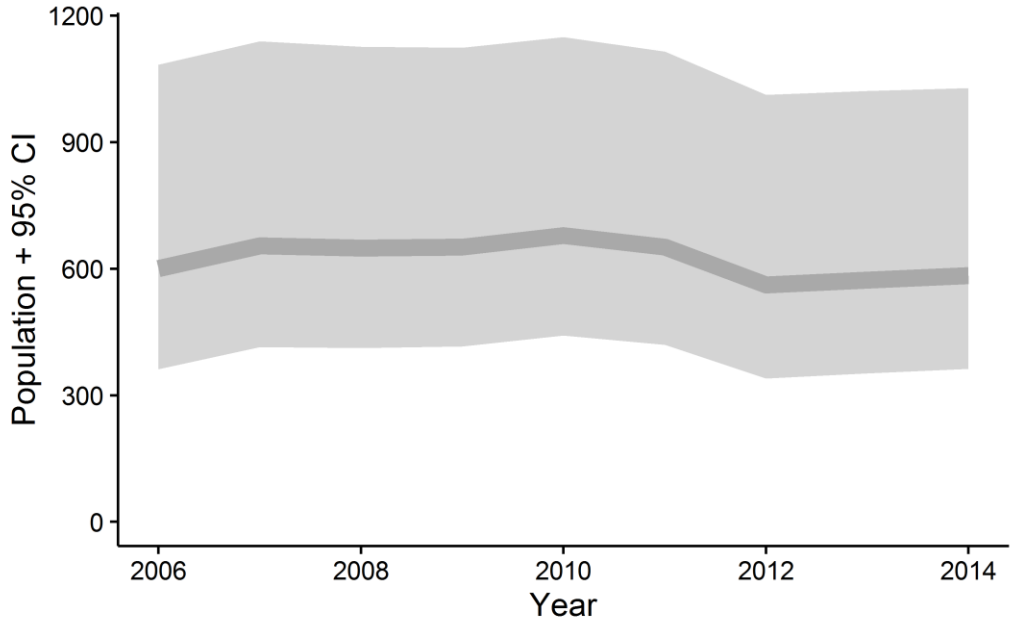
Population estimates are displayed in fig. 1.7. Red-headed Vulture were estimated to be declining, with a growth rate of 0.93 (95% credible interval 0.90–0.96), with a population of 81 (42–153) in 2014, and a net probability of detection at 0.33 (0.13–0.49). Slender-billed Vulture were estimated to be increasing, with a growth rate of 1.08 (1.05–1.12), a population of 104 (71–176) in 2014, a net probability of detection of 0.59 (0.51–0.88), and change in probability of detection *v*, of 1.22 (1.1–1.35). White-rumped Vulture were estimated close to stable over the survey period, with a growth rate of 0.99, (0.97-1), a population of 583 (363–1028) in 2014, a probability of detection of 0.26 (0.14–0.39), and *v* of 1.12 (1.04–1.15).


Population + 95% CI
300
200
100
0
2006
2008
2010
2012
2014
Year

(a)


Population + 95% CI
150
100
50
0
2006
2008
2010
2012
2014
Year

(b)



(c)

Figure 1.7. Population estimates and 95% credible intervals for Cambodian populations of (a) Red-headed Vulture, (b) Slender-billed Vulture, and (c) White-rumped Vulture, from 2006–2014

Discussion

We aimed to develop a method to estimate abundance from simultaneous count data for populations of three critically endangered vultures, which was achieved. The approach applies well to cases with few sites and large differences in counts among them that cannot be accounted for by known covariates with a standard binomial N-mixture model. Because of similarities in their likelihood functions, estimates of abundance are equivalent for the multinomial and binomial versions of the simultaneous-count models (see *Methods* and Figs. 1.2-5), however the more complex multinomial model allows us to estimate the probability an individual is detected at each site (table 1.1, fig. 1.1).

Most models perform poorly with little information, and the simulation results are in line with simulation studies for binomial N-mixture models, which suggest that with low sample sizes, low densities, and low probabilities of detection, estimates can be biased; reliable estimates require large sample sizes (Yamaura 2013; Gomez et al. 2017). Similarly, in our simulations with low probability of detection and larger numbers of sites, the estimates of the multinomial simultaneous-count model were overconfident and biased. When the probability of detection is high, reliable estimates still require many sampling occasions (Fig. 1.3), which may be challenging for many simple or short-term monitoring programmes to achieve. Importantly, both the binomial and multinomial SCMs appears to estimate growth rate very well, even with few observations, few sites, and low net probability of detection (Fig. 1.5). This ability to estimate growth rate could be very useful for monitoring programmes where knowing the trend of a population may be key, however the utility of the SCM approach over simpler generalised linear model (GLM) approaches is reduced if accurate estimates of abundance are not available. The model appears to perform more poorly with larger populations (Fig 1.5), though this may be due to the bulk of the weight of the prior occurring close to zero – which was set the same regardless of the expected population size. Broader priors may be more suitable when larger population sizes are expected and may alleviate this apparent limitation.

The model also appears to perform more poorly with larger numbers of sites particularly when the probability of detection is low. This may occur because of the limited information to estimate the per-site probability of detection is diluted increasingly with more sites, and may be compounded in the prior weight is close to zero, causing underestimation of the population. This behaviour may be worth exploring further, and may be alleviated by alternative choices of prior with les weight on smaller populations.

Monitoring programmes are often interested in abundance, but actually estimating abundance can be difficult if programmes lack the wherewithal to collect data more sophisticated than simple counts or if established robust methods cannot be applied (Banks-Leite et al. 2014). Where only an index of abundance is necessary, a GLM approach may be suitable (Banks-Leite et al. 2014; Barker et al. 2018). GLMs can perform poorly compared with binomial N-mixture models when the probability of detection is low (Yamaura 2013), and detection cannot be known *a priori*. Neither can GLMs estimate absolute abundance where that is desired. However, this is also a concern with identifiability of detection and abundance parameters in N-mixture model approaches (Barker et al. 2018), and these may apply to SCMs. However, with the simultaneous-count model approach, abundance can be estimated from counts over multiple sites based on the assumption that individuals can be detected once at most on each sampling occasion, and that all individuals may be detected on some occasion, without some of the restrictions of binomial N-mixture models (table 1.1).

The SCM approach complements existing methods in circumstances where they are hard to apply. Although the simultaneous-count model is related to the N-mixture model family, it is quite distinct from other approaches (table 1.1). Binomial N-mixture models work best with large spatial replication, and either little variation in abundance or probability of detection, or estimation of covariates that affect abundance and probability of detection (e.g. Royle 2004b; Kéry 2008; Kéry et

al. 2009). While the SCMs estimate abundance of a focal population, N-mixture models primarily estimate density of a population of unknown size. The observation process is modelled in the SCM approach differently from N-mixture models, with the former considering observation over all sites jointly, rather than at each site individually as in the latter. Although the area of the population estimated need not be known with an SCM, binomial N-mixture models assume defined, closed sites, and can produce unreliable estimates of abundance if this assumption is not met (Barker et al. 2018). So binomial N-mixture models are well suited to large-scale monitoring programmes such as national species surveys (Royle 2004a; Kéry et al. 2005, 2009), while the SCM approach would not apply well to them because the assumption of no double-counting may not be met, they may ignore useful site covariates that may improve estimates, and the multinomial model does not perform well with large numbers of sites (fig. 1.3c). Another approach using spatially-explicit methods for estimating density of unmarked individuals work best with dense sampling sites (Chandler & Royle 2013). But for small programmes, rare or highly clustered species such as discrete roost sites, sparse sampling arrays, and populations a distributed unevenly in the landscape, existing approaches may not have access to data with sufficient replication to account for observed variability. These circumstances are where the simultaneous-count model approach performs well. For instance, the high probability of detection of Mediterranean monk seals observed in two breeding caves in West Africa suggests the SCM approach may be well suited for similar studies (Martínez-Jauregui et al. 2012). In simultaneous counts of roosting bats, the SCM approach may be suitable for some species like the spectacled flying-fox, which occurs at few camps, but not others like the grey-headed flying fox, which occurs at a great many locations (Westcott et al. 2015; CSIRO 2017). Furthermore, there is a choice between the simpler binomial simultaneous-count model, or the multinomial simultaneous-count model to provide finer-grained information about detection probability at each site.

Our analyses present the first attempt to estimate the total abundance and trend of vulture populations in Cambodia, though with low probabilities of detection these examples lie at the lower

edge of the reliability of the approach using the multinomial simultaneous-count model. Existing methods to estimate abundance were unsuitable for these populations given the few sites and uneven distribution of vultures, so monitoring had relied on interpreting minimum number alive or using GLMs to estimate trends in counts over time (Loveridge et al. in press; Clements et al. 2013). These existing methods do not account for imperfect detection, and so can be misleading (Guillera-Arroita et al. 2014), but the simultaneous-count approach allows abundance to be estimated. The results suggest that the status of the species is mixed: Red-headed Vulture are declining, while White-rumped Vulture appear to be declining slightly or close to stable, and Slender-billed Vulture may be increasing up to 2014. However, we suggest caution when interpreting our estimates for White-rumped and Red-headed Vulture, given the number of sites, and estimates of net detection (six, and 0.26 and 0.33), are similar to simulations that were over-confident in their estimates of abundance (fig. 1.3c). The model assumed individuals can be detected at any site and satellite tracking suggests this is true for Slender-billed and White-rumped Vultures (Clements et al. 2013), but for Red-headed Vultures this is unknown – they are territorial and may not necessarily move over multiple sites (del Hoyo et al. 1994). Alternative specifications of the SCM such as other growth rate forms or changes in probability of detection may provide better estimates of abundance and growth rate.

A wide variety of statistical methods exist to estimate wildlife population dynamics, but for many species or circumstances, existing methods are not fit for purpose. With ongoing pressure to better manage wildlife, and international initiatives like the Aichi Targets (COP10 2010), demand better wildlife monitoring tools. Monitoring needs cost-effective robust frameworks that are repeatable, scaleable, and avoid conflicting or ambiguous interpretations (Hayward et al. 2015). Our approach fills a particular gap in estimating abundance from simultaneous counts of unmarked individuals. The simulation study presented here indicated circumstances where the models performs well (few sites and at higher probability of detection) and poorly, enabling us to consider this when planning

studies and interpreting results. SCMs may best be avoided where probability of detection is low, sampling occasions are few, where there are many sites, or where other supplementary information like markings may make other robust methods possible. Future work could account for covariation in abundance and detection, examine the implications of failures to meet assumptions such as strictly simultaneous counts or no double-counted individuals, and make use of alternative parameterizations (Lindén & Mäntyniemi 2011). The Cambodian vulture case-study demonstrates the method's use in real-world monitoring. The simultaneous-count model approach provides a useful complementary approach to other existing methods for monitoring biodiversity, and will be the best approach for estimating the abundance of discrete populations of unmarked individuals at a small number of sites (<6), where the net probability of detection is high (>0.5), and where simultaneous counts can be achieved on a higher number of sampling occasions (>8).

Supporting information:

Supporting Information 1: Step-by-step annotated R code to run simulations and plot results per this study (public web-based code repository). https://github.com/geryan/simultaneous_count_models

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Chapter Two: A comparison of analysis methods for monitoring critically endangered vultures in Cambodia

Introduction

Species monitoring is often essential to conservation, to understand species' status, evaluate the impact of interventions, and adapt management (Nichols & Williams, 2006; Possingham et al., 2012). While conducting some monitoring may be easy, useful monitoring can be difficult and expensive (Legg & Nagy, 2006), and resources spent monitoring could instead be spent on other beneficial actions (Knight, Bode, & Fuller, 2010; McDonald-Madden et al., 2010; Moore et al., 2017). A key question then is: can monitoring data be better used to provide more rigorous inference for conservation management?

Many monitoring programs aim to monitor abundance, because it is the key metric of a species' status, and is easily interpretable. However, one major challenge in estimating abundance is that not all individuals will be detected. A wide variety of methods exist to estimate the probability that an individual is detected (Sutherland, 2006). These methods use statistical models to separate the observation process from the underlying state (Royle & Dorazio, 2008), and provide a mechanism for inference and interpretation of results (Warton et al., 2015). Accounting for the probability of detection takes more expense, effort, and analytical expertise than ignoring it (Banks-Leite et al., 2014), may require extensive effort to provide adequate data to assess rare species (Thompson, 2004), and ongoing debate queries the value of some analytic approaches (R. J. Barker et al., 2018). Despite known limitations (Anderson, 2001; Guillera-Arroita et al., 2014), easily collectable data such as counts of individuals, signs, or camera-trapping rates are commonly collected (Jenelle, Runge, &

MacKenzie, 2002; Collier et al., 2007; Keane, Jones, & Milner-Gulland, 2011; Kellner & Swihart, 2014; Stephens et al., 2015).

Improved monitoring is key to the recovery of vultures (Perrig et al., 2019), which are globally in crisis (D. L. Ogada, Keesing, & Virani, 2012; D. Ogada et al., 2016; Safford et al., 2019) Old-world vultures (Accipitridae) are most often monitored by counts of unmarked individuals at artificial feeding sites or "vulture restaurants" (Margalida et al., 2011; Clements et al., 2013), at carcass dumps (V. Prakash et al., 2003), along road-based transects (Cuthbert et al., 2006; Gilbert et al., 2006; D. Ogada et al., 2016; Vibhu Prakash et al., 2019), and at known roosts and nest sites (Gilbert et al., 2007; Chaudhry et al., 2012; D. Ogada et al., 2016). Simple count methods are generally cheap and easy, so can be maintained over longer periods than more intensive methods, and may serve as an 'early-warning signal' of possible declines (R. Barker & Sauer, 1995).

Most of the count-based approaches to monitoring vultures do not account for possible biases in detection probabilities, so results may be misleading (Southwell & Low, 2009; Margalida et al., 2011). For instance, satellite tracking shows that birds present in an area will not necessarily visit a feeding site on a given day, and numbers at feeding sites and roosts in the same landscape may not appear directly comparable (Gilbert et al., 2007). While many programmes try to minimise variation in the probability of detection through standardising field methods (Chaudhry et al., 2012), results may nonetheless be biased in ways that are unknown (Anderson, 2001; Kellner & Swihart, 2014). We do not here impugn previous studies, nor the conclusions that vultures are in crisis: consistent evidence of large declines — some over 90% — have been detected in many populations of many species throughout Asia and Africa (Pain et al., 2008; D. L. Ogada, Keesing, & Virani, 2012; D. Ogada et al., 2016). However, given the focus on vulture conservation in the midst of these crises, any improvements to monitoring inferences will clarify the situation further and better guide effective conservation. Recent work has suggested genetic research on shed feathers as a promising

monitoring technique (Perrig et al., 2019), though such work is likely more expensive than count-based work, will require greater expertise, the capacity for such analyses may be missing in many vulture range countries, and would often constitute a divergent monitoring data set from those historically collected. Therefore, we focus on methods that make more effective use of count data for vulture monitoring.

Here we explore/examine the use of count data in monitoring programmes for the Cambodian populations of three critically endangered vultures: Red-headed Vulture *Sarcogyps calvus*, Slender-billed Vulture *Gyps tenuirostris*, and White-rumped Vulture *Gyps bengalensis* (BirdLife International, 2016a, 2016b, 2016c). The monitoring programme was set up to be cost-effective and technically simple (Clements et al., 2013), and is characteristic of many conservation monitoring programmes world-wide, with unknown variation in detection probability and change in sampling structure over time. Like many monitoring programmes it juggles the need to balance data that are simple and cheap to collect, analyse, and communicate with an ability to detect meaningful trends.

Our aim is to assess how analysis methods affect inferences, and to explore how small changes in monitoring can improve inference. We compare three different and increasingly complex methods for analysing population trends for these vultures in Cambodia: 1) using raw counts to estimate the minimum number alive (Krebs, 1966), 2) fitting a generalised linear model (GLM) to estimate mean count (Loveridge et al., 2019), and 3) using a simultaneous count model to estimate abundance while accounting for imperfect detection (Ryan et al., 2019). The simultaneous count model is a novel approach for estimating the abundance of a population from simultaneous counts of unmarked individuals (Ryan et al., 2019). From these three proposed monitoring methods we consider the assumptions needed to apply each method, what they allow us to infer from their results, and the consequences this has for conservation decision-making. We then make

recommendations to improve current monitoring. Our comparison of increasingly complex data analyses should apply to many small-scale monitoring programmes world-wide.

Study area

We focus on the vulture populations in Cambodia. Decades of hunting and war have led to steep declines of once large populations of wild large ungulates (Loucks et al., 2009; Gray et al., 2011; Singh et al., 2013), reducing food available for vultures (Loveridge et al., 2019), though carcasses of domestic bovids may now meet vulture food needs in the study area. North-East Cambodia is a stronghold for these species in Southeast Asia, and various conservation efforts since 2004, including monitoring, supplementary feeding, nest protection, satellite tagging, and rehabilitating and releasing poisoned birds, have focused on these populations (Clements et al., 2013; Loveridge et al., 2019). Our focal sites are at Chheap Wildlife Sanctuary (CWS), Prey Siem Pang Kang Lech Wildlife Sanctuary (PSPKLWS), Lomphat Wildlife Sanctuary (LWS), Srepok Wildlife Sanctuary (SWS), the Sesan River, and Phnom Prich Wildlife Sanctuary (PPWS). Vulture restaurants surveys (see below) were conducted at each of these sites from 2004-2019? (and are ongoing), except Phnom Prich Wildlife Sanctuary (PPWS), where they were conducted 2004-2014 (Loveridge et al., 2019). In addition to our main focal sites, simultaneous counts were also conducted on a small number of occasions at three other sites, Virachey National Park, Kulen Promtep Wildlife Sanctuary, and the Mekong flooded forest; these sites yielded few individuals (Loveridge et al., 2019) so were ignored/analysed?.

Monitoring methods

Our study design consists of six sites sampled simultaneously on two occasions each year, two weeks apart in June, for 12 years: 2004, and 2006–2016 (except PPWS which was sampled up to 2014, and the three occasional sites, sampled as above). On each occasion ‘vulture restaurants’ were

conducted, where carcasses are provided at each site and all vultures visiting are counted by at least one trained individual over 3 days.

Vulture restaurants are a common tool for the conservation and monitoring of vultures where supplementary, toxin-free food is provided for vultures (Piper, 2005; Gilbert et al., 2007; López-López, García-Ripollés, & Urios, 2014). Vultures can become habituated to regular feeding (Piper, 2005; Donázar, Cortés-Avizanda, & Carrete, 2010; Zuberogoitia et al., 2010), and our sampling programme was integrated with regular vultures restaurants carried out roughly monthly at all sites (Clements et al., 2013; Loveridge et al., 2019). Restaurants at CWS and PSPKLWS were often established more frequently than at other sites, while SWS and PPWS were often alternated between months, given their close proximity to each other (Loveridge et al., 2019). While counts at regular (asynchronous) restaurants can have a role in population monitoring (Clements et al., 2013; Loveridge et al., 2019), here we only consider the use of the synchronous counts in monitoring Cambodian vultures. More detailed descriptions of these programmes are found in Clements et al. (2013) and Loveridge and colleagues (2019).

We consider only counts of known breeding species: Slender-billed, White-rumped, and Red-headed Vulture (Loveridge et al., 2019). Telemetry of tagged Slender-billed and White-rumped Vultures has shown that individuals of these species move among sites, and suggests that our study area covers the likely range of these species in Cambodia (Clements et al., 2013). As Red-headed vultures are territorial (del Hoyo, Elliott, & Sargatal, 1994), and vultures are not recorded regularly in the surrounding areas of Cambodia, Thailand, Laos, and Vietnam, we consider that the populations of each species are likely to be geographically closed within our study area.

Data analysis approaches

We analyse these data using three increasingly complex methods of assessing the abundance and trend of Cambodian vultures. We then compare what inferences these methods allow, and what assumptions they rely upon. We then consider how this affects our ability to make decisions, and what changes we might make to current monitoring programmes to improve our ability to make good management decisions. The methods we compare are:

1. Minimum number alive (MNA)

Simultaneous sampling over all restaurants eliminates double-counting of individuals within each occasion, which enables us to calculate the ***minimum number of individuals alive*** for that occasion (Krebs, 1966), by adding up all population counts across sites?. Assuming the population is closed to migration, births, and mortality within the two-week period between the two sampling occasions each year, the highest overall count is the MNA for that year.

2. Generalised linear models (GLMs)

To estimate the mean number of individuals counted over time, we fit ***generalised linear models*** to our simultaneous counts. We fit GLMs to three subsets of our data:

1) The set of counts from the six main sites as structured in our sampling programme. This subset maintains the data structure and is fully orthogonal, but excludes the few data from infrequently sampled sites.
2) All counts aggregated by occasion (i.e., counts from all sites including the small number of irregular sites were summed on each occasion). This subset included all individuals sampled, but loses the detail of the sampling structure by excluding site level differences.
3) MNA for each year. This results in only a single data point for each year.

For our six main sites, we compared the fit of GLMs where the number of individuals counted varied as: a function of site, or year, or sampling occasion, or as a quadratic function of year, and

combinations of these including interactions between site and year or year (Table 2.1). For the aggregated by occasion and MNA data, we fit subsets of models excluding site, and site and occasion respectively (Table 2.1). We fitted GLMs with log link-functions and quasi-Poisson error terms to account for over dispersion. We compare models using small-sample corrected quasi-Akaike information criterion (QAICc), calculated using the dispersion coefficient from our quasi-Poisson models and the small-sample corrected Akaike information criterion (AICc) from the standard Poisson equivalents following Bolker (2016).

3. Simultaneous count model (SCM)

To estimate abundance and population growth rate, we fitted multinomial simultaneous count models (Ryan et al., 2019). We expected that abundance would change over time, though we were unsure of the direction of change, and fitted models where abundance was either constant, or changed following an exponential or quadratic function; with these functions allowing the population to either continually increase or decrease, or change direction throughout the study period. We were uncertain about how the probability of detection would change, and expected the probability of detection would differ by site. The simultaneous count model approach estimates the joint probability that an individual is either detected at each site or undetected, so estimates a unique probability for each site (Ryan et al., 2019). Vultures often stay near a carcass immediately after feeding and disproportionately use areas with predictable food sources (López-López, García-Ripollés, & Urios, 2014). Given the short period between sampling occasions each year, we considered that birds may remain in the vicinity of restaurants after the first occasion, so may be more likely detected on the second sampling occasion. We also considered the possibility that the probability of detection may vary among years. Therefore, we fitted models where the probability of detection was either constant, varied between occasions while constant among years, or varied among years while constant within year. We fitted all combinations of these abundance and

probability of detection models for each species (Table 2.2), and compare model fit using Deviance Information Criterion (DIC).

We had too few data to estimate unique probabilities of detection in each year in, so to model variation in probability of detection among years, we extended the approach of Ryan et al. (2019). Detection probability was varied from a baseline probability, by the same factor *v* at all sites. If the probability of detection at site *i* on occasion *t* in year *y* is $\pi_{i,t,y}$, then: if probability of detection varies by occasion within a year but is constant among years then $\pi_{i,t+1,y} = v \times \pi_{i,t,y}$; and if the probability of detection varies among years but not within years, then: $\pi_{i,t,y+1} = v \times \pi_{i,t,y}$. In both cases, the probability an individual is not detected varies by a factor of μ, such that if there are *k* sites then: $v = \frac{1-\mu\times\pi_{k+1,t,y}}{1-\pi_{k+1,t,y}}$, and $\pi_{k+1,t,y}$ is the probability an individual in the population is not detected. An assumption of the simultaneous count model is that on a given sampling occasion, every individual in the population must either be detected at one of the sites or remain undetected, such that all detection probabilities and the probability of non-detection sum to one, $\sum_1^{k+1}\pi_i = 1$ (Ryan et al., 2019). To estimate population growth rate in 2016 from the quadratic models, we estimate the first derivative of the quadratic function, i.e., the slope of the curve, in the final year. We did this only for the top models as assessed by DIC.

Our set of count data does not include every single site at each time, so is not fully orthogonal. As well as the six main sites, three other sites without regular restaurants were included in national censuses on a small number of occasions. Of these, vultures were never recorded at one site, with the other two sites mostly recording ≤2 birds of any species. We include these counts in our MNA and GLMs where counts are aggregated by sampling occasion, but exclude them from our GLMs of six-site data, and simultaneous count models. The simultaneous count model approach needs fully orthogonal data or parameters cannot be estimated. Because we had no data for 2005, we only applied simultaneous count models from 2006. As PPWS had no simultaneous counts in 2015 and

2016, in all years we aggregated PPWS with the nearby SWS where regular (non-simultaneous) restaurants were alternated between months, and many of the same birds were likely observed (Loveridge et al., 2019). Based on simulations by Ryan and colleagues (2019), we expected that this would result in less precise estimates of abundance but should not create bias. To test the effect of 'lumping' counts from PPWS and SWS together, we analysed the population up to 2014, when we had data for all sites, with either all six sites separate, or with PPWS and SWS lumped into a single 'site' for a total of five 'sites'.

We used R version 3.2.5 for all data analysis (R Core Team, 2017), and fit the simultaneous count models using JAGS 3.4 (Plummer, 2003), via R. We provide a simple vignette to conduct a simultaneous count model at: https://github.com/geryan/SimultaneousCountModel_vignette.

Results

A minimum of 42 Red-headed Vultures, 34 Slender-billed Vultures, and 90 White-rumped Vultures were alive in 2004, and 26, 37, and 109 in 2016 (Figure 2.1). The maximum MNA was 58 Red-headed Vultures in 2006, 68 Slender-billed Vultures in 2013, and 201 White-rumped Vultures in 2010.

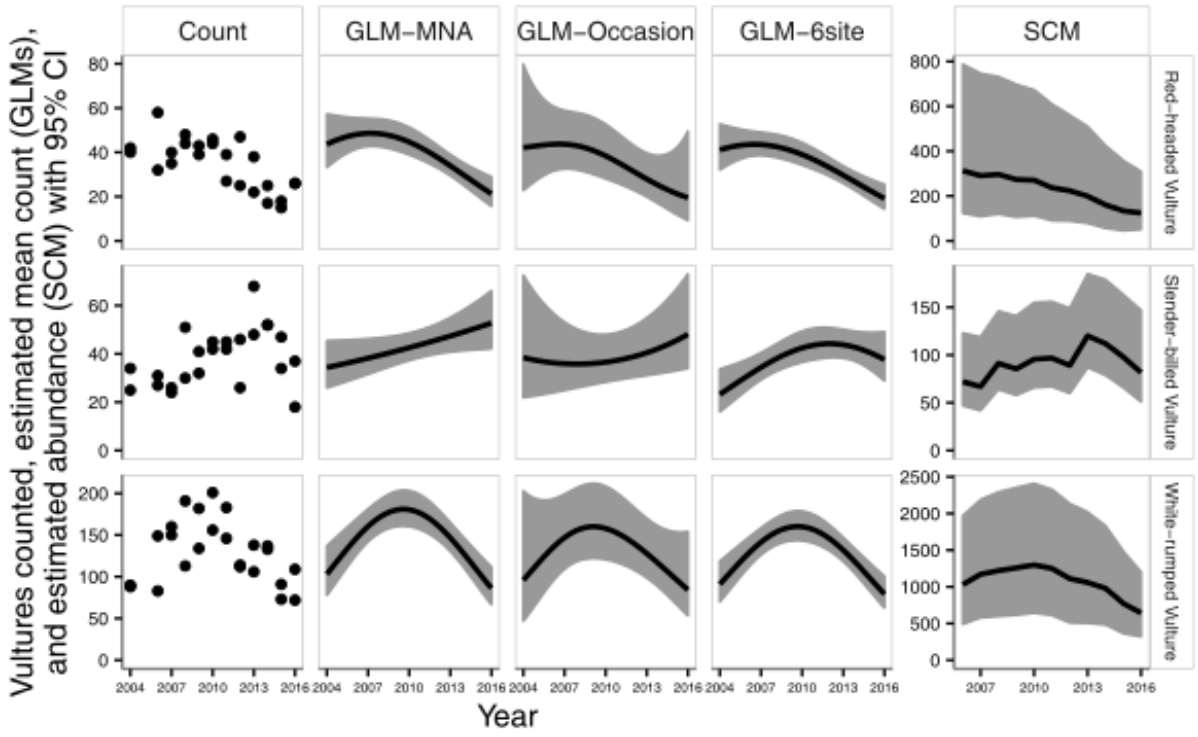

Figure 2.1. Counts of vultures (left column), generalised linear model estimates for mean count of minimum number alive in each year, all data aggregated by sampling occasion, and the six main sites (middle three columns), from 2004–2016, and estimated abundance from simultaneous count model from 2006–2016 (right column), for Red-headed Vulture, Slender-billed Vulture, and White-rumped Vulture (top, mid, and bottom rows, respectively). Grey ribbons show 95% confidence intervals for GLMs, and 95% credible interval for SCM. *NB:* y-axis scale differs between right and other columns.

Quasi-AICc results for the GLMs are presented in table 2.1. The best supported models for both Red-headed Vulture and White-rumped Vulture consistently showed a quadratic trend, with the $year^2$ model the top for MNA and aggregated by occasion, and $year^2 \times site$ the top model where six main site data set is used (Table 2.1). For Slender-billed Vulture, the best model was *year×site* for six main sites, and year for MNA, but the $year^2$ model was best when data were aggregated by occasion.

Table 2.1. Sets of generalised linear models fit to all data, data aggregated by occasion, and minimum number alive per year, with ΔQAICc values among each set.

Model	**Δ QAICc**		
	Red-headed Vulture	**Slender-billed Vulture**	**White-rumped Vulture**
Six main sites			
Constant	84.1	262	251.7
Site	24.7	24.8	46.7
Year	64.3	260.1	252.6
year^2	62.8	261.9	243.7
Occasion	86	262.2	252.8
site × year	3.9	**0**	19.9
site × year^2	**0**	6.4	**0**
site + occasion	26.7	25.1	47.7
year + occasion	66.3	260.1	253.8
year^2 + occasion	64.9	262.1	244.7
site × year + occasion	6.2	0.6	18.4
site × year^2 + occasion	2.6	7.1	1.5
All data aggregated by occasion			
Constant	20.4	3.9	23.2
Year	2.4	2	23.7
year^2	**0**	**0**	**0**
Occasion	22.8	4.3	23.6
year + occasion	5.1	2.7	24.4
year^2 + occasion	3	1	1
MNA per year			
Constant	14.4	2.2	16.5
Year	1.7	**0**	17.8
year^2	**0**	0.7	**0**

DIC results for simultaneous count model fits are shown in table 2.2, with parameter estimates in table 2.3, and abundance estimates and 95% credible intervals in figure 2. The best models for all species modelled abundance as a quadratic function of year (table 2.2). The probability of detection for Red-headed Vulture was modelled as constant, but for Slender-billed Vulture and White-rumped Vulture, modelled as varied by sampling occasion within year – the second occasion estimated as higher (table 2.3). Abundance of Red-headed and White-rumped Vulture were estimated as smaller in 2016 that 2006, while Slender-billed Vulture were estimated more abundant in 2016, though the 95% credible intervals (CI) for all species overlapped between these years (table 2.3). The estimated rate of change in abundance found all populations were declining in 2016, at a rate of −28 Red-headed Vultures per year (95% CI: −8 to −75), −20 Slender-billed Vultures per year (95% CI: −5 to −49), and −172 White-rumped Vultures per year (95% (CI: −93 to −295). The key conclusions from each of the analysis methods, the key assumptions they make, and other considerations, are displayed in table 2.4.

Table 2.2. Set of simultaneous count models, with ΔDIC values, for Red-headed Vulture, Slender-billed Vulture, and White-rumped Vulture.

Model		**Δ DIC**		
Abundance	**Probability of detection**	**Red-headed Vulture**	**Slender-billed Vulture**	**White-rumped Vulture**
Constant	Constant	70.2	42.5	121.9
Constant	Occasion	74.2	38.7	116.4
Constant	Year	7	6.2	2.6
Exponential	Constant	4.5	23.4	70.1
Exponential	Occasion	6.4	11.2	56.0
Exponential	Year	5.1	2.8	1.5
Quadratic	Constant	**0**	10	8.5
Quadratic	Occasion	2.2	**0**	**0**
Quadratic	Year	3.8	1.6	2.5

Table 2.3. Parameter estimates for best fit simultaneous count model, with 95% credible intervals in parentheses, for Red-headed Vulture, Slender-billed Vulture, and White-rumped Vulture.

	Red-headed Vulture	**Slender-billed Vulture**	**White-rumped Vulture**
Abundance (*N*)			
2006	303 (194–913)	94 (50–196)	1031 (491–1969
2016	121 (74–343)	112 (79–253)	641 (472–1200)
Probability of detection in first sampling occasion in first year ($\pi_{i,2006,1}$)			
LWS	0.040	0.043	0.013
SWS–PPWS	0.033	0.015	0.013
CWS	0.057	0.034	0.038
SES	0.038	0.044	0.032
SPKL	0.026	0.16	0.047
Net probability of detection in first occasion in first year ($p' = \sum_1^k \pi_i$)			
	0.19	0.29	0.13
Probability not detected on first sampling occasion in first year (π_{k+1})			
	0.81 (0.62–0.95)	0.71 (0.51–0.88)	0.87 (0.76–0.93)
Quadratic function			
Quadratic term	-0.91 (-3.4–0.68)	-2.2 (-5.5– -0.82)	-15 (-31– -6.5)
Linear term	-8.2 (-44–12)	31 (12–73)	143 (-456–271)
Constant	313 (113–939)	58 (31–139)	928 (452–1752)
Rate of change in abundance (derivative) in 2016	-28 (-73– -7.7)	-20 (-49– -5.1)	-172 (-294– -93)
Change in detection rate (*v*)			
2nd within-year sampling occasion	–	1.20	1.13

Table 2.4. Comparison of conclusions from different methods, confidence in those conclusions, and the assumptions made in drawing those conclusions. Best outcome is bolded, i.e. strongest inference, simplest method, or easiest assumption.

		Minimum number alive	**GLM**	**Simultaneous count model**
Result		Minimum number known alive at given time	Mean count and rate of change of mean count	**Population size and growth rate, with uncertainty**
Conclusion about abundance	Red-headed Vulture	At least 26 in 2016	*Unable to conclude beyond MNA*	**121 (95% CI 74–343) in 2016**
	Slender-billed Vulture	At least 39 in 2016	*Unable to conclude beyond MNA*	**112 (95% CI 79–253) in 2016**
	White-rumped Vulture	At least 109 in 2016	*Unable to conclude beyond MNA*	**641 (95% CI 472–1200) in 2016**
Conclusion about trend in abundance in 2016	Red-headed Vulture	*Unable to conclude*	Possibly declining	**Declining**
	Slender-billed Vulture	*Unable to conclude*	Possibly declining	**Declining**
	White-rumped Vulture	*Unable to conclude*	Possibly declining	**Declining**
Confidence in conclusions		High for minimum abundance, low for absolute abundance	Low	**High for trend, moderate for abundance**
Data needed		Simultaneous counts	**Counts**	Simultaneous counts
Can include occasional sites		**Yes**	**Yes**	No
Predict and infer status?		No	No	**Yes**
Assumptions supporting conclusions		**No double-counting individuals within sampling occasion.**	Probability of detection is constant.	No double-counting, population closure within year.

The comparison of the five and six site approaches, where SWS and PPWS were combined or separated over the years where both sites were surveyed 2006–2014, largely concurred with the

initial modelling. The top models for Red-headed Vulture in 2006–14 in 5 and 5 sites modelled abundance following a quadratic function, and with a constant probability of detection. For Slender-billed Vulture, the top models for both five and six site approaches were the exponential model with probability of detection changing with sampling occasion within year. For White-rumped Vulture, the top model fit abundance following a quadratic function, and probability of detection changing with sampling occasion within year. Figure 2 shows abundance estimates from the five and six site approaches for the top models estimated from the full data set.

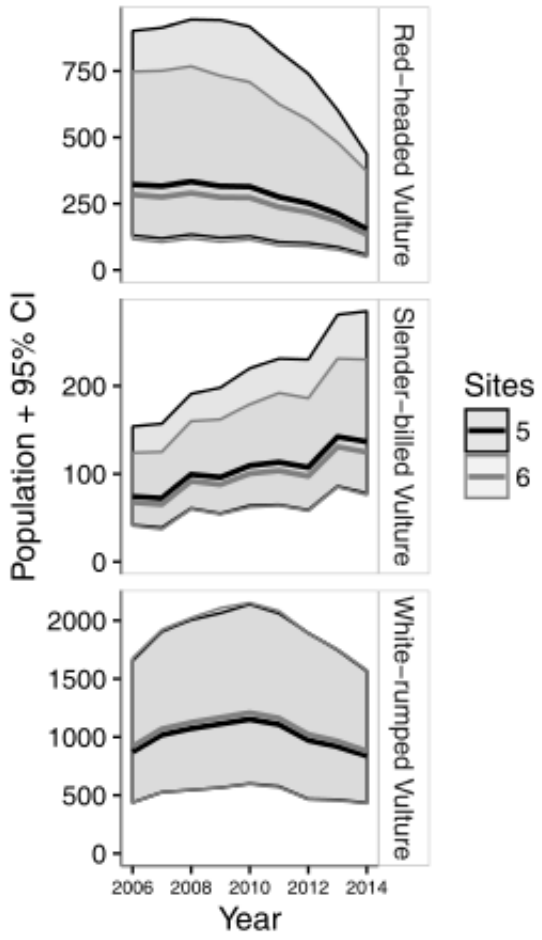

Figure 2.2. Abundance estimates for the three species from the top simultaneous count models for 2006–14, where either SWS and PPWS are combined into a single site for a total of five sites, or are SWS and PPWS remain separate for a total of six sites.

Discussion

We found that small changes to our analyses can greatly enhance the conclusions that we can draw, and we document evidence that Cambodian vulture populations are small and declining. The best estimates from the simultaneous count model are a total population size of 121 Red-headed Vulture in 2016, declining at 28 individuals per year, 112 Slender-billed Vulture declining at a rate of 20 individuals per year, and 641 White-rumped Vulture declining at a rate of 172 individuals per year. These trends should be considered in context with the overall trajectories (Fig 2.1), but if these trends continue, the vulture species that breed in Cambodia will be extirpated within the next decade. So while it was previously difficult to draw firm conclusions from counts as to the absolute state of the population (Clements et al., 2013; Loveridge et al., 2019), here we can conclude that in 2016, all populations were small and rapidly declining.

Our ability to draw firm conclusions is neither trivial, nor purely of academic interest: it can and should affect the management actions taken for species, the funding available, and the priorities given (Ferraro & Pattanayak, 2006; Nichols & Williams, 2006; Lindenmayer, Piggott, & Wintle, 2013). For example, each of the vulture species is listed on the IUCN Red List of Threatened Species as Critically Endangered under Criterion A (reduction on population size, within three generations; IUCN, 2001; BirdLife International, 2016a, 2016c, 2016b). If scientists are unable to establish the trajectory of the population relative to population size, this criterion would cease to apply. Here we establish current, ongoing declines of high magnitude for the all three populations, suggesting they remain Critically Endangered under Criterion A. Although the species were initially classified in part through declines observed through simple counts and GLMs (e.g., V. Prakash et al., 2003; Cuthbert et al., 2006), the magnitude and proportion of the change was so large as to demonstrate unequivocal declines (>90% over three generations). In a small highly dispersed population such as Cambodian vultures, changes may be harder to detect, and in such cases model-based approaches such as the SCM can help.

Although the general conclusion that each species is declining does not differ greatly between analytical methods we applied, the strength of the conclusions do. With MNA, we can only conclude that the population is larger than some number. The GLMs model the mean count, so we can assess the trend in individuals counted, but this approach only corresponds to actual abundance if the probabilities of detection are constant or accounted for by known covariates. By modelling detection with the simultaneous count model we are able to evaluate this assumption and relax it if necessary. We find evidence that the probability of detection varies temporally for Slender-billed Vulture and White-rumped Vulture (table 2.3). This result is expected for these wider-ranging species, compared with the more territorial Red-headed Vulture. In addition, modelling the detection process allows us to account for uncertainty and make assessment of the quantities we are really interested in: abundance of the population, and its trajectory over time.

The strength of inferences from monitoring often involves trade-offs among the simplicity of field methods, the complexity of analyses, and the strength of the assumptions involved. Here the SCM does involve more sophisticated modelling than the GLMs. Efforts to bridge technical modelling work to easily implemented analyses are key to improving monitoring works (e.g., Borchers, 2012; Kéry & Royle, 2016). To that end we provide a simple vignette demonstrating the application of the method, which can be reproduced by researchers (see Methods). The SCM does not however require an assumption of constant detection needed for the GLM to index abundance, which is unlikely to be true (Kellner & Swihart, 2014). We do assume though, that on a given occasion sampling is simultaneous (or that individuals are counted at most once), which are also assumptions of the MNA, and that the population is geographically closed. We believe we have met these assumptions here. While a GLM can be fit to count data that is not simultaneous as an index of abundance (Clements et al., 2013; Loveridge et al., 2019), relating this to abundance requires either the strong assumption that the probability of detection is constant, or that probability of detection

varies randomly and that there are sufficient data to overcome such noise. Yet there is much evidence to suggest it is more appropriate to assume *a priori* that the probability of detection will be less than one, and will vary (Collier et al., 2007; Southwell & Low, 2009; Kellner & Swihart, 2014). Accounting for the probability of detection requires more sophisticated analyses than ignoring it, and cases are made for sometimes ignoring detection processes (e.g., Johnson, 2008; Banks-Leite et al., 2014). Here the SCM estimates abundance with uncertainty while accounting for imperfect detection, without changes to sampling design or additional assumptions.

Although the SCM approach allows significantly improved inferences, there were limitations in this case. The model needs orthogonal data, which were not available, necessitating combining PPWS and SWS into a single site for analyses. This seems to work well (fig. 2). Where we have data in both sites for all years to 2014, comparison of lumping and separating them shows similar estimates of trend and abundance, though with slightly smaller credible intervals when separate. That the use of more information reduces uncertainty is expected from theory, and from simulation trials (Ryan et al., 2019). We were also not able to include the small numbers of individuals at the infrequently included sites, however these individuals will be accounted for in the 'undetected' portion of the estimated population. The SCM can also poorly estimate true abundance if the probability of detection is low (Ryan et al., 2019). Simulations found that with net probability of detection (the sum of the detection probabilities over all sites) of 0.1 or 0.25, and number of sites and sampling occasions similar to this study, the model tended to underestimate true abundance (Ryan et al., 2019), although estimates of population change were reliable. Here our estimates of net probability of detection are 0.19, 0.29, and 0.13 for Red-headed, Slender-billed, and White-rumped Vulture respectively (table 2.3), suggesting that we accept these estimates of abundance with caution. We were also in this case only able to account for probability of detection that varied evenly among sites over sites, rather than independently. Model selection also generates a degree of uncertainty in our findings. Although here we have focussed on the top SCM and GLM via DIC and QAICc, several

models rank close to these top models and may potentially alter the conclusions of the study. Here, as our focus is on the difference between methods, we have chosen not to focus on model selection issues, further exploration of approaches to model selection may be useful either through statistical methods or by comparing the effect of alternative models on the conclusions or resulting conservation actions.

Some small changes to the sampling design could further improve the inference from this monitoring. Increased sampling increases confidence in estimates and power to detect changes in the population (Legg & Nagy, 2006; Guillera-Arroita & Lahoz-Monfort, 2012). Simulation studies on a similar time frame to this study and low net probability of detection suggest that increasing from two to four sampling occasions per year can reduce bias by up to half (Ryan et al., 2019; Ryan unpublished data). For Slender-billed and White-rumped Vulture, the probability of detection is higher for the second sampling occasion within a given year (table 2.3 & 4), so additional sampling within the same closed period may further increase the probability of detection for these species. Recently, two additional simultaneous counts have been carried out in September and March (Loveridge et al., 2019). These occasions are too far apart to be considered a closed period, but shifting all of these counts into one or two closed periods with multiple samples, e.g. all in July, would increase sampling effort to reduce bias and increase the probability of detection for Slender-billed and White-rumped Vulture. If detection continues to increase with repeated samples, estimates of abundance could become much more reliable. Additional sampling occasions within each closed period would also allow modelling unequal variation in probability of detection among sites, which we are not able to achieve in this study. If resources permit, even more additional sampling occasions per year should improve estimates further. While one may be generally more confident in one's results the more data one has, with the SCM additional data tangibly increase precision in the estimates of abundance, while this is not the case for GLMs or MNA.

Our general conclusion that the populations are small and declining is reached through all our analysis approaches. The simple MNA and GLM analyses can provide some information on the population status that is easily conducted, and we have information here to support that the assumption of constant probability of detection among years. The more complex simultaneous count model provides a framework to estimate the quantities that we are actually interested in – abundance and population growth rate – and uncertainties in these, but at the cost of substantially more analytical expertise. Specific to this study, clustering of simultaneous sampling effort to a single closed period per year with four or more occasions should significantly improve the precision and accuracy of estimates without additional field effort. More generally, focussed strategic sampling, and careful changes to analyses can improve inference in many wildlife monitoring programmes; not a new message, but one worth reiterating given the importance of quality monitoring for conservation.

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Chapter Three: A general method for assessing the risks and benefits of secrecy in conserving 'Lazarus species'

This chapter is the basis for the following publications:

Ryan, G.E. and Baker, C.M., 2016. A general method for assessing the risks and benefits of secrecy in conserving 'Lazarus species'. *Biological Conservation*, *100*(203), pp.186-187.

Ryan, G.E. and Baker, C.M., 2019. Corrigendum to "A general method for assessing the risks and benefits of secrecy in conserving 'Lazarus species' [Biol. Cons. 203, 186–187]. *Biological Conservation*, *230*, p.47.

Deciding whether to publicize the discovery of rare, or presumed-extinct species can be challenging. Publicity can have positive impacts, such as increased funding, and negative effects, like increased poaching. In their article "Secrecy considerations for conserving Lazarus species", Meijaard and Nijman (2014) frame this trade-off. While it is a welcome advance, they only discuss three possible decision scenarios from a continuum of problems. They present an unclear interpretation of risk, cost, and benefit, and do not provide solutions for dealing with the trade-off. Here we clarify these concepts using decision-theory and develop simple equations to provide a solution for the problem of whether to publicize the discovery of "Lazarus species".

A common definition of risk in conservation is "the chance, within a time frame, of an adverse event with specific consequences" (Burgman, 2005, p.1). Meijaard and Nijman (2014), however, present a muddled description of risk; defining "risk" as "the probability of something bad happening" (p. 23). They define "cost" as the product of "risk" and the non-specific "impact that would have on the species" (p. 23). It is unclear from usage of 'costs' throughout whether these are monetary costs, and if they are potential or incurred. They do not define benefit. These definitions make interpretation of their figure 1 arduous. The limited scenarios explored imply that 'benefits' are fixed, and that changes in risk depend only on intentional publicity. Neither is always true.

If one considers risk to be the probability of extinction of the target population in a given time frame, one can decide whether to publicize or not by calculating which decision will minimize risk. To do this, both benefits and costs must be considered in comparable terms. The natural measure for benefits is the potential funding increase. Hence, the cost must be defined in monetary terms too,

for example to defray poaching to deal with increased law enforcement. This approach provides an explicit decision problem to solve.

Consider a Lazarus species with location known only to us. Our objective is to minimise its probability of extinction in the next 100 years, and our decisions is whether to announce the finding, $(\delta = 1)$ or not $(\delta = 0)$. The parameter p_0 is the species' current probability of extinction within 100 years and p_p is the probability that poachers will discover the location, even if it is not announced. Finally, d represents the expected damages from poaching and B is the benefit from publicity. We use the logistic equation $f(x) = \frac{1}{1+e^{-x}}$ to model how these quantities affect the species' probability of extinction, p:

$$p = f\left(\log\left(\frac{p_0}{1-p_0}\right) + d\big(p_p + \big(1-p_p\big)\delta\big) - B\delta\right) \qquad \textbf{(1)}$$

We seek to minimise Eq. (1), and as δ can only be 0 or 1, the decision to announce is preferable if

$$B > d\big(1-p_p\big). \qquad \textbf{(2)}$$

Announcing the finding will be preferable if the benefits are greater than the poaching damages multiplied by the probability that poachers would not discover the location independently.

Meijaard and Nijman (2014) discuss the discovery of an unknown population of the Endangered Sumatran rhinoceros (*Dicerorhinus sumatrensis*). Using our method, there are several scenarios to consider: managers can keep silent, subject to no additional investment (*B = 0*) and a small probability of discovery (low p_p). Managers could tell trusted agencies and donors, accepting a larger chance of discovery (higher p_p) for larger investment, or managers could tell everyone, increasing the chance of discovery and perhaps increasing investment further. Our equation provides one way to solve the decision problem introduced by Meijaard and Nijman (2014). Deciding what to do in high-profile situations would still be contentious because of parameter uncertainty and because the decision cannot be reversed. Although that decision may change depending on uncertain parameters, quantitative methods in decision theory can deal with this (Canessa et al. 2015).

We have presented one specific formulation of Meijaard and Nijman's (2014) problem, and one interpretation of risk; alternatives exist in this and other contexts. For instance Meijaard and Nijman (2014) introduce the problem as temporal, and a dynamic model where benefits, costs and risks could accrue or change though time would be more realistic. However, this introduces many more parameters, so may not be practical. We believe our simple model — with only three key parameters — is a practical approach that should work in many cases.

Acknowledgements:

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Chapter Four: The costs and benefits of publicising species discoveries.

Introduction

New species continue to be found, hundreds of species considered extinct have been rediscovered, and yet more populations are discovered in areas from where they were extirpated or previously unknown (Keith & Burgman 2004; Scheffers et al. 2011; Meijaard & Nijman 2014). These discoveries are sources of public interest and rare environmental good news (Smith et al. 2010; Watson & Davis 2017), and provide data invaluable for managing biodiversity (Tulloch et al. 2018). Environmental news has long been dominated by sensational negativity (Lowe & Morrison 1984), and conservation science traditionally focussed on crises (Soulé 1985). Yet positive messaging and the promotion of hope are necessary to solve complex environmental problems (Beever 2000; Chawla & Cushing 2007; Garnett & Lindenmayer 2011). Species discoveries are a key part of environmental good news (Smith et al. 2010), and publicity can be expected to bring support through funding or protection for such species (Scheffers et al. 2011; Veríssimo et al. 2017). The drive to rediscover species can also bring funds, research, and support to protect poorly known species (Butchart et al. 2005; Watson & Davis 2017). There is also an impetus to make biodiversity data open and accessible, to allow for more powerful ecological inferences, reproducibility of results, better use of existing information (Reichman et al. 2011; Costello et al. 2013; Hampton et al. 2013), and to make better decisions for managing biodiversity (Tulloch et al. 2018). Clearly publicising discoveries of new species and populations can be beneficial.

However, publicising discoveries can be detrimental too (Meijaard & Nijman 2014; Ryan & Baker 2016; Lindenmayer & Scheele 2017). Species can be harmed by disturbance (Kelly et al. 2003), exposed to disease (NSW Department of Environment and Conservation 2006), and risk poaching if their location is known (Webb et al. 2002; Lindenmayer & Scheele 2017), even if their published location is vague (Meijaard & Nijman 2014). Species are often more valuable when rare (Angulo et al. 2009), and so newly discovered or rediscovered species may be at particular risk of exploitation if their existence or location is public (Stuart 2006). As data become more accessible, rapid growth in internet access and social media use increases the spread and sourcing of information about

biodiversity, so understanding the nature of this trade-off in costs and benefits is increasingly important.

Recently there has been heated scientific debate about whether to release information about species' locations when new species or populations are found (Meijaard & Nijman 2014; Lindenmayer & Scheele 2017). Illustrating the problem in several recent discoveries, researchers and managers have chosen to withhold locations from the public domain, such as the finding of the night parrot in Australia (Worthington 2013), or the silver-backed chevrotain in Vietnam (Nguyen et al. 2019). Such decisions to withhold information rely on mangers' knowledge and intuition; decision support tools could help explore the trade-offs in the range of decisions available to managers, to account for uncertainty, and to consider risk attitudes.

There are some methods to assist decision-making around publicising species' locations, but none of these fulfil all desirable criteria (Ryan & Baker 2016, 2019; Tulloch et al. 2018). Meijaard and Nijman (2014) present a graphical model of relative costs and benefits, and suggest that publicity should only occur if the subsequent benefits to the species will increase relative to the subsequent costs. This is a simple heuristic, but it provides a discrete solution to a continuum of options. Alternatively, Tulloch and colleagues (Tulloch et al. 2018) provide a decision-tree approach to publishing biodiversity data in general, dependent on relevant threats. This approach is a useful guide for decision-making, but it doesn't explicitly allow managers to explore trade-offs, adapt to their own attitude to risk, or consider the probabilities of different outcomes, but instead relies on discrete alternatives. Ryan and Baker (2016, 2019) constructed a general theoretical framework to balance the costs and benefits when deciding to publicise the discovery of species, and can incorporate uncertainty. Their approach also considers the probability of adverse outcomes whether the information is made public or not. Although Ryan and Baker's method can compare a suite of options, it is designed to be calculated as a binary choice between disclosing information in one scenario or not, rather than as a comparison of a suite of options. No studies that attempt to provide guidance for decisions about publicising discoveries thoroughly explore how such decisions are made. Further, none have been tested in a real-world context and compared with the decisions made based on perceived costs and benefits.

In this study we examine the costs and benefits identified in such decisions and use decision theory to assess them. First we generalise Ryan and Baker's (2016, 2019) method to trade-off costs and benefits, and examine with four simulated species the state space of decisions, costs and benefits. We then examine how real-world examples fit into this state space, by asking decision-makers to estimate the costs and benefits of disclosing information about real species discoveries and rediscoveries. We apply our method to these case studies whilst accounting for uncertainty and consider the suite of types of potential benefits and costs that decision-makers identify. This is the first such study to analyse this emergent problem in species conservation, and the methods provided can be used directly to inform future decisions about publicising species discoveries.

Methods

An updated decision analysis for assessing publicity decisions

Various options confront decision makers, from publishing all information, to publishing none, and gradations in-between. This decision is made considering the potential costs and benefits of the decision against some objective. A typical objective might be minimising the species' probability of extinction in some time-frame (Ryan & Baker 2016; Tulloch et al. 2018). If the decision causes some change in the resourcing available for conservation of the species, such as increased funding or increased costs, the species probability of extinction, PE, may change from some baseline PE_0, may to some PE_d (figure 4.1). Here we propose a method to make the decision to publicise a species discovery whilst minimising the probability of extinction based on the methods of Ryan and Baker (2016, 2019).

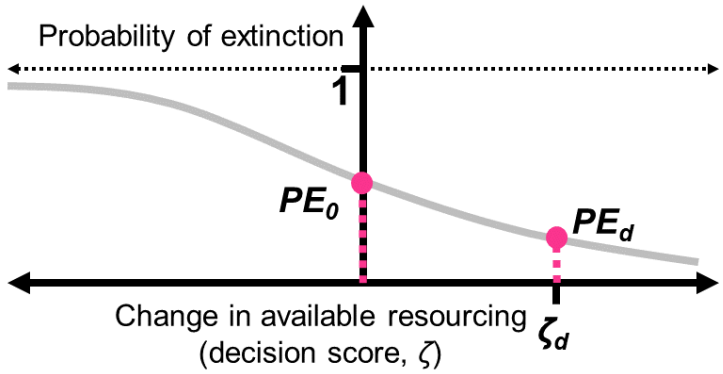

Figure 4.1. Grey line shows one possible relationship between probability of extinction (y-axis) and change in available resources or decision score (x-axis), with pink points showing baseline probability of extinction, and an example probability of extinction resulting from some decision *d*.

If one considers a decision *d*, there will be some expected benefit of that decision B_d, and some expected cost of the decision C_d. If the information were entirely public, the expected cost is C_p. Regardless of the decision, there is some probability p_d, that the information may become public anyway (such as a leak or accidental discovery), and that the public scenario may be realized. If the decision is to publicise all information, then p_d equals one. Using these values we can calculate a decision score ζ_d, that represents the change in expected available resources (i.e., net benefit) towards conserving the species such that:

$$\zeta_d = B_d - C_d - p_d(C_p - C_d) \quad \text{Eq 1.}$$

This calculates the expected net benefits while accounting for the probability that information may become inadvertently public. If the relationship between the probability of extinction and the change in available resourcing resulting from the decision is monotonically decreasing with a range between 0 and 1 (e.g. figure 4.1), then the decision that maximises decision score ζ_d is the one that minimises the species probability of extinction, so meets the objective. The derivation of equation 1 is explained in detail in supporting information 1.

Simulated species

To explore the behaviour of this method and check that results are useful, we simulate four decision scenarios:

1. a species with high value on illegal markets and high risk of poaching,
2. a species with high potential tourism value, and therefore potential for disturbance due to visitation,
3. a species where its major value is intrinsic, rather than direct monetary values, and
4. an exotic and possibly invasive species at risk of spread by the general public.

For each species we consider a set of five decision choices where both the amount of information publicly disclosed, and the group of people who are informed of the species exact location varies (table 4.s1, Supporting information 1). These choices were:

- Public disclosure of the exact location of the species,
- Partial public disclosure of the location, e.g. the species' name and protected area, and inform government and local community groups of the exact location,
- Partial public disclosure of the location, e.g. the species' name and protected area, and inform government of the exact location,
- Secret, don't publicly disclose any information, but inform government and local community groups of the exact location, or,
- Secret, don't publicly disclose any information, but inform government of the exact location.

These possible decisions represent a gradient of levels of control, formality, and number of people with knowledge. The expected cost of management associated with the decision was varied with the level of public disclosure, the expected benefits were varied with the groups informed, and probability of the exact location becoming public was varied with both level of disclosure and group involved. (Values table 4.s1 in Supporting Information 1). We applied equation 3 to these scenarios to estimate decision scores.

We broadly expect that: the best decision for the species at risk of poaching and the invasive species would tend toward secrecy because of the high costs of publicity; partial publicity would not be beneficial for the tourism species because of the high management costs, greater risk of publicity than secrecy, and high benefits of publicity; and publicity would be the best result for the species with primarily intrinsic values.

Case studies

To obtain information on the costs and benefits of real decisions about whether to publicise information about species locations, we identified recent cases studies. Each case study species had either been newly discovered, rediscovered after considered extinct, or a new population was discovered in an area where it was not known to occur, and some or all information about this discovery was withheld from the public. For each species, we identified a key informant with knowledge of the decision to withhold all information. Informants were asked to complete a structured, written questionnaire about the decision.

Regardless of the actual decision made, informants were asked to provide estimates for three decision scenarios: if the discovery was made public, partially public, or not public (secret). We defined public as "releasing the species identity and a location that could reasonably expect the species to be found", partially public as "by releasing the species identity, but vague or no information about its location", and not public such that "they may inform other management agencies, scientists, or donors, in such a way that the information is not intentionally publicly released". We asked informants to provide numeric estimates of the costs and benefits associated with the case study. We used a four-point elicitation method to obtain estimates of benefits and costs, where informants were asked to provide the lowest and highest possible expected values, a most likely value, and the percentage degree of confidence that the true value lay between within this range of values (Speirs-Bridge et al. 2010; McBride et al. 2012). Informants were also asked for a single best estimate of the probability of information becoming unintentionally public. Informants were instructed to consider all kinds of benefits and costs, and make an estimate of their equivalent monetary value, in the currency of their choice.

We asked informants to name the types of benefits and costs they expected to accrue for this case study, what kinds of entities were expected to accrue these benefits, and the source of such benefits. We then asked informants to name the types of benefits and costs associated with species discoveries in general, and to specifically consider if there were any additional costs or benefits to the species, the individuals, and the organisations involved in the discovery. Lastly informants were given the opportunity to add any comments they wished.

To protect the privacy of informants and information about discoveries that are not public, we only name species and the continent on which they occur if such information was already public and we received the express written consent of informants. The questionnaire was administered with approval of the University of Melbourne Faculty of Science Human Ethics Advisory Group, project ID 1750658.1.

Data analysis

All quantitative analyses were conducted using R 3.6.2 (R Core Team 2019). We use Monte Carlo simulation to explore our results and represent uncertainty (Burgman 2005). We encoded elicited estimates of costs and benefits into probability distributions using numerical approximation. For

each parameter, the fitted mode was equal to informants' estimates of the most likely value, and the fitted density between their upper and lower estimates was equal to their confidence that the true value occurred there. We fitted lognormal distributions to most elicited responses. Exceptions were that exponential distributions were used when the lower and most likely estimates were equal to zero, and triangular distributions were used either when informants' confidence was equal to one or (in a single instance) where the lower and most likely value were equal and greater than zero, and the confidence interval was large such that a lognormal distribution could not be fit. Distribution parameter estimates are in table 4.s3. We consider this fitting to be illustrative rather than definitive because we did not ask informants the distributions they expected and other distributions may also be reasonable (McBride et al. 2012).

After constructing the probability distributions to represent uncertainty in the costs and benefits, we drew 1000 replicate random samples of costs and benefits for each scenario (public, part, and secret) and calculated decision scores. For a given replicate, the decision scores for each scenario used their scenario-specific sample of costs, C_d, and benefits, B_d, and shared the replicate estimate of costs when public, C_p, (equation 1). To discriminate among scenarios we determined for each replicate which decision was best or worst, i.e., had the highest or lowest the decision score, and whether a given decision resulted in an expected net benefit, i.e., the decision score was greater than zero, and calculated the cumulative density of decision scores and first-order stochastic dominance (Canessa et al. 2016). Stochastic dominance is a decision-analytic tool that compares the probability distributions of alternative actions to determine whether some actions are preferential to others over the range of uncertainty – Canessa and colleagues (2016) provide a concise overview of this in the conservation context.

Lastly, we consider informants' qualitative responses to the types of costs and benefits by coding their responses into several generic sub-classes (Supporting information 2), and we calculated the frequencies of response types.

Results

Decision scores for simulated species' decision scenarios are shown in figure 4.2 and table 4.s3, showing divergent patterns among the four species, and largely in line with expectation. Namely that secrecy was better for species that may be poached or interfered with through tourism, and involving fewer groups, while openness and inclusion better for species with purely intrinsic values.

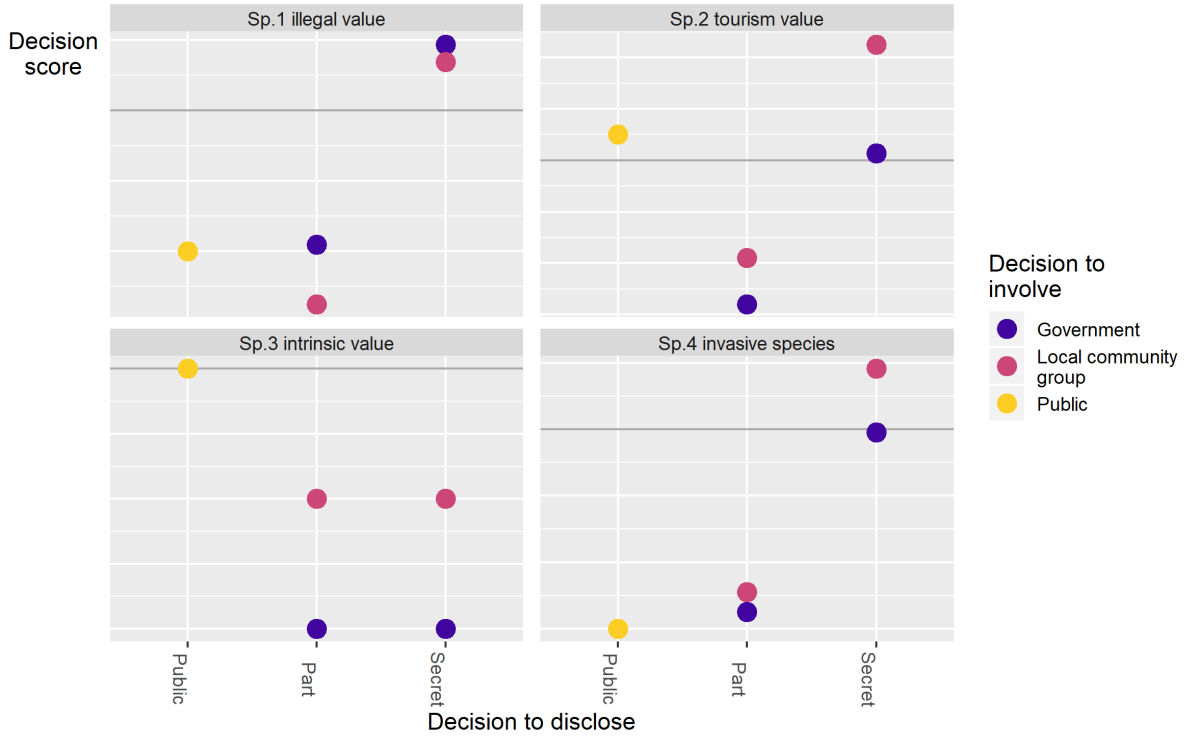

Figure 4.2. Decision scores, ζ, for simulated species, for each combination of disclosure of location (x–axis) and involvement of group of people (colour). Grey line indicates a score of zero, and the y-axis is relative to the range of scores for each decision scenario.

Eight informants returned the questionnaire, with minor redactions to maintain privacy. Two of the case studies are not public (secret), and no public information exists about their existence; we refer to these species in results as “Species1” and “Species2”. Six species have some information about the species’ identity and location made public (i.e. made partly public). For Species2 the informant was unable to provide quantitative estimates, however completed the text responses to the questionnaire.

Estimated decision scores show generally high overlap and long-tailed distributions (figure 4.3 and figure 4.s1). Smooth newts are the only species with a first-order dominant scenario — public. For alpine tree-frog, Giant Ibis, and red handfish part-public dominates secret, and for tiger, public dominates secret. Often decisions that may dominate for much of the range of values (figure 4.3) do not necessarily dominate at the tails (figure 4.s1), and tails, particularly lower bounds, may be of concern to decision makers in this context. Partial publicity is most frequently the best decision, while secret was the most frequent worst decision (figure 4.4, table 4.s4). Often the decision that

was most frequently the best decision was also beneficial, i.e., the decision score was usually greater than one (figure 4.s2, table 4.s5). Many decisions likely result in a net cost, and all of them for Species1 (fig 1, and figure 4.s2).

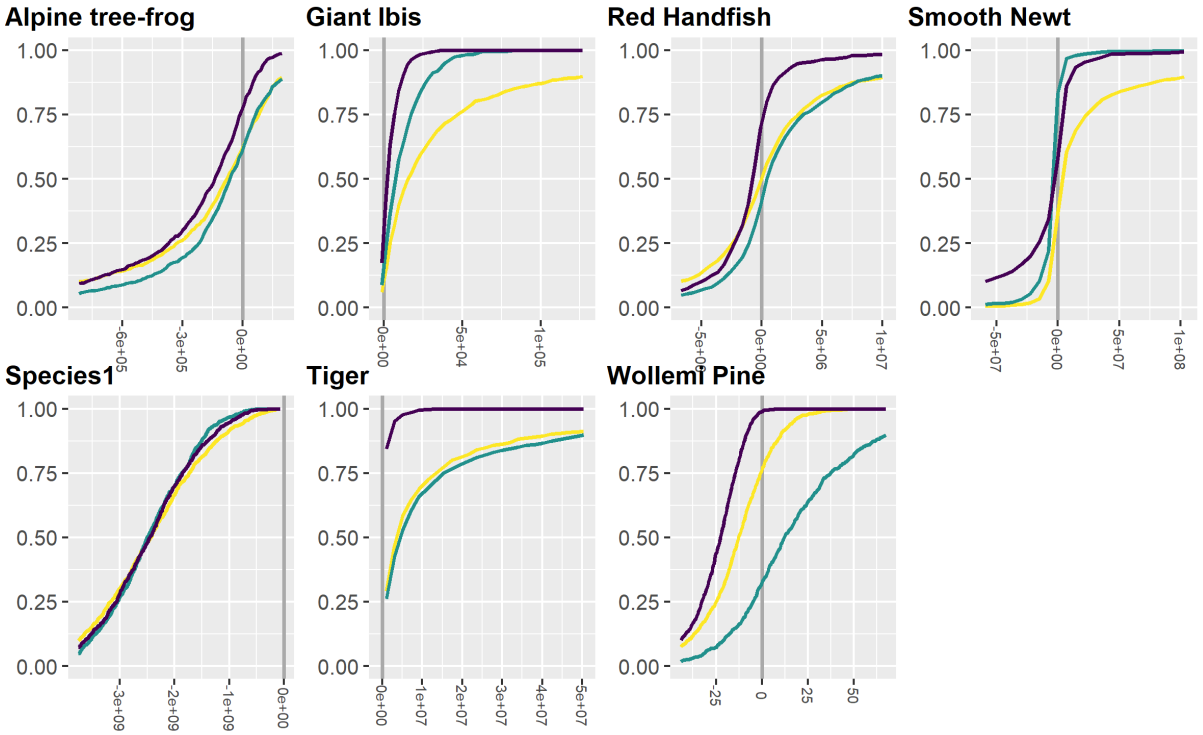

Figure 4.3. Cumulative densities (y-axis) of estimated decision scores, ζ, (x-axis), for case study species, for each of disclosure decision — public (yellow), part public (green) and secret (purple). For each species, panels show the middle 80th percentile ranges of all scenarios for that species (full range in figure 4.s1). Grey line equals zero, and x-axis is relative to the range of scores for each species.

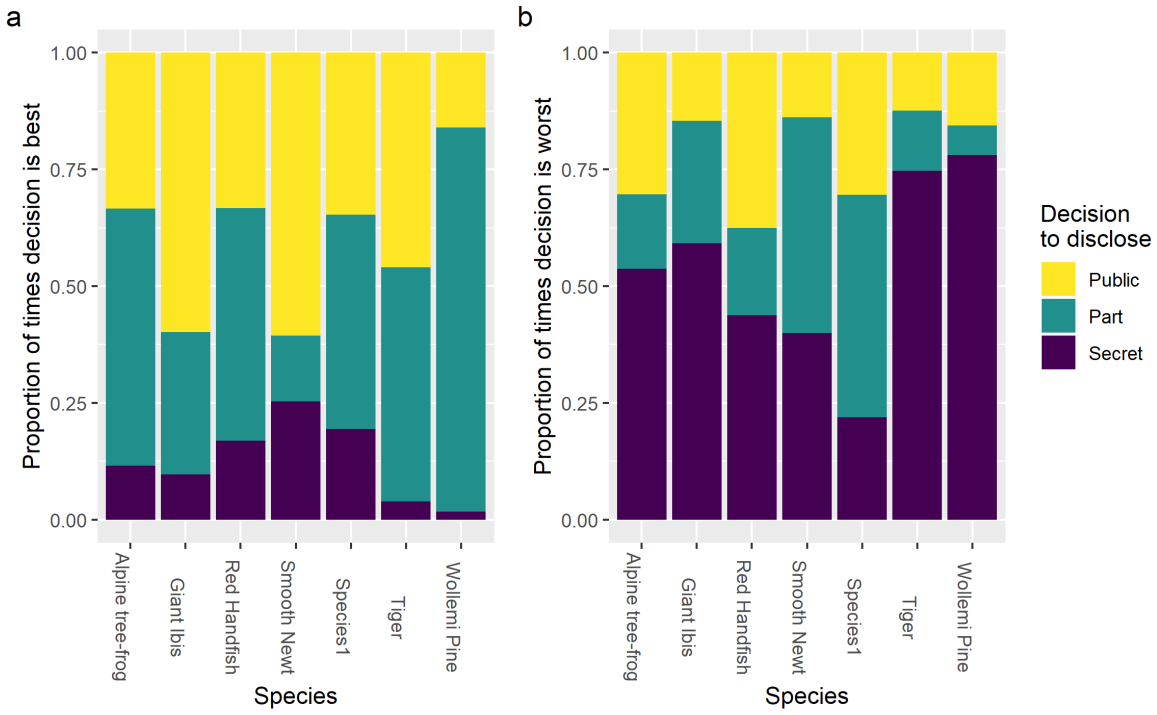

Figure 4.4. Proportion of simulation replicates that a given decision is (a) the best decision, i.e. highest decision score, or (b) the worst decision, i.e., lowest decision score.

All informants identified funding as a key benefit, and most also identified awareness and public support, and efforts to protect and recover species (figure 4.5). Benefits were most often perceived as flowing to government agencies and NGOs, rather than necessarily to species themselves, though government agencies and NGOs were also perceived to be the sources of benefits too (figure. 5). Poaching was the most frequently identified cost, and government agencies and the species themselves were the most frequently identified bearers of costs (figure 4.5). The range of sources of costs had no identifiable patterns (supporting information 1).

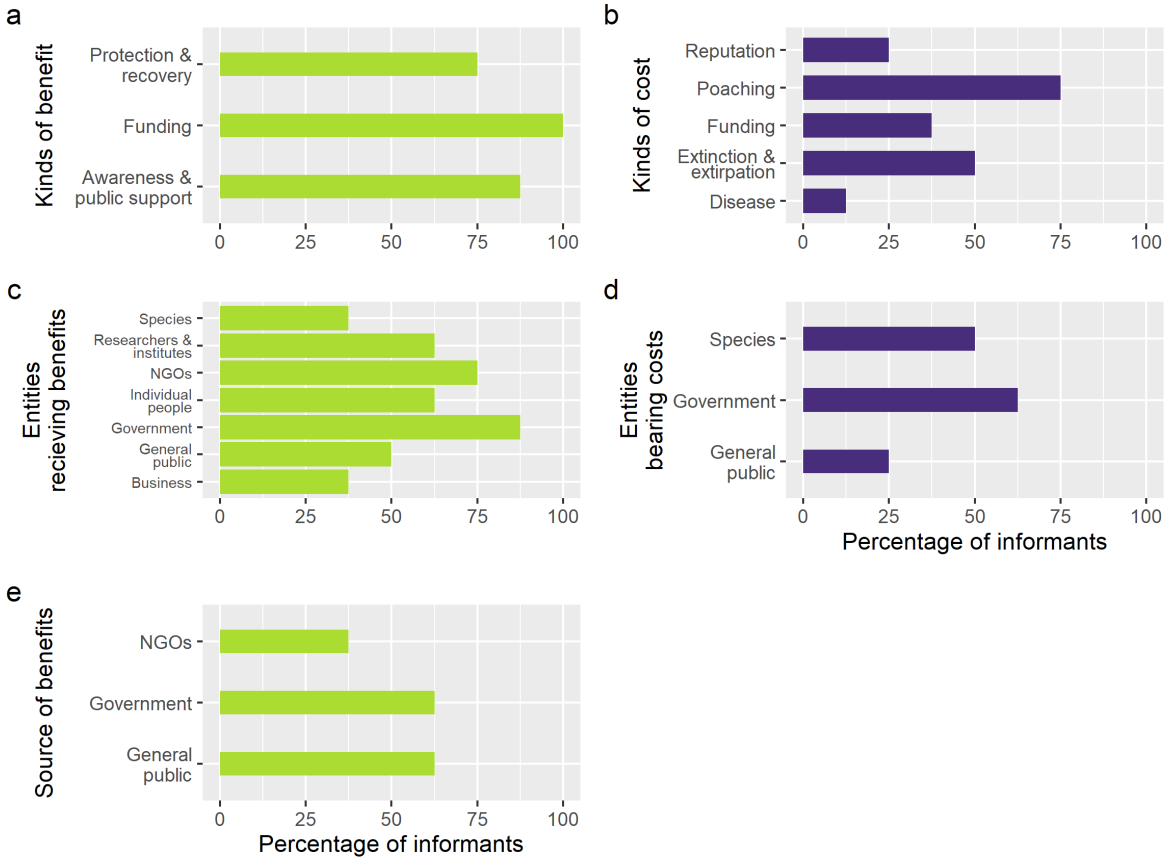

Figure 4.5. Percentage of informants providing types of responses to questionnaire about kind, recipient, and sources of benefits and costs.

Informants also provided a range of additional comments on their decision-making process and the questionnaire. Several made it clear that they had considered a range of benefits and costs and risks in making their decisions, though none claimed to have used a structured method to do this. Several informants identified difficulties in obtaining or estimating the magnitude of possible costs and benefits. Informants mentioned a range of motivations for not disclosing information, including to avoid taxonomic vandalism (Kaiser et al. 2013), and respect the wishes of local Indigenous peoples.

Discussion

We aimed to develop a method to help make decisions about publicising species discoveries, to understand decision-makers' perceptions of the costs and benefits involved in real decisions, and to apply our method to real case studies. Our method appears to be appropriate, as results from the simulated species match intuitive expectations (figure 4.2). For instance, the largest relative benefits

of publicity are expected for the species with mainly intrinsic values, as there is little cost to publicity, and scores reflect this. Species with high illegal value are best kept secret to avoid large costs. The better options for species with tourism value are either secret, where costs are not incurred, or public, where benefits are realised, rather than part-public, where greater costs are incurred than secret, but without realising the benefits of full publicity. The method can be applied usefully to our case studies too. For the smooth newt, publicity is the best decision over the range of possible outcomes, regardless of risk attitude, and is both the most often best and least often worst decision. Other species give less clear but still helpful outcomes. For the Wollemi Pine, partial publicity is clearly dominant over much (though not all) of the range of possible values (fig. 2), and is mostly the best, and least often the worst decision. For Species1 all outcomes resulted in net costs to the species, while for tiger and Giant Ibis, almost all outcomes resulted in benefits, regardless of the best decision. Such results can provide decision-makers with confidence.

In many conservation decisions, the best outcome may depend on the decision maker's attitude to risk (Tulloch et al. 2015; Canessa et al. 2016), and may change depending on uncertainty in the state of the system (Regan et al. 2005; Nicholson & Possingham 2007); this is true in many of our case studies, and our method can help elucidate the process identifying attitude and uncertainty. In many cases the uncertainty about the state of the system, i.e., the range of possible costs or benefits, is larger than the differences in expected utility from a given decision (e.g. long-tailed, overlapping distributions in fig. 3). Where the system does not show clear first-order dominance, decision-makers may still defer to other tools such as assessing second-order dominance given their own risk preference (Canessa et al. 2016), choosing from the most-likely best or least-likely worst option (fig. 4), the most likely to return a positive outcome (which is also least-likely to return a negative one, figure 4.s2), or explore the range of uncertainty necessary to change the optimal decision. We did not assess risk attitudes of our informants, so do not draw conclusions about what may be the best option, however decision-makers applying the method can make such judgements for themselves. Our method also provides a straightforward mechanism for reassessment of decisions considering additional information and changing circumstances. For instance it may be desirable to ensure protections are in place prior to publishing information (Stuart 2006), and increasing amounts of information released as suitable protections are enacted, such as happened with the night parrot (Murphy et al. 2017). This method allows for assessment of the utility of all such scenarios together.

A common objective in conservation is to minimise the probability of extinctions, such as here and elsewhere (Tulloch et al. 2018). Here we assume this is the main objective of decision makers too, and this is corroborated by informants' comments. Informants identified a wide range of costs and benefits to both species concerned, and those involved in their discovery, but reported some were not considered as part of the decision-making – such as benefits to researchers and their reputations. There may be internal tensions between agencies that may expect to receive benefits from releasing information, such as through donations and esteem, against the risks of harm borne by species, and costs borne by agencies tasked with protection. Although this method compares costs and benefits among decisions, it does not directly compare differing objectives. Where decision-makers identify a range of objectives, broader approaches such as structured decision-making (Gregory et al. 2012; Guerrero et al. 2017) can incorporate our method. Costs and benefits may covary (Armsworth 2014), and though here we assume they are independent, our framework can incorporate could account for this. Costs are important to maximise conservation outcomes (Naidoo et al. 2006; Joseph et al. 2009), and the direct incorporation of costs and benefits into this method is an important differential from alternative approaches (e.g., Meijaard & Nijman 2014; Tulloch et al. 2018).

Although there is a public interest in discoveries of species from unknown locations (Watson & Davis 2017) and wider benefits to the systematic cataloguing of biodiversity data (Tulloch et al. 2018), there is also a clear tension with the potential harms to species if their location is known (Meijaard & Nijman 2014; Lindenmayer & Scheele 2017). Our method can interrogate this tension, and systematically and transparently justify choices. Using such a framework may help reduce perverse outcomes like suppression of information for arbitrary purposes (Hannam 2017), or overeager sharing against the best interests of a species (Meijaard & Nijman 2014). This tension is increasingly recognised. We hope to have provided methods that will be widely applicable in future, and to have illuminated the path for further study.

Supporting information

Supporting information 1: Supplementary text, figures, and tables.

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Supporting Information 1 to "The costs and benefits of publicising species discoveries"

GE Ryan, E Nicholson, CM Baker, and MA McCarthy

Supporting methods: Derivation of equation 1.

The methods we present in this paper simplify and generalise the solution to the problem of deciding which decision to publicise a species' discovery is optimal as described Ryan and Baker (2016, 2019; hereon RB). Their equation 1 (p. 186 Ryan & Baker 2016, corrected p. 47, 2019) allows for the benefits of some decision for some amount of publicity to be compared with a decision for no publicity, and these benefits to be offset by the likelihood and possible costs associated with information leaking out in the event of no publicity (and no benefits). The RB formulation does not need different data to what we propose here, however it has several drawbacks which we have sought to ameliorate. The RB formulation

considers only a logistic type relationship between available resourcing and probability of extinction, while this may not necessarily be the case. A greater difficulty is that the RB approach sets up a binary problem: publicity or not, and 'benefits' are turned on or off with publicity. Although as RB note, it is possible to compare several different publicity scenarios with a no publicity scenario, this is not a straightforward or intuitive means to compare a range of scenarios. This mechanism means that if there are a range of scenarios from no-publicity to full publicity and gradations in-between (e.g., releasing some information such as the discovery of the Night Parrot, but not the location), costs must be accounted for in one of several unintuitive ways. One way is that for in-between scenarios, the costs ("damages" in RB) incurred if information unintentionally becomes public despite a decision not to publicise will only be the costs for that in-between scenario, not for information becoming fully public which may be more likely. The alternative is that costs for each decision are directly accounted into the benefit term, making it actually a net-benefit term, and that the costs term represents the costs of associated with a fully public scenario. Another implication of this RB binary approach is that there are no benefits associated with a no-publicity scenario. This therefore means that if there may be benefits with such a scenario, the benefits for other scenarios must be adjusted to be relative to the no-publicity scenario. Lastly, the RB formulation assumes that costs and benefits are already scaled as relative to their functional relationship with probability of extinction, and the nature of this scale may not be known, though it is not required to be known to produce an answer (RB).

We can therefore propose an formulation similar to RB such that:

$$PE_d = f\left(g(PE_0) + z\left(C_d + p_d\left(C_p - C_d\right) - B_d\right)\right) \qquad \text{Eq. S1.,}$$

Were for some decision *d*:

PE_d is the probability of extinction of a species' given that decision,

f is some function of the relationship between probability of extinction and resources available for conservation, and monotonically decreases from 1 to 0 with range -∞ to ∞,

g is the inverse function of f,

PE_0 is the species' baseline probability of extinction,

z is a scaling coefficient,

C_d are the costs associated with that decision,

C_p are the costs associated with that a decision to fully publicise the discovery,

p_d is the probability that information will become fully public despite the decision, and

B_d are the benefits associated with this decision.

Using equation S1, the best decision is the one that minimises PE_d. This approach solves several of the issues raised above with RB, namely it allows the inclusion of any functional form of *f*, rather than just logistic, it separately accounts for the costs and benefits of a decision, meaning that any given scenario can be calculated rather than some binary comparison, and removing the problems associated with this. While we may not know *f*, *g*, PE_0, or *z*, these terms to not change with the decision, so we can simplify the solution further by extracting the multiplicand of *z*, and multiplying it by negative one to get equation 1 in the main text:

$$\zeta_d = B_d - C_d - p_d(C_p - C_d)$$

Because the terms are now negated, the decision that maximises ζ_d is the one that minimises PE_d and so is optimal for the species.

Table 4.s1. Potential costs, benefits, and probabilities, for decision scenarios of four simulated species. Costs are listed on right, and dependent on information disclosed to the public. Benefits are listed below, and are dependent on stakeholder groups involved. Probabilities that information will become public anyway are in the central matrix, dependent on both stakeholders and level of publicity.

S1a: Species 1 – High value on illegal markets

	Publicly Disclose				**Cost (C_d)**
Inform and involve	**Probabilities of Publicity (p_d)**	*Government*	*+ Local Community Groups*	*Public*	
	Secret	0.01	0.1		10,000

	Part	0.4	0.8		1,500,000
	Public			1	5,000,000 (C_p)
Benefit (B_d)		1,000,000	1,500,000	3,000,000	

S1b: Species 2 – High tourism value

	Publicly Disclose				**Cost (C_d)**
Inform and involve	**Probabilities of Publicity (p_d)**	*Government*	*+ Local Community Groups*	*Public*	
	Secret	0.01	0.05		20,000
	Part	0.6	0.8		4,000,000
	Public			1	4,500,000 (C_p)
Benefit (B_d)		200,000	2,500,000	5,000,000	

S1c: Species 3 – Intrinsic value

	Publicly Disclose				**Cost (C_d)**
Inform and involve	**Probabilities of Publicity (p_d)**	*Government*	*+ Local Community Groups*	*Public*	
	Secret	0.01	0.02		20,000
	Part	0.05	0.1		20,000
	Public			1	20,000 (C_p)
Benefit (B_d)		10,000	15,000	20,000	

S1d: Species 4 – Invasive species

	Publicly Disclose				**Cost (C_d)**
Inform and involve	**Probabilities of Publicity (p_d)**	*Government*	*+ Local Community Groups*	*Public*	
	Secret	0.01	0.02		500,000
	Part	0.5	0.7		1,500,000
	Public			1	5,000,000 (C_p)
Benefit (B_d)		500,000	1,500,000	2,000,000	

Table 4.s2. Decision scores for each simulated species in each decision scenario.

species	involve	Secret	Part	Public
Sp.1 illegal value	Government	940100	-1900000	
	Local community group	691000	-2750000	
	Public			-2000000
Sp.2 tourism value	Government	135200	-2800000	
	Local community group	2256000	-1900000	
	Public			500000
Sp.3 intrinsic value	Government	-10000	-10000	
	Local community group	-5000	-5000	
	Public			0
Sp.4 invasive species	Government	-45000	-2750000	
	Local community group	910000	-2450000	
	Public			-3000000

Table 4.s3. Numeric estimates of cost and benefit from questionnaires for each case study species and decision scenario, statistical distribution fit to those estimates, and estimates of parameters corresponding to the relevant distribution.

species	decision	type	Lower estimate	Most likely estimate	Upper estimate	confidence	distribution	sigma	mu	lambda	a	b	c
Alpine tree-frog	Public	Benefit	25000	150000	4.00E+05	0.9	lognormal	0.538738	12.20863				
Alpine tree-frog	Public	Cost	0	1.00E+05	1.00E+06	0.9	lognormal	1.006397	12.52576				
Alpine tree-frog	Part	Benefit	25000	1.00E+05	4.00E+05	0.9	lognormal	0.694365	11.99507				
Alpine tree-frog	Part	Cost	0	50000	2.00E+05	0.9	lognormal	0.699705	11.30936				
Alpine tree-frog	Secret	Benefit	25000	25000	3.00E+05	0.9	triangular				0	361111.1	25000
Alpine tree-frog	Secret	Cost	0	0	2.00E+05	0.9	exponential			1.15E-05			
Giant Ibis	Public	Benefit	1000	2000	20000	0.5	lognormal	1.485846	9.808641				
Giant Ibis	Public	Cost	0	0	2000	0.5	exponential			0.000347			
Giant Ibis	Part	Benefit	0	0	10000	0.5	exponential			6.93E-05			

Giant Ibis	Part	Cost	0	0	2000	0.8	exponential			0.000805
Giant Ibis	Secret	Benefit	0	0	10000	0.8	exponential			0.000161
Giant Ibis	Secret	Cost	0	0	2000	0.8	exponential			0.000805
Red Handfish	Public	Benefit	0	250000	2.00E+06	0.5	lognormal	1.442027	14.50866	
Red Handfish	Public	Cost	20000	5.00E+05	2.00E+06	0.5	lognormal	1.177353	14.50852	
Red Handfish	Part	Benefit	0	250000	2.00E+06	0.5	lognormal	1.442027	14.50866	
Red Handfish	Part	Cost	0	20000	5.00E+05	0.5	lognormal	1.794123	13.12236	
Red Handfish	Secret	Benefit	0	75000	5.00E+05	0.5	lognormal	1.37736	13.12236	
Red Handfish	Secret	Cost	0	20000	5.00E+05	0.5	lognormal	1.794123	13.12236	
Smooth Newt	Public	Benefit	0	50000	1.00E+06	0.2	lognormal	2.20205	15.6688	
Smooth Newt	Public	Cost	0	8.00E+05	2.00E+06	0.35	lognormal	1.169087	14.95913	
Smooth Newt	Part	Benefit	0	20000	1.00E+05	0.2	lognormal	1.757418	12.99201	
Smooth Newt	Part	Cost	0	7.00E+05	2.00E+06	0.35	lognormal	1.235224	14.98461	
Smooth Newt	Secret	Benefit	0	8.00E+05	2.00E+06	0.3	lognormal	1.254692	15.16662	
Smooth Newt	Secret	Cost	0	1.00E+05	1.00E+06	0.2	lognormal	1.995506	15.49497	

Species1	Public	Benefit	50000	750000	1.50E+07	0.66	lognormal	1.536246	15.88788				
Species1	Public	Cost	0	2.50E+09	5.00E+09	1	triangular				0	5.00E+09	2.50E+09
Species1	Part	Benefit	50000	750000	1.50E+07	0.66	lognormal	1.536246	15.88788				
Species1	Part	Cost	0	2.50E+09	5.00E+09	1	triangular					5.00E+09	2.50E+09
Species1	Secret	Benefit	50000	1.00E+06	1500000	0.5	lognormal	0.636761	14.22098				
Species1	Secret	Cost	0	2.50E+09	5.00E+09	1	triangular				0	5.00E+09	2.50E+09
Tiger	Public	Benefit	50000	2.00E+05	2.00E+07	0.8	lognormal	1.758138	15.29712				
Tiger	Public	Cost	0	0	180000	0.3	exponential			1.98E-06			
Tiger	Part	Benefit	50000	2.00E+05	2.00E+06	0.3	lognormal	1.793519	15.42278				
Tiger	Part	Cost	0	0	180000	0.3	exponential			1.98E-06			
Tiger	Secret	Benefit	0	70000	2.00E+05	0.3	lognormal	1.319825	12.89819				
Tiger	Secret	Cost	0	0	180000	0.3	exponential			1.98E-06			
Wollemi Pine	Public	Benefit	0	25	50	0.95	lognormal	0.347844	3.339871				
Wollemi Pine	Public	Cost	5	35	75	0.95	lognormal	0.376959	3.697446				
Wollemi Pine	Part	Benefit	0	40	70	0.7	lognormal	0.530494	3.970304				
Wollemi Pine	Part	Cost	5	8	50	0.7	lognormal	1.036047	3.152835				
Wollemi Pine	Secret	Benefit	0	10	20	0.95	lognormal	0.347844	2.42358				
Wollemi Pine	Secret	Cost	5	7.5	20	0.95	lognormal	0.298059	2.103742				

Table 4.s4. Data corresponding to figure 4.3 – proportion of times a decision is the best (left) or worst option (right), given in simulations. Highest proportions in bold.

Species	**Proportion of times best option**			**Proportion of times worst option**		
Decision	*Public*	*Part*	*Secret*	*Public*	*Part*	*Secret*
Alpine tree-frog	0.334	**0.55**	0.116	0.303	0.16	**0.537**
Giant Ibis	**0.598**	0.305	0.097	0.146	0.262	**0.592**
Red Handfish	0.333	**0.498**	0.169	0.375	0.187	**0.438**
Smooth Newt	**0.606**	0.141	0.253	0.138	**0.462**	0.4
Species1	0.347	**0.459**	0.194	0.304	**0.477**	0.219
Tiger	0.46	**0.501**	0.039	0.124	0.129	**0.747**
Wollemi Pine	0.16	**0.823**	0.017	0.156	0.063	**0.781**

Table 4.s5. Data corresponding to figure 4.s2 — proportion of times a given decision resulted in a net benefit, i.e., a decision score greater than zero. “Best” is whichever decision had the maximum score in a given simulation replicate.

Species	**Best**	**Public**	**Part**	**Secret**
Alpine tree-frog	0.527	0.377	0.386	0.221
Giant Ibis	0.984	0.903	0.836	0.7
Red Handfish	0.778	0.492	0.584	0.268
Smooth Newt	0.782	0.622	0.136	0.405
Species1	0	0	0	0
Tiger	0.995	0.893	0.909	0.539
Wollemi Pine	0.708	0.22	0.66	0.006

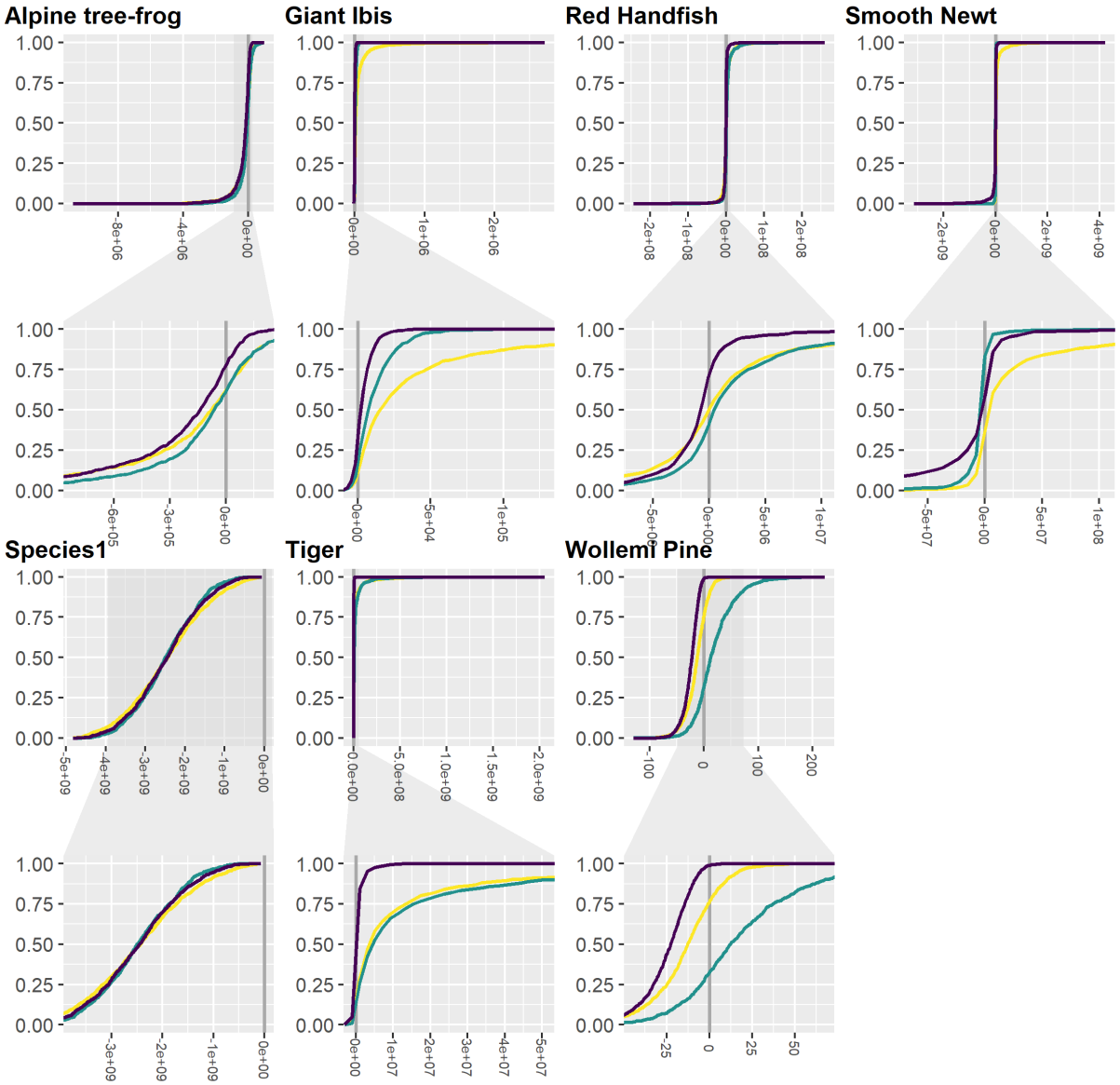

Figure 4.s1. Cumulative densities of estimated decision scores, ζ, for case study species, for each of disclosure decision — public (yellow), part public (green) and secret (purple). For each species panels above show the full range of values, while panels below zoom to encompass the middle 80th percentile ranges of all scenarios for that species. Grey line equals zero, and x-axis is relative to the range of scores for each species.

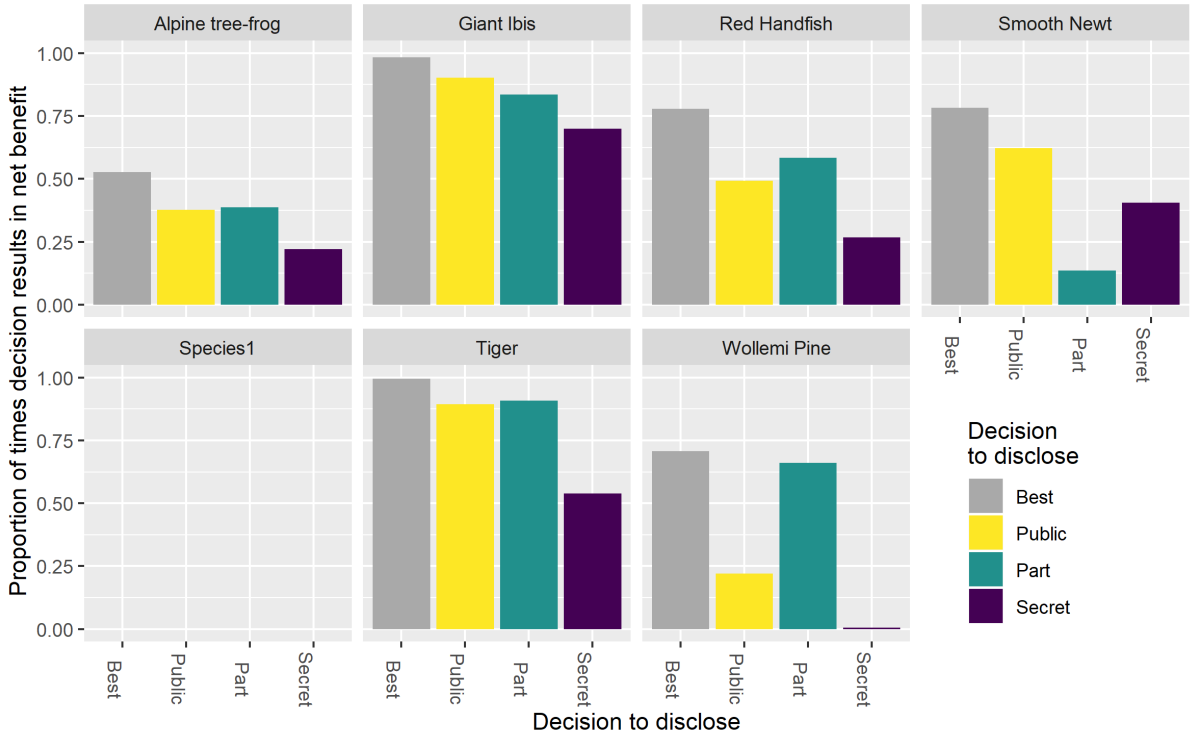

Figure 4.s2. Proportion of simulation replicates that a given decision resulted in a net benefit, i.e., the decision score was greater than one. “Best” decision is the one with the highest decision score in each replicate.

Chapter Five: Strategies to maximise outcomes from investments in species conservation

Introduction

Funding to conserve biodiversity is well below the levels need to meet many national and global targets and prevent extinctions (McCarthy et al. 2012; Wintle et al. 2019). Allocation of conservation funds is driven by a range of priorities (Pressey & Bottrill 2009; Wilson et al. 2009; Dayer et al. 2016), and may be biased towards certain taxa (Clark & May 2002) or places (Larson et al. 2016). Such influences on allocation of funds can lead to poorer conservation outcomes than may be possible (Game et al. 2013; Larson et al. 2016). A large body of research has explored methods to improve conservation outcomes through strategic allocation of limited funding (Wilson et al. 2009; Game et al. 2013), such as methods to prioritise species conservation activities (Joseph et al. 2009), threat abatement actions (Carwardine et al. 2012), or maximise reserve assets (Moilanen 2007). Such methods can significantly improve biodiversity outcomes when compared to less structured approaches (Pressey & Bottrill 2009) or in the absence of considering costs (Naidoo et al. 2006), however differences among various resource allocation methods are not always well understood.

At the core of many strategic approaches to conservation investment decisions is some measure of cost-efficiency, where investors may target actions that are expected to achieve the best outcomes per unit of investment, given some objective (Davis et al. 2006; Wilson et al. 2007). This type of approach can result in funding some species or projects, while other less efficient projects are not funded, and is sometimes referred to as 'conservation triage' (Bottrill et al. 2008). A popular approach to the cost-efficient selection of actions for species conservation is the Project Prioritization Protocol (PPP; Joseph et al. 2009). The PPP approach moves systematically through a list of projects or actions funding them in order from the most cost-effective action to the least, up to the available budget, and may be weighted to account for a range of values (Joseph et al. 2009; Gerber et al. 2018). Several programmes follow this type of return-on-investment approach to priority setting for species conservation (Brazill-Boast et al. 2018), threat management (Carwardine et al. 2012; Auerbach et al. 2014), land acquisition (Withey et al. 2012), or biosecurity (Dodd et al. 2017). The PPP is conceptually appealing and relatively simple to apply, but inevitably simplifies a complex problem; such as either assuming a whole project is funded, or if partially funded, that each

additional unit of funds spent on a given project is assumed to be just as effective as the last (i.e. a linear function between spending and benefit). An alternative approach to allocate conservation funding is to consider the relationship between efficiency for a given action, and the amount of funding spent. For instance, some actions or projects may show a linear relationship between funding and efficiency, such as systematic habitat restoration, where more funding results in more units of habitat restored. Others may show non-linear behaviour, for example all-or-nothing, such as the purchase of a key piece of land where nothing can be bought for less than the full price. More complex relationships between the amount of funding and efficiency may also occur, for example as increasing ranger patrols in an effected area may initially show increasing efficiency in deterring poaching, but past a certain level may show diminishing returns.

Alternatively, an optimisation approach can account for the relationship between funding and efficiency. For instance, the relationship between funding and changes in a species' IUCN Red List status (IUCN 2019) as a measure of extinction risk (Keith et al. 2004) was exploited to optimise funding allocation for Australian birds to meet a range of objectives (McCarthy et al. 2008). This study considered how funding affected changes in the conservation status of species, while assuming effects were the same for all species of the same status, which is unlikely to be true. For instance, management may be more effective if targeted to species with relatively smaller populations rather than larger ones, or populations occupying smaller rather than larger areas.

Species' biological traits provide some predictive generalisation about their ecology or biology (McGill et al. 2006), and can be related to a species' extinction risk (Bennett & Owens 1997; Purvis et al. 2000; Machado & Loyola 2013). Therefore species traits may have affect the efficiency of conservation management actions and funding. However, we know of no research previously that examines the effect of species' biological traits and management characteristics on the efficiency of conservation investments. Furthermore, this type of optimisation approach may be more cost-efficient than a PPP approach because it can target funding using the relationship between outcomes and funding across all funding levels, not just the specific amount required for each project. The relative efficiency of these approaches has not yet been explored.

In this study we explore approaches to efficient allocation of funding and compare their outcomes for conservation. We aim to answer two questions: first, can information on species traits be used to improve the efficiency of conservation spending? Second, is such an optimisation approach more

efficient than a PPP approach? We build on research by McCarthy and colleagues (McCarthy et al. 2008) by including a range of species traits and management characteristics when examining optimal conservation investments for Australian birds. We expected that the inclusion of this additional information would improve our estimates of funding efficiency. Based on the results of this optimisation we compare a PPP approach with our optimisation approach, based on which minimises the expected number of extinctions. A key difference between the continuous optimisation approach and the discrete project-by-project funding approach of the PPP is that the PPP approach only allows for either the allocation of a full complement of funding for each species or no funding to each species, while the optimisation allows for partial funding across many species at once. Because of this difference, we expected that the optimisation approach would produce greater expected outcomes than the PPP. Our approach builds on the use of decision theory in conservation of species to demonstrate methods to improve the efficiency of funding conservation actions.

Methods

Data

To explore funding efficiency on conservation outcomes we used a case study of Australian birds. We used information on species biological traits, conservation status, and other characteristics for Australian birds (Garnett et al. 2015), information on the funding spent on bird conservation in Australia from 1993-2000 (Garnett & Crowley 2000; Garnett et al. 2003) and their IUCN Red List regional status in Australia at the start and end of this period (Garnett 1992; Garnett & Crowley 2000), which included a number of retrospective reclassifications of status based on improved information (Garnett et al. 2015) and changes of taxonomy. Reclassifications of status are for the year 1990 (Garnett et al. 2015), however it is assumed here that species would have had the same status in 1992. These data include a range of taxonomic units such as sub-species and sub-populations, but for simplicity we refer to them all as “species” here.

The Red List status is based on the categories and criteria of the IUCN Red List of Threatened Species (IUCN 2020). Based on rules and quantitative thresholds relating to population size, distribution size and declines in either, species are placed in ordinal categories of risk, ranging from Extinct and Extinction in the wild, to threatened categories (in order of decreasing risk) critically endangered (CR), endangered (EN), and vulnerable (VU), and non-threatened categories, near threatened (NT) or least concern (LC). We considered 106 threatened species and 154 non-threatened species deemed

by Garnett and Crowley (2000) to be of conservation concern. Because of reclassifications of Red List status and taxonomy, the numbers of species in each category used here differ slightly from those presented by McCarthy and colleagues (2008); compare table 5.1 with their table 5.1 (p. 1430, McCarthy et al. 2008). Our description of direction of movements among risk categories where 'down' refers to a reduction in risk status (e.g. Critically Endangered to Endangered), and 'up' refers to an increase in risk (e.g., Critically Endangered to Extinct), is also in contrast to the use of these terms by McCarthy and colleagues (2008), but is intended to be more consistent with the use of 'uplisting' and 'downlisting' elsewhere in the conservation literature (e.g. Butchart and colleagues (2004), Mallon and Jackson (2017)).

Table 5.1. Number of funded and unfunded species in each IUNC Red List category, and outcomes in change of status between 1992 and 2000. 'Down' refers to a reduction in risk status (e.g. Critically Endangered to Endangered), while 'up' refers to an increase in risk (e.g., Critically Endangered to Extinct); Up 2 refers to an increase of two risk categories (e.g. Vulnerable to Critically Endangered).

Initial conservation status	**Outcome: change in conservation status**				
	Up 2	**Up 1**	**Stay**	**Down 1**	**Total**
Unfunded species					
CR	-	0	5	0	5
EN	0	1	9	0	10
VU	0	1	21	0	22
NT/LC	0	0	108	-	108
Funded species					
CR	-	0	8	2	10
EN	0	0	32	2	34
VU	1	0	24	0	25
NT/LC	2	7	37	-	46

We explore the effect of a range of species' characteristics on the probability of changes in Red List status. Body mass and density are known to correlate with extinction risk (Bennett & Owens 1997; Purvis et al. 2000); additionally, we considered area of occupancy (AOO, a measure used in one of the sub-criteria for Red List assessment), and proportion of population in Australia, and degree of ecological specialization, as we expected that these variables might influence the effectiveness of management actions and extinction risk. Specifically, we expected more tightly concentrated

populations may be easier to efficiently manage, as well as those mostly located in Australia, though we were unsure what direction the effect of specialization would have on efficiency. We also considered a species' IUCN Red List status in Australia because the ability for species to move among categories might depend on the category they are in. These data were drawn from (Garnett et al. 2015).

Estimating species characteristics and funding efficiency

To understand the effect of species characteristics on funding efficiency, we expanded on the methods of McCarthy and colleagues (2008), and use a multinomial regression to model the probabilities of changes in species' Australian Red List status from 1992 to 2000. We model the probability of threatened species either declining one or two categories, or increasing one category, model the probability of non-threatened species becoming threatened (table 5.1). We then calculate the probability of remaining in the same category as the complement of the probabilities of changing category. We collectively refer to these changes or non-changes in status as "outcomes".

We used an exponential function to model these probabilities of change with main effects of funding, species' characteristics, and interactions between characteristic and funding. We model the probability of outcome *j*, for species *i*, with a set of characteristics, as:

$$p_{i,j} = e^{(\alpha_j + \beta_j \times X_i + \gamma_j \times Y_i + \delta_j \times X_i \times Y_i)} \qquad \text{eq 1.}$$

With the intercept α_j, coefficient of funding β_j, funding X_i, coefficient of species' characteristic γ_j, characteristic value Y_i, and the interaction coefficient δ_j.

Additional terms and interactions can be added to or removed from the exponent for additional variables, and separate models were fit for threatened species, and non-threatened species. We estimated these probabilities in a Bayesian framework using JAGS (Plummer 2003, 2017) through R (R Core Team 2019). We used vague priors for our coefficients and constrained estimates in several ways. The probability of being uplisted by one category was constrained to be greater than the probability of being uplisted by two categories; thus critically endangered species were at greater risk of extinction than endangered species. The effect of funding was constrained to reduce the probability of decline, or to increase the probability of improving a species' conservation category. Finally, we constrained the effect of funding to be greater on the probability of declining two categories, than of declining one category. Because of the reasonably small sample size – only seven changes in category for threatened species, and nine non-threatened species becoming threatened

(table 5.1) — rather than model all possible combinations of characteristics, we ran a subset series of models with either:

- Cost only,
- Cost plus one of abundance, AOO, body mass, density, specialization, proportion of the population in Australia, and for threatened species only, IUCN Red List status or
- Cost plus one of abundance, AOO, body mass, density, specialization, proportion of the population in Australia, and for threatened species only, IUCN Red List status, with an interaction term between cost and the other variable.

Thus, we had 15 models for threatened species, and 13 models for non-threatened species. Models were run for up to 10^6 iterations with a burn-in of $5x10^5$, and those failing to converge were excluded from further consideration.

Optimisations of funding

Using our estimates of funding efficiency from above, we explored the optimal investment strategy for how to allocate funding to minimise the expected number of extinctions over eight years (the period of our estimates from above). Given the lack of evidence for effects of species characteristics, and large uncertainty around interaction terms (see results below), we explore this optimisation for only a limited subset of possible model as an illustration of the process. We conduct the optimisation using the funding-only model as per McCarthy and colleagues (2008), and the area of occupancy and funding model with no interaction term for budgets from zero to AUD 30 million. For the funding only model we use the analytic solutions derived by McCarthy and colleagues (equations 4 and 5, p. 1431, 2008) where the optimal amount to spend on each critically endangered species, X^*_{CR} is:

$$X^*_{CR} = \frac{bB+(a-c+\ln\left(\frac{d}{b}\right))n_{EN}}{bn_{CR}+dn_{EN}} \qquad \text{eq.2}$$

And the optimal amount to spend on each endangered species X^*_{EN} is:

$$X^*_{EN} = \frac{B-X^*_{CR}n_{CR}}{n_{EN}} \qquad \text{eq.3}$$

Where the the probability of a threatened species being uplisted by two classes is given funding of X is e^{-a-bX}, and the probability of a threatened species being uplisted by one class is e^{-c-dX}, and a budget B, and numbers of critically endangered n_{CR} and endangered n_{EN} species.

For the AOO and funding model the optimisation is a high dimensional problem as the optimal funding differs by species, rather than IUCN status, and likely has no analytic solution. Instead we estimate the near-optimal amount to spend on each species using a numerical optimisation tool in R (R Core Team 2019).

Comparison of project prioritisation protocol and optimisation

To compare the efficiency of investment via a PPP approach with the optimisation approach described above, we consider a portfolio of projects where each project requires funding to a level that would reduce the extinction risk to <1% over 80 years, i.e., ten times the original period over which we estimated parameters. As above, we restrict this analysis to critically endangered and endangered species, and approximate risk over 80 years based on the estimates for a single 8 year period. Estimates of optimal funding to minimise risk over longer time-frames by McCarthy and colleagues (2008) suggest that the estimate over 8 years is very similar to that for a longer-time frame. We prioritise projects based on return-on-investment measured as expected avoided extinctions per dollar, and using the PPP approach fund projects in decreasing order of efficiency. Where projects have equal efficiency, we fund them one after the other in alphabetical order. As funding increases, projects are added to the portfolio of funded projects once the level of funding is sufficient to fully fund a project.

We therefore compare the benefit in terms of expected avoided extinctions over 80 years, against budget per 8 year period, for four investment strategies:

- Optimisation based on the funding only model
- Optimisation based on the funding and AOO model
- PPP based on the funding only model
- PPP based on the funding and AOO model

Results

In general, our results showed low evidence for a clear effect of any of the species characteristics on the probability of changes in status, and high uncertainty about interactions between cost and those

characteristics (figures 1 and 5.2). For threatened species, almost no models converged including variables for Red List status or the proportion of the population occurring in Australia, so we excluded these models from further consideration. For both the set of models for threatened and non-threatened species, we found that the models including cost only had the lowest deviance information criterion (DIC), and models including cost and area of occupancy had the lowest DIC among models including at least one species characteristic. We therefore focus on these two models for further investigations.

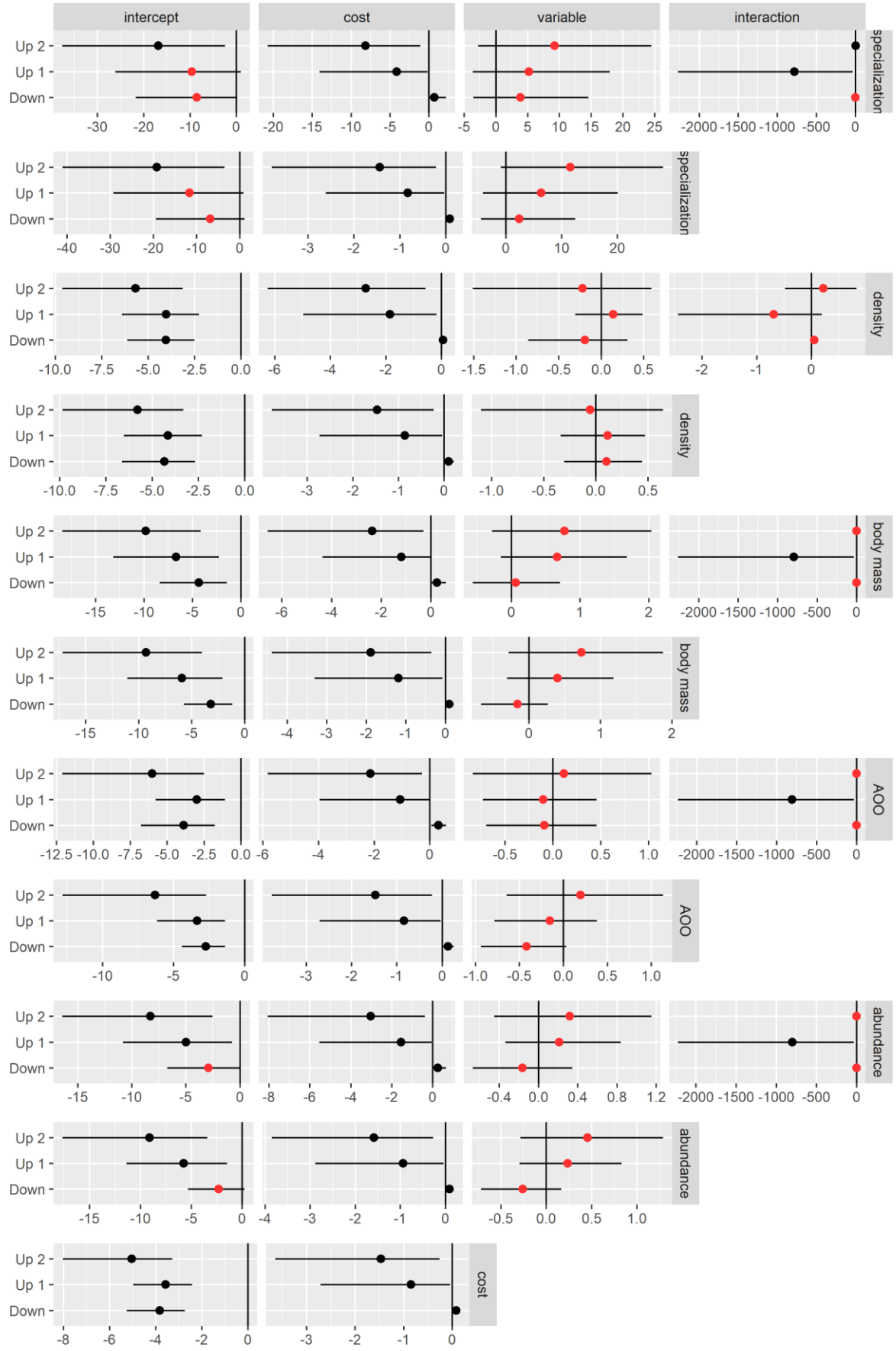
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Figure 5.1. Parameter estimates for models of threatened species. Estimates of values (x-axis) of intercepts, and coefficients of cost, species characteristic variables, and interactions between cost and those variables (columns) for probabilities of change of status (y-axis), for models with cost only or a single characteristic with or without interaction terms (rows). Points are mean of the posterior and lines represent 95% credible interval. Red points indicate credible interval bounds zero.

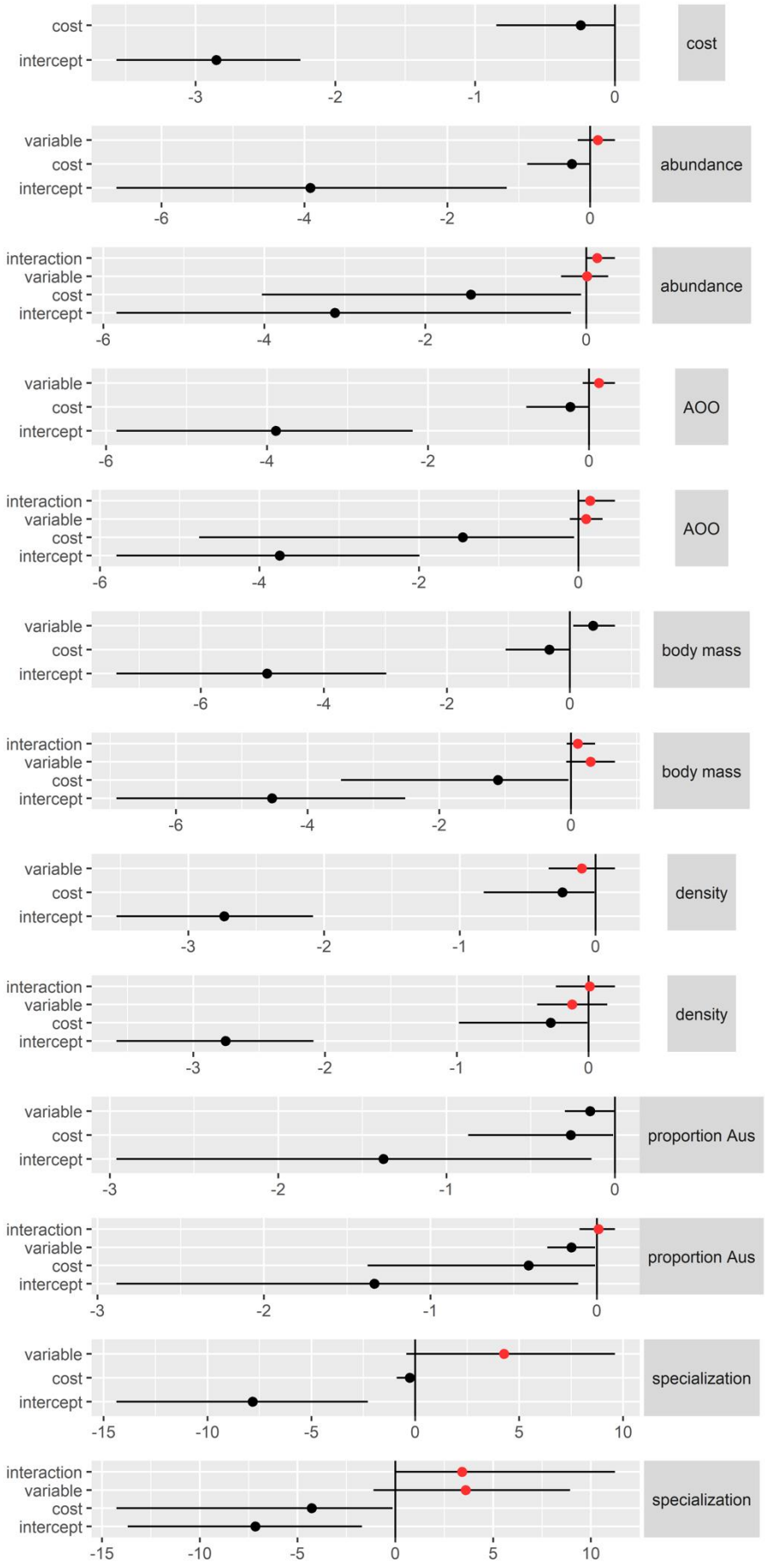
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Figure 5.2. Parameter estimates for models of non-threatened species. Estimates of values (x-axis) of intercepts, and coefficients of cost and species' characteristic variables, and interaction terms, for models with cost only or a single characteristic with or without interaction (rows). Points are mean of the posterior and lines represent 95% credible interval. Red points indicate credible interval bounds zero.

Comparing our results with those of McCarthy and colleagues (2008), we find a similar overall pattern, although notably the probability of non-threatened species becoming threatened is much higher (figure 5.3, cf. figure 5.1., p. 1431 McCarthy and colleagues (2008)). The optimisation of funding to minimise the number of extinctions over an eight-year period showed a slightly different pattern, with critically endangered species being funded before endangered species at lower budgets (figure 5.4, cf. figure 5.2., p. 1432 McCarthy and colleagues (2008)). The optimisation including AOO as well as cost showed a similar broad pattern to the cost-only model (figure 5.5).

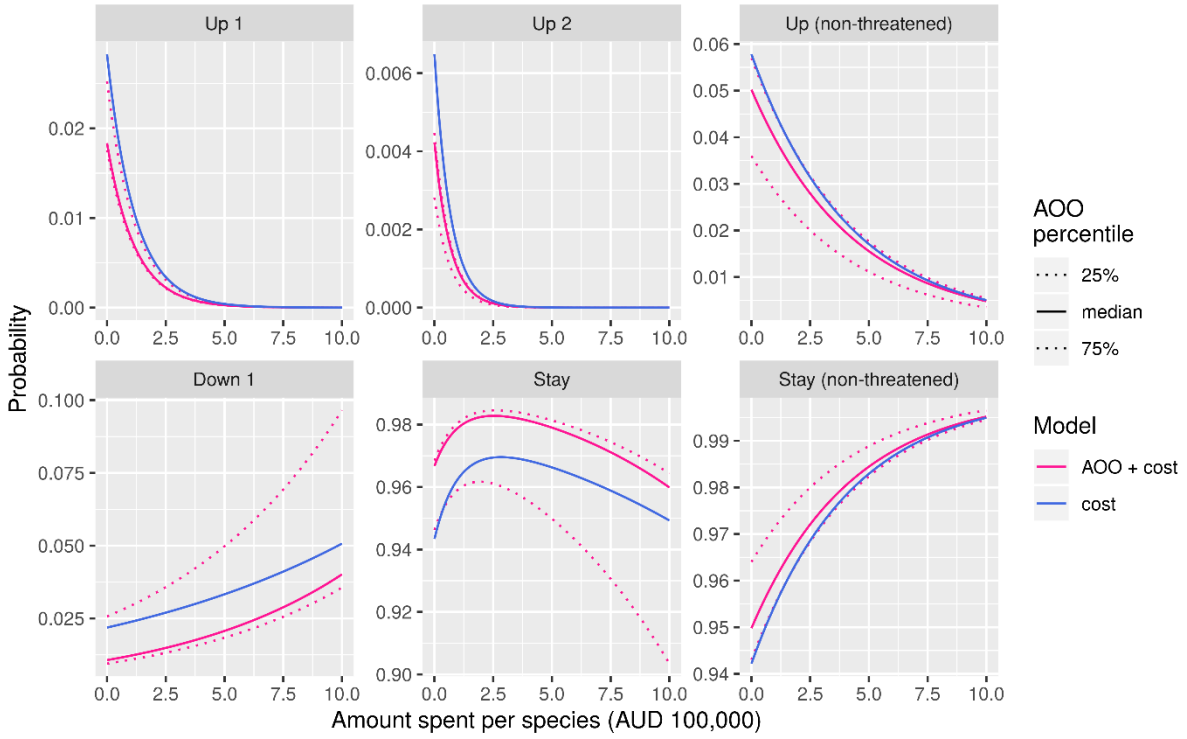

Figure 5.3. Estimated probability of change or stasis in a species' status in a single 8-year period for a given budget from cost-only models (blue), or the cost and AOO model (magenta) for a species with median (solid), and 25th or 75th percentile (dotted) AOO.

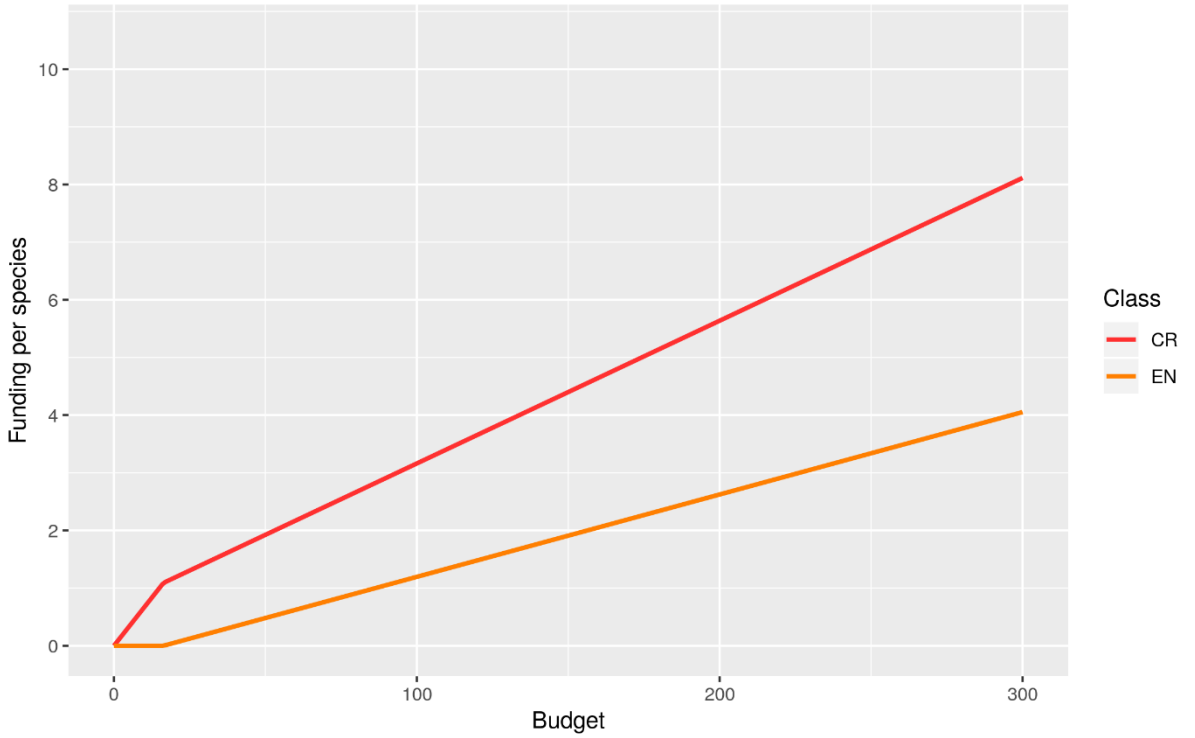

Figure 5.4. Optimal amount of funding per species (y) for a given budget (x) to minimise the number of extinctions over a single 8-year period for critically endangered species (red) and endangered species (orange), based on the cost-only model.

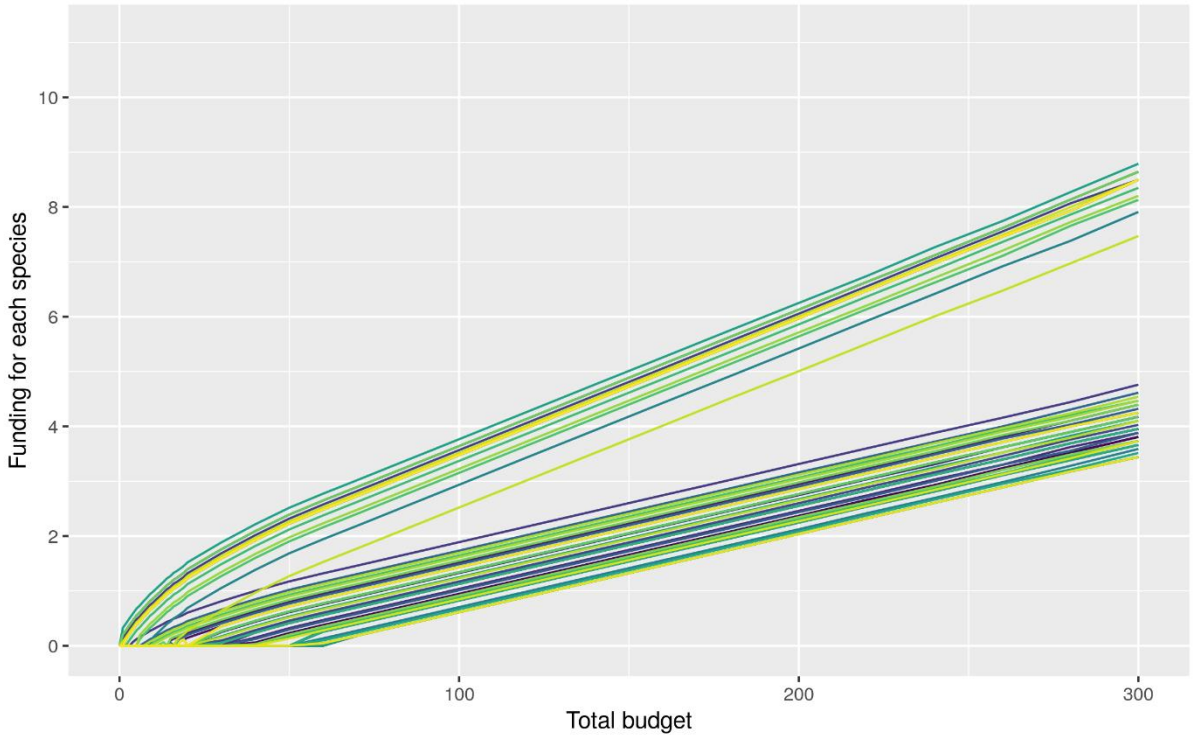

Figure 5.5. Optimal amount of funding per species (y) for a given budget (x) to minimise the number of extinctions over a single 8-year period for each critically endangered or endangered species based on the cost and AOO model. Each line represents a different species.

Comparing the PPP approaches with the optimisation shows that the optimisation is more efficient than the PPP approach regardless of the model used (figure 5.6). This difference is proportionally largest at low levels of funding, and narrows to the point where all PPP projects are "fully funded" (figure 5.6). In the cost-only model, at the point where projects are "fully funded", the proportion of funding and benefits to each class is similar in both the PPP and optimisation approaches (figure 5.7), so therefore the expected benefits are also similar.

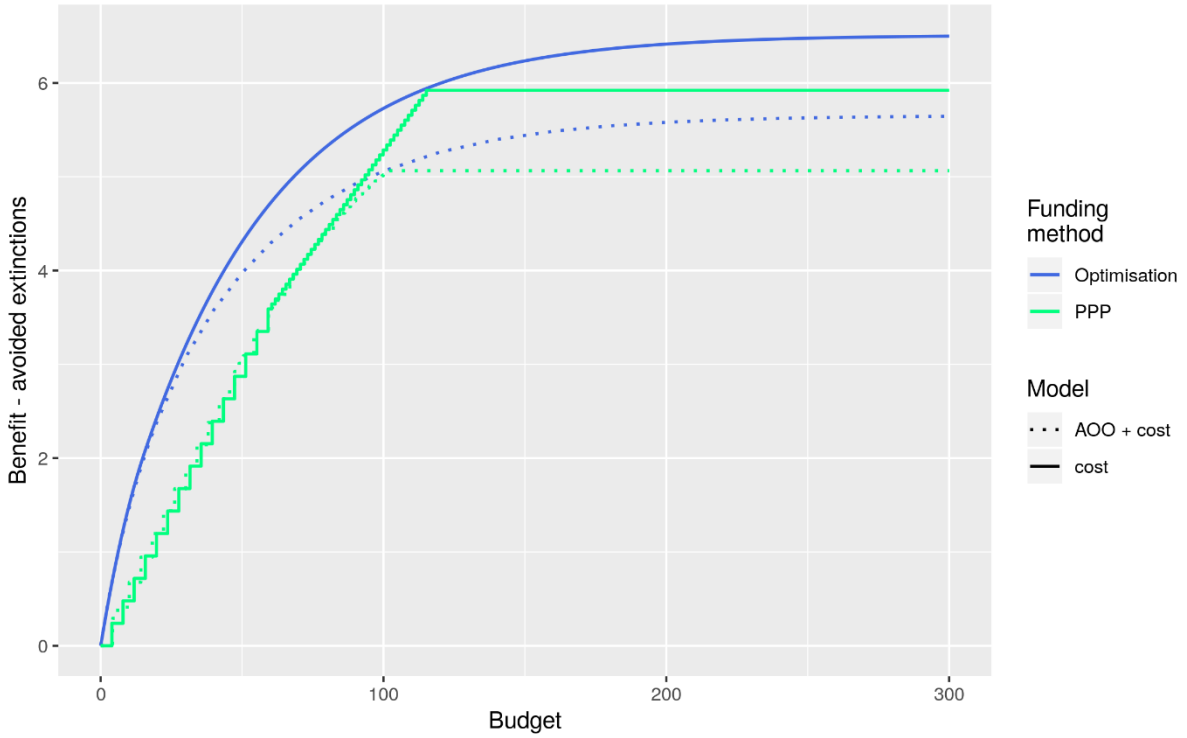

Figure 5.6. Comparison of expected benefit in terms of avoided extinctions over 80 years (y) for a given 8-year budget (x) based on funding using an optimisation (blue) or PPP approach (green) using the cost-only model (dashed line) or AOO plus cost model (solid line).

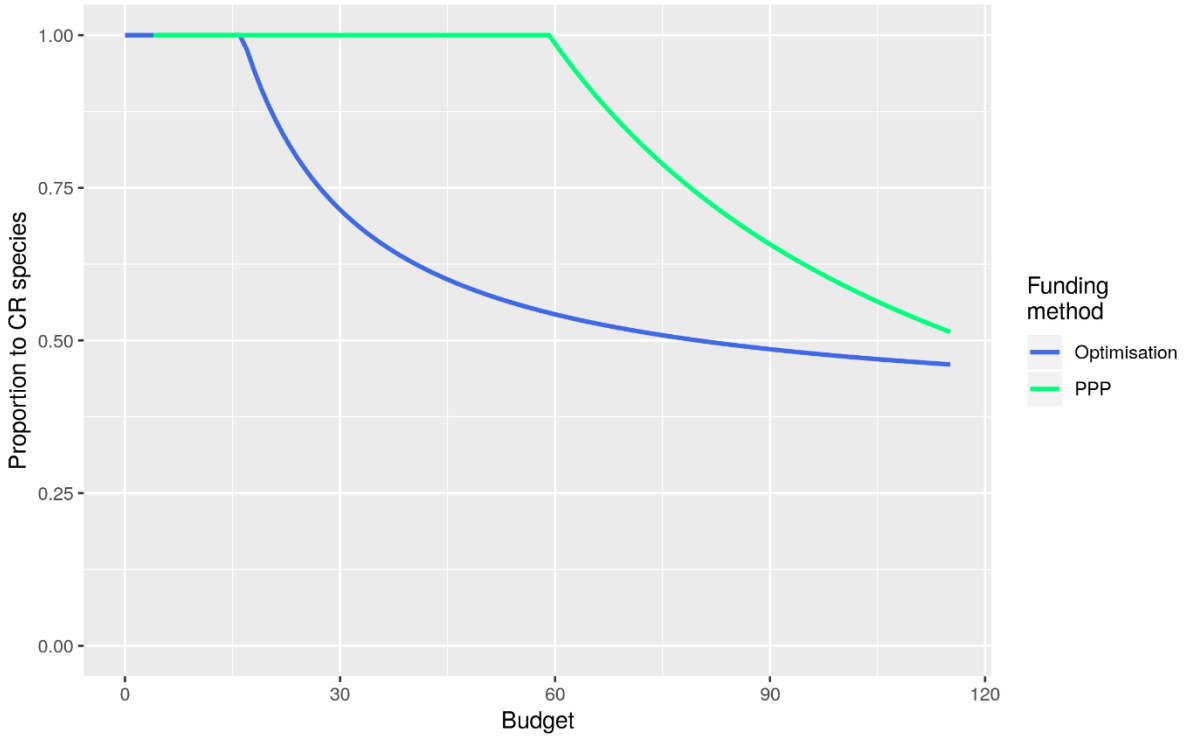

Figure 5.7. Proportion of proportion of funding to critically endangered species (y) for a given budget (x), using an optimisation (blue) or PPP approach (green) based on the cost-only model. Budget extends to the point where all PPP projects are fully funded.

Discussion

It is vital that we find the most efficient methods to allocate scarce conservation funds to achieve the best outcomes possible. We found that that the choice of how to cost-effectively allocate funding to species can greatly affect conservation outcomes, and the difference in outcomes between the PPP and optimisation approaches are largest at low levels of funding (figure 5.6). Our findings have ramifications for the allocation of funding among conservation programmes. Although both approaches aim to maximised return-on-investment, this difference in outcomes is due to the degree of understanding of the relationship between the level of funding and efficiency. The cost-efficiency of conservation management may often be assumed to show diminishing returns (Hone et al. 2017), and has been estimated to this this system previously (McCarthy et al. 2008). It is most beneficial to fund species where the slope of the objective function is steepest, which occurs in this case at the smallest budgets. So if the first few thousand dollars achieve more for a given species that later dollars, then it makes sense that in general one may get the greatest outcomes from spending lots of first dollars, and fewer later dollars. The PPP approach does not allow this however – projects must be fully funded, and added wholly one after another. It therefore should make

intuitive sense that the optimisation approach, which models the relationship between cost-efficiency and the funding spent on a species should be more efficient than the PPP. Both methods aim to maximise return-on-investment, however the optimisation is better equipped to deal with it through leveraging more explicit information on how return relates to investment. This does not invalidate the PPP approach as a systematic means of prioritising funding decisions. However, it is clear that if more information about the relationship between funding and efficiency is available, the use of an optimisation approach can improve outcomes.

This study does not find clear evidence for the effect of a range of species traits and characteristics on cost-efficiency, but this should not necessarily be viewed as evidence of the lack of effect. A number of factors combine in this study to make it difficult to disentangle signal and noise, but the small sample size is of particular concern. Although we consider 260 species — all Australian bird species, subspecies, and populations considered threatened or of conservation concern at the time — few of these actually change status. Those that did chance status are split into separate models for threatened and non-threatened species (table 5.1), and thus the range of values over which we can estimate coefficients for traits and characteristics is small. Furthermore, our response measure in this study, change in IUCN status over 8 years, is a coarse measure, making it difficult to detect modest effects. In addition, the nature of effects of traits on extinction risk may be complex and interacting (Freville et al. 2007). We did not test for complex interactions nor do we have the sample size in this system to explore this further. It seems likely to be work continuing to explore how biological traits and a range of other characteristics (e.g., social, political) effect the efficiency of funding (and therefore conservation activity) to reduce extinction risk.

This study benefited from improved information from that used by previous work on these data by McCarthy and colleagues (2008), though this made conclusions less certain. The resulting retrospective reclassifications of IUCN Red List Status and taxonomic changes changed the estimates of cost-efficiency, from those in the previous work. The smaller number of changes in Red List status however made these estimates less certain, providing fewer data points. In addition, the down-listing of a species from Near Threatened to Vulnerable, suggested that the model for non-threatened species might benefit from the inclusion of two estimated classes of down-listing, rather than a single combined non-threatened to threatened class. Prioritisation of investments may not be a routine univariate return-on-investment exercise – there are a range of ethical and values-based considerations at play too (Wilson & Law 2016). Although these are important considerations in

decision-making, they lie outside of the scope of our study here. There may be methods to explicitly incorporate a range of values through weightings, e.g. for taxonomic groups that have been used with these methods previously (McCarthy et al. 2008; Joseph et al. 2009), and can be incorporated into future approaches that may make better use of the relationship between weighted efficiencies and funding. Our example here is a relatively simple one, and the project prioritisation protocol approach we consider – where all critically endangered and endangered species either receive the same amount within IUCN category as in the cost only model, or with adjustments for AOO in the alternative. There may be much larger, or much smaller differences between the optimisation and PPP approaches in other circumstances, such as where projects differ more greatly in terms of efficiency or total budget. Future research would do well to explore this.

Despite these limitations this research, it highlights a fertile area for improving conservation outcomes, and suggests directions for future research. There is growing evidence that, although doubtless useful, simple cost-efficiency measures may result in cub-optimal conservation outcomes (Hanson et al. 2019). The PPP approach is certainly simpler to apply than the optimisation, and may generally be more easy to obtain suitable data for. However this may be changing as more studies focus on understanding the relationship between funding and conservation outcomes (Gerber 2016; Hone et al. 2017; Waldron et al. 2017), and improved information on the costs of conservation becomes available (Iacona et al. 2018). Although optimisation is a relatively more complex tool, it is still well known in natural resource management, and complexity is not necessarily a barrier to uptake (Gibson et al. 2017), so much as suitability to policy objectives. Enunciation of objectives is key to maximising conservation outcomes (Nicholson & Possingham 2006), and the use of optimisation approaches may be better able to maximise (or minimise) policy objectives. Many recent PPP approaches select complementary projects that may each effect multiple species (Martin et al. 2018). This is a particularly challenging problem, but optimisation algorithms have been shown to improve potential outcomes in the step-by-step selection of projects (Hanson et al. 2019). It seems likely that optimisation using information about the relationship between funding and cost-efficiency as in this study would improve outcomes for multi-species projects as well.

Future applications of funding allocation problems may take a ‘hybrid’ approach if sufficient information on the relationship between funding and cost-efficiency were available for some projects, and not others. Where information is missing, such an approach may assume a linear relationship, or even fit a diminishing exponential relationship if preferred, but use modelled relationships where they are known. Improving understanding of the relationship between funding

level and efficiency can clearly make large improvements to investment outcomes where budgets are limited and should be a priority for future investment schemes. Where further efforts to collect data and improve knowledge are may be warranted, value-of-information type approaches may be useful to determine if such data are worth collecting (Canessa et al. 2015).

We believe that our findings here can be used to improve investment decisions in conservation by leveraging the relationship between efficiency and funding to improve the expected return-on-investment. Improvements can be largest at low levels of funding — this finding is important because many conservation investment portfolios fall well short of the funding levels desired to reach their goals (McCarthy et al. 2012; Wintle et al. 2019). Better use of optimisation approaches such as this may be able to help make up some of the shortfall.

Acknowledgements and Data

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Discussion

The aim of this thesis was to develop and explore the use of quantitative methods to improve decision-making processes in conservation, and therefore achieve better conservation outcomes. I focussed on three key case studies – estimating vulture abundance, decision-making for species discoveries, and optimizing the allocation of funding. Across these case studies, I considered under- or un-used sources of information that can help reduce uncertainty in the decision-making process, provide structure to unclear decision-making processes, and to improve outcomes for conservation.

Dealing with uncertainty is a critical part of effective conservation decision-making (Regan et al. 2005; Nicholson & Possingham 2007). Uncertainty takes a range of forms (Regan et al. 2002), but here I have primarily focused on epistemic uncertainties — uncertain knowledge of the state or structure of the system, such as how many vultures there are in Cambodia. While previous regular monitoring provided baseline minimum population sizes and a guide to possible trends in vulture populations (Clements et al. 2013; Loveridge et al. 2019), these may not be representative of the true population, if for example a large proportion of individuals are not observed, or there is a change in the rates of detection over time. The development of the "simultaneous count model" in Chapter One enabled estimation of the proportion of individuals not detected, and thus improves understanding of the true status of the population. In Chapter Two, I considered how this improved understanding affected inference from monitoring compared with less intensive analyses approaches, and considered the advantages and disadvantages of these approaches. I dealt further with uncertainty in decision-making in Chapter Four. Informants were asked to estimate a range of values related to the costs and benefits of decisions to publicise information on the discovery of species. Current best-practice for expert elicitation exercises like this is to elicit responses covering

the range of possible values (Speirs-Bridge et al. 2010; McBride et al. 2012), resulting in often large uncertainty. In this case we demonstrate methods to overcome these uncertainties to inform decision-making through either accounting for risk preferences, or through the use of stochastic dominance methods. At the core of these approaches to overcoming uncertainty is the use of models to structure and inform the decision-making.

Model-based approaches provide a useful structure to account for uncertainty and clarify the problem at hand (Addison et al. 2013). In the vulture chapters my new model provides a means to understand the key uncertainty in the system: the unknown number of unobserved individuals. In the third and fourth chapters, I develop a model as the structure around which to make explicit trade-offs among costs and benefits, and to clarify the objective of the decision – in this case to maximise persistence. In the last section, chapter five, I compare the potential benefits of two structured approaches: an optimization and a rank-based approach. It is the explicit nature of these structures — the continuous reallocation of funds in the optimization, and the stepwise funding of the project prioritisation protocol — that provides the hypothesis we test and explanation for why the methods perform differently.

Across these approaches I aimed to draw in information that was otherwise available but going to waste, in an effort to clarify the situation and to facilitate better-informed decisions. In the vulture chapters, with several reasonable assumptions allowed estimates of detection probability. This probability enabled estimation of the actual quantity of interest – the abundance of the populations in question — when previously the same data were only able to provide minimum known populations. In the next section of the thesis, I considered the problem of deciding what information, if any, should be publicised when a new species is discovered. It may appear that there is often little or no information at hand to address this decision problem, and thus one must fall back

on intuition and experience to make decisions and weigh costs — in fact I received this exact type of comment from several quarters over the course of investigating the problem. However this experience and intuition is itself a form of information that, unguided, may not be used to its full potential (Hajkowicz 2007; Addison et al. 2013). Although several approaches previously described do provide a decision-making structure for the problem of publicising species discoveries (e.g., Meijaard & Nijman 2014; Tulloch et al. 2018), these are coarse at best, and do not provide a direct means for incorporating uncertainty or specific data. Through conducting elicitation and providing a formal model structure to use this information, I enabled a fuller exploration of the range of possible outcomes from the decision, that could empower decision-makers to act according to their own risk tolerance rather than a prescribed framework. In the final section of the thesis I examined whether a range of additional data can improve optimal funding allocations. This was perhaps a less successful endeavour than the previous chapters — for although the framework to include these data was reasonable, the few data points available due to the small number of species changing IUCN Red List status prevented the uncovering of any additional benefits in this particular case. However, this is unlikely to be true in other cases, and indeed there is extensive scope to take this approach to other optimisation problems in conservation.

Like much research, the findings in this thesis raised new questions and suggest new areas for research. The 'simultaneous count model' developed in the first chapter invites a range of future research questions about its performance under a variety of conditions beyond those examined in my simulations, such as changing population growth rates or varying probability of detection. Other important explorations would include accounting for possible covariation in abundance and detection, or the implications of failures to meet certain key assumptions in the model like as simultaneity and avoiding the double-counting of individuals. There are also a range of difficulties with parameter identifiability in related N-mixture models (Barker et al. 2018), and it is not clear the

degree to which these concerns may apply to this model too. A more general question about the model, as raised in chapter two, is that given the specialised nature of hierarchical Bayesian modelling, will this preclude use of this modelling approach? And can the model be extended into more accessible frameworks?

The trade-off between the effort or technical training and skill needed to apply a method, and the utility of results also played out in the second section of the thesis. Although I provided a framework to compare and trade-off costs and benefits, did the effort and knowledge required to do this outweigh the ease of using unaided intuition? That several other frameworks have been developed to address this problem of public release of information (Meijaard & Nijman 2014; Lindenmayer & Scheele 2017; Tulloch et al. 2018) suggests that there is indeed interest in using these tools. The framework I provided may not be necessarily well suited to all applications, and the development of alternative decision-making models for the broader problem of public accessibility of sensitive biodiversity data is an obvious target for of potential future research.

In the last section of the thesis, I demonstrated that optimisation approaches can outperform the popular step-wise PPP approaches in the expected conservation outcomes. The example under consideration was compelling, though limited in scope in that the only alternatives were species either classified as Endangered and Critically Endangered under IUCN Red List criteria. An interesting extension of this work may be to apply the comparison of an optimisation approach to a diverse project prioritisation list of projects or species (e.g., as found in Joseph et al. 2009; Brazill-Boast et al. 2018). The difficulty in that case is likely to be understanding the shape of the response function between funding level and outcome for each project on the list, however there may be means to estimate this from previous conservation actions, or simulate a range of plausible response functions like diminishing return curves or step functions.

Conservation action and conservation science is chronically underfunded — there are many worthy candidates for the shallow resource pool, and this competes with many other human demands. It is likely in my lifetime that there will never be enough resourcing available to halt, let alone reverse, the global decline of biodiversity. My approach in this thesis was to explore how to wring more information out of existing data to reduce uncertainty, improve decision-making and hope to generate better conservation outcomes with the resourcing to hand. I have found fertile ground for this – it appears that there is indeed much more we can learn from the information we have. But this is not a free lunch – work needs to be done to uncover opportunities, and technical skills are often needed to make best use of them. We also must often make a set of assumptions in order to gain our results, assumptions that may be reasonable or not. Understanding the influence of these assumptions on the decisions will be important – unreasonable or unmet assumptions may not lead to better decisions.

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