Adaptive management improves decisions about where to search for invasive species

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Abstract

Invasive species managers must decide how best to allocate surveillance and control effort through space. Doing this requires the predicted location of the invasive species, and these predictions come with uncertainty. While optimal surveillance designs have been developed for many invasive species, few have considered uncertainty in species distribution and abundance. Adaptive management has long been recommended for managing natural systems under uncertainty, but has not yet been applied to searching for invasive species. We investigate whether an adaptive management approach can increase the number of individuals found and removed, as compared to a naïve allocation of search effort or “common sense” rules of thumb. We develop a simple illustrative model where search effort must be allocated to maximise plant removals across two sites in which species abundance is unknown. We tested the performance of both passive and active adaptive strategies through simulation. There are substantial benefits to employing an adaptive strategy, although the two forms of adaptive management performed similarly. The optimal active adaptive strategy is complex to calculate, whereas the passive strategy could be calculated for a large number of sites using widely accessible spreadsheet software. We therefore recommend the passive practical strategy for achieving approximately the same outcome while being much more problems in a way that is accessible to managers.

Keywords: abundance estimation, imperfect detection, optimisation, search effort, surveys, weeds.
1 Introduction

A primary concern for invasive species managers is how best to allocate surveillance and control effort through space (Chadès et al. 2011; Epanchin-Niell et al. 2012; Hauser and McCarthy 2009; Regan et al. 2011). Achieving this requires the predicted location of the invasive species, now and/or in the future. Expert opinion (Williams et al. 2008), species distribution models that correlate occurrence with environmental attributes (Elith et al. 2010; Guisan et al. 2013), or other spatial population and spread models (Adams et al. 2015; Caplat et al. 2012; Coutts et al. 2011; Gallien et al. 2010) can provide these predictions.

However these predictions are made, they will come with some uncertainty. Expert judgements can be biased, although bias can be minimised by using structured elicitation processes (Martin et al. 2012; Sutherland and Burgman 2015). Predictive models are simplifications that will imperfectly represent biological relationships (Levins 1966). In addition, imperfect detection means that occupancy or abundance cannot be known perfectly, even if a landscape were comprehensively surveyed (Chen et al. 2013; Garrard et al. 2008; MacKenzie and Kendall 2002; Moore et al. 2011; Royle et al. 2005). If we ignore this uncertainty and treat our point predictions as the true species distribution, our survey designs may be suboptimal. This increases the risk of missing infestations where they occur, and applying excessive effort where they do not.

While optimal surveillance designs have been developed for a wide range of species invasions, few consider uncertainty in species distribution and abundance. Methods for optimally allocating search effort generally assume that occurrence probabilities are accurately predicted by models (Chadès et al. 2011; Hauser and McCarthy 2009; Regan et al. 2011) or species abundance is uniform across the landscape (Epanchin-Niell et al. 2012; Rout et al. 2014; Rout et al. 2011). Alternatively, search effort can be allocated to maximize the probability of achieving an acceptable outcome in the face of uncertainty (McCarthy et al. 2010). None of these approaches aim to reduce uncertainty about abundance in different locations. A notable exception is Baxter and Possingham (2011), who modelled the Receiver Operating Characteristic curve of an uncertain distribution map and calculated the trade-off between searching for the species and reducing uncertainty in the distribution map. They found that under long management time frames, initial investment in learning about species distribution increased the likelihood of eradication. Acknowledging and planning for uncertainty in distribution and abundance when designing surveys can, therefore, improve invasive species management outcomes.

Adaptive management is a solution to the problem of managing systems under uncertainty (Parma et al. 1998). This approach to management not only acknowledges uncertainty and its effect on decision-making, but also seizes opportunities to reduce this uncertainty (Walters 1986). The two types of adaptive management, passive and active, both use the information learned through management to improve future decision-making. Active adaptive management involves planning ahead for future learning opportunities, and may involve decisions that sacrifice current management performance in return for information that will improve management performance in the future (Williams 2001). In contrast, passive adaptive management takes the best action at each time point given the current state of knowledge, updating that knowledge after the results of the action are observed.

Optimal adaptive management theory has been applied to harvesting of fish (Walters 1981; Walters et al. 1993; Walters and Hilborn 1976) and waterfowl (Nichols et al. 1995; Williams and Johnson 1995), vegetation restoration (McCarthy and Possingham 2007), reintroduction
(McCarthy et al. 2012; Rout et al. 2009), metapopulation management (Southwell et al. 2016), and threatened species management (Chadès et al. 2012; Moore and Conroy 2006). While it is potentially useful for invasive species management (Shea et al. 2002), there have been no applications thus far.

This paper investigates whether adaptive management is a useful approach for spatially allocating search and management effort for invasive species under uncertainty. We outline a simple illustrative problem of allocating effort between two sites of uncertain habitat suitability for a species, with the aim of finding and removing as many individuals as possible. Searching a site not only finds individuals, but also increases confidence in estimates of total abundance at that site, which should in turn improve future allocation decisions. Although searching for invasive plants usually occurs across a much greater number of sites, condensing this to the simplest two-site problem is necessary to find the optimal active adaptive management strategy. We investigate the extent to which active and passive adaptive management approaches can increase the number of individuals found and removed, as compared to a naïve allocation or common sense rules of thumb. We then discuss the implications for landscape-scale search and removal of invasive plants.

2 Material and methods
2.1 Optimisation framework

We considered two sites to be surveyed for a plant population. Across a series of $T$ surveys, a searcher aims to find as many plants as possible. However, the abundance of plants in each site $i$ is unknown, and could be between 0 and $N_{i,\text{max}}$ individuals. We developed an optimisation model to find the best way to allocate search effort between the two sites.

Each survey ($t = 1, ..., T$) has a budget of effort $B_t$ to be allocated between the sites. The decision variable is the amount of effort allocated to site 1 ($x_{1,t}$), with the remainder allocated to site 2 ($x_{2,t}$). The effort allocated to site $i$ will determine the probability of detecting each individual in that site:

$$p_{i,t} = 1 - e^{-\lambda_i x_{i,t}}, \quad (1)$$

where $\lambda_i$ is the detection rate at site $i$. The probability of detection is the same for each individual in a site, and is independent of the detection (or non-detection) of other individuals in space and time. This exponential detection-effort curve is based on predictions from search theory (Frost and Stone 1998), assuming that individuals are distributed throughout the sites and are encountered randomly. (If individuals are clustered, detection rates can increase with abundance (McCarthy et al. 2013)). This functional form is supported by the few studies that have measured the detection-effort relationship in the field (Chen et al. 2009; Garrard et al. 2008; Moore et al. 2011).

We assume that surveys are carried out close enough in time that there is no reproduction or mortality; thus only the detection and removal of individuals affects the plant abundance in each site. The number of plants newly found in site $i$ during survey $t$ ($c_{i,t}$) can be used to estimate the number of plants in each site before surveys began ($N_{i,0}$). The number of undetected individuals remaining after survey $t$ ($N_{i,t}$) can then be estimated from the estimate of $N_{i,0}$ and the number of individuals found. Found individuals are marked and/or removed and thus do not contribute to detections in future surveys.
Before surveys begin, we assume that our prior belief regarding plant abundance at site \(i\) follows the distribution:

\[
Pr\left(N_{i,0} = n | \alpha_i, \beta_i \right) = \begin{cases} 
\frac{\left( \alpha_i + n \right)^{n} e^{-\lambda_i n}}{\sum_{k=0}^{\Psi_i} \left( \alpha_i + k \right)^{k} e^{-\lambda_i k}} & \text{for } n = 0, 1, 2, ..., N_{i,\text{max}}^i 
\end{cases}
\]

(2)

where parameters \(\alpha_i\) and \(\beta_i\) determine the shape of the distribution. Parameter \(\alpha_i \geq 0\) is a counting number and is measured on the same scale as plant abundance; it is indicative of the distribution’s centre of mass. Parameter \(\beta_i \geq 0\) is any positive real number and is measured on the scale of search effort. When \(\alpha_i = \beta_i = 0\) we recover a discrete uniform distribution over \(n = 0, 1, 2, ..., N_{i,\text{max}}^i\).

We can update our understanding of plant abundance after each survey using effort data \((x_{i,j}, j = 1, 2, ..., t)\), detection data \((c_{i,j}, j = 1, 2, ..., t)\) and Bayes’ theorem. At any time \(t\), the number of plants detected \(c_{i,t}\) is drawn from a binomial distribution with probability of success \(p_{i,t}\) (eqn 1) and number of trials \(N_{i,0} - \sum_{j=1}^{t-1} c_{i,j}\) (i.e. the number of plants not yet detected and removed from the site).

We find that after survey \(t\), the posterior probability distribution for the initial plant abundance in site \(i\) is given by:

\[
Pr\left(N_{i,0} = n | \alpha_i, \beta_i, C_{i,t}, X_{i,t} \right) = \begin{cases} 
\frac{\left( \alpha_i + n \right)^{n} e^{-\lambda_i (X_{i,t}) n}}{\sum_{k=0}^{\Psi_{i,t}} \left( \alpha_i + C_{i,t} + k \right)^{k} e^{-\lambda_i (X_{i,t}) k}} & \text{for } n = C_{i,t}, C_{i,t} + 1, C_{i,t} + 2, ..., N_{i,\text{max}}^i 
\end{cases}
\]

(3)

where \(C_{i,t} = \sum_{j=1}^{t} c_{i,j}\) is the total number of plants found in site \(i\) across the first \(t\) surveys, and \(X_{i,t} = \sum_{j=1}^{t} x_{i,j}\) is the total time spent searching site \(i\) (see Appendix A for derivation).

The probability distribution for the number of undetected plants remaining in site \(i\) after survey \(t\) is then:

\[
Pr\left(N_{i,t} = n | \alpha_i, \beta_i, C_{i,t}, X_{i,t} \right) = \begin{cases} 
\frac{\left( \alpha_i + C_{i,t} + n \right)^{n} e^{-\lambda_i (X_{i,t}) n}}{\sum_{k=0}^{\Psi_{i,t}} \left( \alpha_i + C_{i,t} + k \right)^{k} e^{-\lambda_i (X_{i,t}) k}} & \text{for } n = 0, 1, 2, ..., N_{i,\text{max}}^i - C_{i,t} 
\end{cases}
\]

(4)

(see Appendix A for derivation). We can then calculate the expected number of undetected plants remaining in site \(i\) after survey \(t\) as:

\[
E\left(N_{i,t} | \alpha_i, \beta_i, C_{i,t}, X_{i,t} \right) = \sum_{n=0}^{N_{i,\text{max}}^i - C_{i,t}} nPr\left(N_{i,t} = n | \alpha_i, \beta_i, C_{i,t}, X_{i,t} \right).
\]

(5)

Passive adaptive management aims to maximise expected performance given current levels of uncertainty, while active adaptive management aims to maximise long-term performance while acknowledging changes in uncertainty. Active adaptive management can therefore involve sacrificing short-term performance to gain information that will allow better
performance in the long-term. Under passive adaptive management, survey effort at time \( t \) is allocated to maximise the expected number of plants found in that survey. We find the best search allocation for each state of the system, where a state refers to each possible combination of the number of plants previously found in each site \( (C_{1,t-1}, C_{2,t-1}) \), the previous effort allocation \( (X_{t-1}) \), and the time step \( (t) \). The value of the best search allocation for each state is calculated as:

\[
V(C_{1,t-1}, C_{2,t-1}, X_{1,t-1}, X_{2,t-1}, t) = \max_{0 \leq x_{i,t} \leq B_t} \left( E(c_{i,t} | \alpha_1, \beta_1, \alpha_2, \beta_2, C_{1,t-1}, X_{1,t-1}) + E(c_{2,t} | \alpha_2, \beta_2, C_{2,t-1}, X_{2,t-1}) \right)
\]

(6)

where \( X_{2,t-1} = \sum_{j=1}^{t-1} B_j - X_{1,t-1} \).

\[
E(c_{i,t} | \alpha_i, \beta_i, x_{i,t}, C_{i,t-1}, X_{i,t-1}) = \sum_{m=0}^{N_i^{\text{max}} - c_{i,t-1}} \sum_{n=0}^{N_i^{\text{max}} - c_{i,t-1}} m \Pr(c_{i,t} = m | x_{i,t}, N_{i,t-1} = n) \Pr(N_{i,t-1} = n | \alpha_i, \beta_i, C_{i,t-1}, X_{i,t-1}),
\]

(8)

and

\[
\Pr(c_{i,t} = m | x_{i,t}, N_{i,t-1} = n) = \left( \frac{n}{m} \right) p_{i,t}^m (1 - p_{i,t})^{n-m} = \left( \frac{n}{m} \right) (1 - e^{-\lambda_i x_{i,t}})^m (e^{-\lambda_i x_{i,t}})^{n-m}.
\]

(9)

Data from the results of each survey \( (c_{i,t}, x_{i,t}) \) are then used to update the previous effort allocation \( (X_{i,t}) \) and previous finds \( (C_{i,t}) \), and this informs how search effort is allocated in the subsequent survey. Learning can therefore happen incidentally as a result of management actions, but is not planned for as part of the optimal search action. Under active adaptive management, we may search in a site with the purpose of gaining more information about abundance, if that information will allow us to find more individuals in the future. For example, searching a site for some time without finding any plants may signal that there are few remaining plants to be found. The aim is to maximise the total number of plants found across the series of surveys. The value function for the final survey is therefore:

\[
V(C_{1,T}, C_{2,T}, X_{1,T}, T) = C_{1,T} + C_{2,T}.
\]

(10)

We used stochastic dynamic programming (SDP) to solve for the optimal active adaptive strategies in each time step (Bellman 1957). For each survey prior to the final time step, all possible decisions \( (x_{1,t}, t = 1, 2, \ldots, T) \) are evaluated for every state, that is, every combination of possible previous effort allocations \( (X_{1,t-1}) \) and number of plants found \( (C_{1,t-1}, C_{2,t-1}) \). The dynamic programming equation, which calculates the value of the best option for each state at each time step, is:

\[
V(C_{1,t-1}, C_{2,t-1}, X_{1,t-1}, X_{2,t-1}, t) = \max_{0 \leq x_{i,t} \leq B_t} \sum_{c_{1,t}=0}^{N_1^{\text{max}} - c_{1,t-1}} \sum_{c_{2,t}=0}^{N_2^{\text{max}} - c_{2,t-1}} \Pr(c_{1,t} | \alpha_1, \beta_1, x_{1,t}, C_{1,t-1}, X_{1,t-1}) \Pr(c_{2,t} | \alpha_2, \beta_2, x_{2,t}, C_{2,t-1}, X_{2,t-1}) \times V(C_{1,t-1} + c_{1,t}, C_{2,t-1} + c_{2,t}, X_{1,t-1} + x_{1,t}, t + 1)
\]

(11)

where the probability distributions for number of finds at each site are calculated using the approach given in equations (8) and (9).
2.2 Case study

To illustrate the optimisation approach we used detection estimates derived from a search experiment for Australian native seedlings (McCarthy et al. 2013). The experiment took place in a grassland area of Royal Park, a 170-ha park in inner suburban Melbourne, Australia. Nine 15 x 15 m quadrats were planted with Lomandra longifolia at randomly assigned locations and densities of 2, 4, 10 or 30 individuals per quadrat. Participants were asked to search each quadrat for 15 minutes, and record the time of their first and second detections for the species. The 14 searchers each had between 2 and 30 years of plant survey experience.

We used the mean detection estimates for the species (λ = 0.07392, McCarthy et al. 2013) and additionally considered a hard-to-search site with a halved detection rate.

We considered a scenario with 10 surveys (T = 10), each consisting of two minutes of search time that must be allocated between two sites (Bi = 2) in increments of one minute (possible decisions x1,t = 0, 1, 2, where x2,t = B - x1,t). We explore cases where our prior information regarding plant abundance at each site is completely uninformative (discrete uniform over [0, N\text{max}], α = β = 0 in equation 2) or partially informative (see Appendix B for specific values).

To predict the performance of optimal adaptive strategies, we simulated their implementation in scenarios where the actual number of plants in each site varied between 0 and N\text{max} = 30 (961 scenarios). We generated 1000 simulations, recording for each simulation the total number of plants that had been found at the end of the ten surveys.

As a basis for comparison, we simulated the performance of a uniform allocation strategy, which is a strategy of always splitting search effort equally between the sites. We also assessed the performance of two other rules of thumb for search effort allocation. The first was to allocate all search effort to the site where most plants have already been found (i.e., with the largest C). The second was to allocate all search effort to the site where most plants have been found per minute of searching (i.e., largest C/X). For both rules of thumb, search effort was evenly split if these metrics were equal between the sites.

3 Results

3.1 Optimal adaptive strategies

The prevalence of different search allocations (i.e., the percentage of states for which each allocation is optimal) differed under passive and active adaptive management (Figure 1). In the first survey (t = 1) there has been no prior searches of either site, so there is a single possible state (X1 = 0, C1 = 0, C2 = 0). Under passive adaptive management with uninformative priors, the optimal allocation for this state was to split search effort equally between the two sites. Splitting search effort is expected to yield the most finds in the first survey. In contrast, under active adaptive management it was optimal to allocate all search effort to one site only, although it did not matter which site this was. Concentrating effort in a single site will increase the expected number of plants to be found by the end of the ten surveys, showing there was a benefit to the extra information gained about the density of plants in that site.

The number of states increased with the number of surveys undertaken because the number of previous search allocations (X1,t-1) and previous numbers of plants found (C1,t-1, C2,t-1) expanded with each survey (see Figure 1 caption for the number of states before each survey). From the second to the ninth survey (t = 2 to 9), it was more often optimal to split...
search effort equally between sites under active adaptive management than under passive adaptive management. It was also more common under active adaptive management for more than one allocation to be equally optimal. For example, in the second survey there were 30 states for which searching a single site and splitting effort between sites were equally good decisions under active adaptive management.

More differences in best allocation decisions between passive and active adaptive management occurred early in the decision time frame than later. This reflects the short- and long-term focus of passive and active adaptive management, respectively. Passive adaptive management maximises the immediate number of finds, while active adaptive management maximises the total number of finds across the entire survey period. As more surveys were carried out and fewer plants remained, the active adaptive objective became increasingly similar to the passive adaptive objective. In the final survey \((t = 10)\), the objectives of the two approaches were identical, and thus so were the corresponding optimal strategies.

### 3.2 Benefit of searching adaptively

We examined the performance of each strategy (passive adaptive, active adaptive, and two rules of thumb) in terms of the total number of plants found over ten surveys. To provide context, we also assessed the performance of a uniform allocation of search effort, where the search budget is always divided equally between the two sites. We calculated the benefit of each search strategy as the improved performance compared to uniform allocation.

Passive and active adaptive management provided similar benefits, and they consistently outperformed other search rules across a range of scenarios (Appendix B). Under uninformative uniform prior distributions for abundance at each site, passive adaptive management found an average of 5.1% more plants than uniform allocation, while active adaptive management found an average of 5.5% more plants. Both rules of thumb performed worse than uniform allocation, finding an average of 6.5% (rule 1) and 2.6% (rule 2) fewer plants. Uniform allocation of effort is a particularly poor strategy when there is some prior belief that one site has a low plant abundance (e.g. \(\alpha_2 = 0\) and \(\beta_2 > 0\) in Appendix B).

Adaptive management can yield up to 22% more finds, while the rules of thumb also offer benefits of up to 17%.

All five search strategies performed best when there were many plants in both sites (Appendix C), but the benefit of the adaptive strategies and rules of thumb over uniform allocation increased with the difference in plant abundance between sites (Figure 2, Appendix D). In these abundance scenarios, the rules of thumb performed marginally better than the adaptive approaches, delivering a slightly higher benefit. However, both rules of thumb performed much worse than uniform allocation across a large number of scenarios where the number of plants in each site was approximately equal (Figure 2, Appendix D). This was markedly worse than both adaptive strategies, which performed the same or slightly worse than uniform allocation when abundance was approximately equal at both sites. There was a marked exception to this performance using a passive adaptive search strategy when one site is thought to have low plant abundance but actually has high abundance (Figure D1); without active adaptive probing it is possible that these many plants will not be discovered. Nevertheless, this outcome is relatively improbable and the prior-averaged passive adaptive performance still exceeds the uniform allocation and two rules of thumb.
Examining individual simulation trajectories can reveal the reasons behind similarities and differences in performance. In a scenario with 30 plants in each site, the passive and active adaptive strategies performed similarly by mostly splitting effort equally between sites. The passive adaptive strategy began by splitting effort equally (Figure 3a), while the active adaptive strategy allocated all effort into site 1 and subsequently all effort into site 2 (Figure 3b), reflecting the different strategies apparent in Figure 1. In contrast, the rules of thumb mostly allocated effort to a single site (Figure 3c,d), a disadvantage in this case given that the number of plants in each site was equal. The adaptive strategies provided more precise estimates of the number of plants remaining across both sites, although all methods underestimated the actual number (Figure 3).

In a scenario with 30 plants in one site and 0 in the other, the rules of thumb performed better than the adaptive strategies (Figure 4). The adaptive strategies wasted some effort searching the empty site, with the active adaptive strategy spending the most time there (Figure 4a). In contrast, both rules of thumb allocated minimal effort to the empty site, splitting effort equally in the first survey and subsequently allocating all effort to the occupied site (Figure 4b). However, the adaptive strategies again gave more precise estimates of the number of plants remaining, although the 95% credible intervals encompassed the true number for all methods.

The ranking of search strategies is unchanged when the two sites are known to have different detection rates (Appendix B). The adaptive strategies explicitly accommodate detection rate in their predictions of future plant finds, while the rules of thumb receive implicit feedback on detection rate via the number of plants found (although they cannot distinguish detection rate and abundance). When one site is known to have a lower detection rate, it has less influence on overall performance under all non-uniform strategies because fewer plants are likely to be found and little search time is allocated there (Figures C2, D1).

In summary, the adaptive strategies can be outperformed by the rules of thumb or even uniform allocation in specific situations. The two rules of thumb mostly allocate all effort to a single site, which is optimal if there is a large difference between the number of plants in each site. Conversely, uniform allocation is optimal if the number of plants in each site is equal. However, the rules of thumb and uniform allocation can perform very poorly outside of these specific situations. The ability to learn means that the adaptive strategies perform well across the entire range of the numbers of plants in each site, which is an advantage given that this quantity is unknown.

4 Discussion

Our study demonstrates that adaptive management can help allocate search and management effort for invasive species. We found clear benefits to employing an adaptive search strategy over uniform search effort allocation or simple rules of thumb when species abundance and distribution are uncertain, and when aiming to maximise the number of individuals found and removed. However, the benefits of adaptive management will depend on the management objective. A different objective, for example, aiming to maximise certainty of species abundance, could alter optimal strategies (Probert et al. 2011) and the benefit of an adaptive approach. For invasive species management, it can be advantageous to develop ‘proof of absence’ in order to delimit a population (Hauser et al. 2016) or rapidly detect and remove new or outlier low-abundance infestations to contain impacts (Chadès et al. 2011). Our chosen objective of maximising removals implicitly assumes that each individual causes...
equal damage; it is better suited to impact-mitigation scenarios where the species has saturated its local range (e.g. Giljohann et al. 2011).

Several previous adaptive management studies have found optimal passive and active adaptive strategies to be similar (Johnson et al. 2002; McCarthy and Possingham 2007; Moore and McCarthy 2010; Moore et al. 2008). In this management scenario, we found marked differences in optimal active and passive adaptive strategies (Figure 1), and yet little difference in the performance of these strategies. This is not unprecedented. Other studies have found little difference in the performance of optimal passive and active adaptive strategies (Johnson et al. 2002; McCarthy and Possingham 2007; Rout et al. 2009; Smith and Walters 1981; Walters 1981), even when the strategies themselves are quite different (Rout et al. 2009).

Active adaptive management is characterised by strategies that sacrifice short-term performance for information that will improve management performance in the long-term. Differences in the optimal passive and active adaptive strategies indicate that these sacrifices do exist within this management scenario. For example, investing all initial search effort in a single site to learn about abundance there (Figure 1) sacrifices short-term performance if that site is empty (Figure 4). Yet, a similarity in the performance of active and passive adaptive approaches means that the short-term sacrifice is too great or the long-term benefit of additional information is too little to increase performance overall. An outcome similar to an active adaptive management approach can be achieved simply by acknowledging uncertainty and learning from the results of actions taken, i.e., passive adaptive management.

The similarity in performance of the two adaptive strategies has practical benefits. The optimal active adaptive strategy is complex to calculate, requiring the time, effort, and skills to write an optimisation program. This is not necessary for the passive adaptive strategy. As it only looks ahead one time step, the passive adaptive strategy can be calculated using a single equation (eqn. 3). Therefore, although an active adaptive strategy is often considered the gold standard for management, for this search scenario we recommend a passive adaptive strategy for achieving approximately the same outcome while being much more practical to implement. An optimal passive adaptive strategy could be calculated for numerous sites using programmable spreadsheet software with optimisation capabilities. This development would facilitate application to much larger and more realistic search problems and improve the technique’s accessibility to managers (Giljohann et al. 2011; Hauser 2009; Hauser et al. 2016; Moore et al. in press).

Aspects of this problem were simplified to allow us to calculate exact optimal active adaptive strategies. For tractability, we assumed a definite maximum to the number of plants that could be in each site. While it is feasible to estimate such a maximum given the area of the site and the minimum area occupied by an individual, for most real problems this number will be much larger than our limit of 30 individuals. Finding optimal active adaptive strategies given a larger maximum number of plants per site poses problems computationally because of the well-known ‘curse of dimensionality’ in SDP (Nicol et al. 2010). For example, increasing the number of plants from 30 to 40 in each site increases the number of states at \( t = 10 \) from 16,399 to 28,659. However, larger problems such as this could be feasible to solve approximately (Chadès et al. 2016; Nicol and Chadès 2011; Nicol et al. 2010). In contrast, a passive adaptive approach can easily accommodate a larger maximum number of plants per site, again making it a more practical approach for realistic search problems.
We used a general prior distribution form to describe the abundance of plants at each site before searching began (equation 2). Its parameter values could be informed by species distribution models or other sources of information about potential plant abundance at a site. Our Bayesian updating approach (equation 3) allows a seamless integration of knowledge where a manager initially allocates search effort based on a habitat suitability map, but wishes to learn about the accuracy of their map as management progresses and adjust their future allocation accordingly. Our conjugate distributions (equations 2 and 3) allow for compact storage of knowledge where a small set of parameters \( \{ \alpha_i, C_{it}, \beta_i + X_{it} \} \) can be carried through the active adaptive optimisation as state variables, fully characterising the likelihood of each possible site abundance (Chadès et al. 2016).

Detection rate affects the capacity to find plants and thus the overall performance of management. Detection rates can differ among sites with different terrain, and this affects the optimal allocation of resources among sites. We used the mean estimates of detection rate for \textit{L. longifolia} and did not acknowledge uncertainty around these estimates. Estimating detection rates directly can be resource-intensive and will rarely resolve all of this parameter uncertainty (Hauser et al. 2015). Previous work has considered how accounting for uncertainty in detection rates changes search strategies (McCarthy et al. 2010) or how to optimise search effort when detection rates vary (Moore et al. 2014). Adaptively searching for an invasive species with an uncertain detection rate, perhaps in addition to an uncertain distribution, is a more realistic management scenario and an exciting avenue for future research.

Our simple illustrative model has clearly demonstrated benefits in applying a formal adaptive management framework to invasive species survey design. Although a complex active adaptive strategy may not be necessary to maximise removals, acknowledging uncertainty during decision-making and learning is highly valuable. We hope this analysis will pave the way for future applications of adaptive surveillance strategies.

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Figure legends

Figure 1. The percentage of states for which each decision is optimal through time under passive (left column in each pair) and active (right column in each pair) adaptive management. Both sites use the estimated *Lomandra longifolia* detection rate, and have prior belief in plant abundance that is discrete Uniform[0, 30]. The number of states increases with each survey undertaken; a general formula to calculate the number of states is:

\[ N_{states} = N_1^{max} + 1 + N_2^{max} + 1 + ((B(t - 1) - 1)(N_1^{max} + 1)(N_2^{max} + 1)) \]

Figure 2: The benefit of each strategy over uniform allocation of search effort for *Lomandra longifolia*, in terms of the expected number of individuals found over ten surveys. Prior belief in plant abundance is discrete Uniform[0, 30] for both sites. For each true abundance state, we calculated the mean benefit from 1000 simulations. Rule of thumb 1 is to search the site where the most plants have already been found. Rule of thumb 2 is to search the site where the most plants have been found per minute searched.

Figure 3: Example trajectories under a single simulation when there are 30 plants in each site, for a) passive adaptive management, b) active adaptive management, c) rule of thumb 1, and d) rule of thumb 2. Each simulation used the same seed for random number generation. This means that given the same allocations, the number of plants found will be the same in each simulation. Markers show the optimal search allocation (right axis), lines show the number of plants remaining (left axis, solid = actual number, dashed = estimated mean given the total number found and total search effort, dotted = estimated 95% credible intervals given the total number found and total search effort).

Figure 4: Example trajectories under a single simulation when there are 0 plants in site 1 and 30 plants in site 2, for a) passive adaptive management, b) active adaptive management, c) rule of thumb 1, and d) rule of thumb 2. Each simulation used the same seed for random number generation. This means that given the same allocations, the number of plants found will be the same in each simulation. Markers show the optimal search allocation (right axis), lines show the number of plants remaining (left axis, solid = actual number, dashed = estimated mean given the total number found and total search effort, dotted = estimated 95% credible intervals given the total number found and total search effort).
**Figures**

![Bar chart](image)

**Figure 1**
Figure 2
Figure 3
Figure 4
Appendix A: Uncertainty distributions for plant abundance given find data

Before surveys begin, we assume that our prior belief regarding plant abundance at site $i$ follows the distribution:

$$
Pr(N_{i,0} = n | \alpha_i, \beta_i) = \frac{\left(\frac{\alpha_i}{\alpha_i + n}\right)^{\frac{n}{\alpha_i}} e^{-\lambda_i \beta_i n}}{\sum_{k=0}^{N_{i,\max}} \left(\frac{\alpha_i}{\alpha_i + k}\right)^{\frac{k}{\alpha_i}} e^{-\lambda_i \beta_i k}} \text{ for } n = 0, 1, 2, \ldots, N_{i,\max}.
$$

In our first survey, we allocate effort $x_{1,i}$ and $x_{2,i}$ to plots 1 and 2, respectively, and we find $c_{1,i}$ and $c_{2,i}$ plants, respectively. Given that individuals are detected independently according to equation 1, we can update our belief in the initial plant abundance at each plot:

$$
Pr(N_{i,0} = n | \alpha_i, \beta_i, c_{1,i}, x_{1,i}) = \frac{Pr(c_{1,i} | N_{i,0} = n, x_{1,i}) Pr(N_{i,0} = n | \alpha_i, \beta_i)}{\sum_{k=0}^{N_{i,\max}} Pr(c_{1,i} | N_{i,0} = k, x_{1,i}) Pr(N_{i,0} = k | \alpha_i, \beta_i)}
$$

$$
= \frac{\left(\frac{n}{c_{1,i}}\right) p_{1,i} (1 - p_{1,i})^{n - c_{1,i}} \left(\frac{\alpha_i + n}{\alpha_i}\right)^{\frac{n}{\alpha_i}} e^{-\lambda_i \beta_i n}}{\sum_{k=0}^{N_{i,\max}} \left(\frac{n}{c_{1,i}}\right) p_{1,i} (1 - p_{1,i})^{n - c_{1,i}} \left(\frac{\alpha_i + k}{\alpha_i}\right)^{\frac{k}{\alpha_i}} e^{-\lambda_i \beta_i k}}
$$

$$
= \frac{\left(\frac{n}{c_{1,i}}\right) (1 - e^{-\lambda_i \beta_i x_{1,i}})^{c_{1,i}} \left(\frac{\alpha_i + n}{\alpha_i}\right)^{\frac{n}{\alpha_i}} e^{-\lambda_i \beta_i n}}{\sum_{k=0}^{N_{i,\max}} \left(\frac{n}{c_{1,i}}\right) (1 - e^{-\lambda_i \beta_i x_{1,i}})^{c_{1,i}} \left(\frac{\alpha_i + k}{\alpha_i}\right)^{\frac{k}{\alpha_i}} e^{-\lambda_i \beta_i k}}
$$

$$
= \frac{n! \left(\frac{\alpha_i + n}{\alpha_i}\right) e^{-\lambda_i \beta_i x_{1,i}}}{c_{1,i}! (n - c_{1,i})! \alpha_i! n! e^{-\lambda_i \beta_i n}}
$$

$$
= \sum_{k=0}^{N_{i,\max}} \frac{\left(\frac{\alpha_i + k}{\alpha_i}\right) e^{-\lambda_i \beta_i x_{1,i}}}{c_{1,i}! (k - c_{1,i})! \alpha_i! k!} \left(\frac{\alpha_i + n}{\alpha_i}\right) e^{-\lambda_i \beta_i n}
$$

$$
= \frac{(\alpha_i + n)!}{(\alpha_i + c_{1,i})! (n - c_{1,i})!} e^{-\lambda_i (\beta_i + x_{1,i}) n}
$$

$$
= \sum_{k=0}^{N_{i,\max}} \frac{\left(\frac{\alpha_i + k}{\alpha_i}\right) e^{-\lambda_i (\beta_i + x_{1,i}) k}}{c_{1,i}! (k - c_{1,i})!} \left(\frac{\alpha_i + n}{\alpha_i}\right) e^{-\lambda_i (\beta_i + x_{1,i}) n}
$$

$$
= \frac{\left(\frac{\alpha_i + n}{\alpha_i}\right) e^{-\lambda_i (\beta_i + x_{1,i}) n}}{\sum_{k=0}^{N_{i,\max}} \left(\frac{\alpha_i + k}{\alpha_i}\right) e^{-\lambda_i (\beta_i + x_{1,i}) k}} \text{ for } i = 1, 2 \text{ and } n = c_{1,i}, c_{1,i} + 1, \ldots, N_{i,\max}.
$$

The above posterior distribution for initial population size in consistent with our general formula with $t = 1$. 

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At some future survey period $t$ we will have accumulated finds $C_{i,t} = \sum'_{j=1} c_{i,j}$ having applied total effort $X_{i,t} = \sum'_{j=1} x_{i,j}$ to each plot $i$. For a moment let’s assume that our given formula accurately represents our posterior Bayesian belief for the initial plant abundance at each plot $i$. Then after survey $t+1$ we find $c_{i,t+1}$ plants using effort $x_{i,t+1}$ at each plot $i$, and our updated belief is:

$$\Pr\left(N_{i,0} = n \mid \alpha_t, \beta_t, C_{i,t}, X_{i,t}, c_{i,t+1}, x_{i,t+1}\right)$$

$$= \frac{\Pr\left(c_{i,t+1} \mid N_{i,0} = n, C_{i,t}, X_{i,t}, x_{i,t+1}\right) \Pr\left(N_{i,0} = n \mid \alpha_t, \beta_t, C_{i,t}, X_{i,t}\right)}{\sum_{k=C_{i,t}}^{\max N_{i}} \Pr\left(c_{i,t+1} \mid N_{i,0} = k, C_{i,t}, X_{i,t}, x_{i,t+1}\right) \Pr\left(N_{i,0} = k \mid \alpha_t, \beta_t, C_{i,t}, X_{i,t}\right)}$$

$$= \frac{\left(n - C_{i,t}\right)! k^{-C_{i,t}} \left(1 - p_{i,t+1}\right)^{k-C_{i,t}} \left\{ \alpha_t + k \right\} e^{-\lambda (\beta_t + X_{i,t})k} \left\{ \alpha_t + C_{i,t}\right\}^{k-C_{i,t}} e^{-\lambda (\beta_t + X_{i,t})k}}{\sum_{k=C_{i,t}}^{\max N_{i}} \left(n - C_{i,t}\right)! k^{-C_{i,t}} \left(1 - p_{i,t+1}\right)^{k-C_{i,t}} \left\{ \alpha_t + n \right\} e^{-\lambda (\beta_t + X_{i,t})n} \left\{ \alpha_t + C_{i,t}\right\}^{n-C_{i,t}} e^{-\lambda (\beta_t + X_{i,t})n}}$$

Again, this posterior belief regarding initial plant abundance is consistent with our formula. Given that we know it to be true for $t = 1$, we now know by induction that the formula holds for $t = 2, 3, 4, ..., T$.

We derive the belief distribution for the number of plants remaining in plot $i$ after survey $t$ by noting that $N_{i,t} = N_{i,0} - C_{i,t}$. Then
\[ \text{Pr}\left( N_{i,j} = n \mid \alpha_i, \beta_i, C_{i,j}, X_{i,j} \right) = \text{Pr}\left( N_{i,0} - C_{i,j} = n \mid \alpha_i, \beta_i, C_{i,j}, X_{i,j} \right) \]
\[ = \text{Pr}\left( N_{i,0} = n + C_{i,j} \mid \alpha_i, \beta_i, C_{i,j}, X_{i,j} \right) \]
\[ = \frac{\left( \alpha_i + n + C_{i,j} \right) e^{-\lambda_i(\beta_i + X_{i,j})(n + C_{i,j})}}{\sum_{k=n-C_{i,j}}^{N_{i,0}^{\max}} \left( \frac{\alpha_i + k + C_{i,j}}{\alpha_i + C_{i,j}} \right) e^{-\lambda_i(\beta_i + X_{i,j})(n + C_{i,j})}} \]
\[ = \frac{\left( \alpha_i + C_{i,j} + n \right) e^{-\lambda_i(\beta_i + X_{i,j})n}}{\sum_{k=0}^{N_{i,0}^{\max} - C_{i,j}} \left( \frac{\alpha_i + k + C_{i,j}}{\alpha_i + C_{i,j}} \right) e^{-\lambda_i(\beta_i + X_{i,j})k}} \]
for \( i = 1, 2 \) and \( n = 0, 1, ..., N_{i,0}^{\max} - C_{i,j} \),

which is given in equation 2.
Appendix B: Average performance and benefit across scenarios

Table B1. The expected total number of plants found from two sites over ten surveys under various detection rates, prior abundance beliefs and decision rules. In all cases, site 1 has parameter values $N_{\text{max}} = 30$, $\lambda_1 = 0.07392$ (same as *Lomandra longifolia*), $\alpha_1 = \beta_1 = 0$ (i.e. prior belief regarding plant abundance is Uniform[0, $N_{\text{max}}$]). We calculated the prior-weighted mean performance from 1000 simulations of each true abundance state.

<table>
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<tr>
<th>Scenario</th>
<th>$\lambda_2$</th>
<th>$\alpha_2$</th>
<th>$\beta_2$</th>
<th>$E(N_{2,0})$</th>
<th>St Dev($N_{2,0}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Passive</td>
<td>0.07392</td>
<td>0.03696</td>
<td>0.07392</td>
<td>0.03696</td>
<td>0.07392</td>
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<tr>
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<td>5.96</td>
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</tr>
<tr>
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<td>12.47</td>
<td>10.95</td>
<td>9.68</td>
<td>15.66</td>
</tr>
</tbody>
</table>

Table B2. The benefit of each strategy over uniform allocation of search effort, in terms of the expected number of plants found. Scenarios include two sites over ten surveys under various detection rates, prior abundance beliefs and decision rules. In all cases, site 1 has parameter values $N_{\text{max}} = 30$, $\lambda_1 = 0.07392$ (same as *Lomandra longifolia*), $\alpha_1 = \beta_1 = 0$ (i.e. prior belief regarding plant abundance is Uniform[0, $N_{\text{max}}$]). We calculated the prior-weighted mean performance from 1000 simulations of each true abundance state.

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Appendix C: Survey strategy performance

Figure C1: The performance of each strategy, in terms of the expected number of individuals found over ten surveys. Detection rate in both sites is estimated for *Lomandra longifolia*. Prior belief in plant abundance is discrete $\text{Uniform}[0, 30]$ for both sites. Results have high visual similarity for the other abundance priors investigated (see Appendix B). Rule of thumb 1 is to search the site where the most plants have already been found. Rule of thumb 2 is to search the site where the most plants have been found per minute searched.
Figure C2: The performance of each strategy, in terms of the expected number of individuals found over ten surveys. Detection rate in site 1 is estimated for *Lomandra longifolia*, and in site 2 is half this rate. Prior belief in plant abundance is discrete Uniform[0, 30] for both sites. Results have high visual similarity for the other abundance priors investigated (see Appendix B). Rule of thumb 1 is to search the site where the most plants have already been found. Rule of thumb 2 is to search the site where the most plants have been found per minute searched.
Figure D1. The benefit of each strategy over uniform allocation of search effort, in terms of the expected number of individuals found over ten surveys. Detection rate in site 1 is estimated for *Lomandra longifolia*, and in site 2 is half this rate. Prior belief in plant abundance is discrete Uniform[0, 30] for both sites. Rule of thumb 1 is to search the site where the most plants have already been found. Rule of thumb 2 is to search the site where the most plants have been found per minute searched.
Figure D2. The benefit of each strategy over uniform allocation of search effort, in terms of the expected number of individuals found over ten surveys. Detection rate in both sites is estimated for *Lomandra longifolia*. Prior belief in plant abundance is discrete Uniform[0, 30] in site 1 and has parameters \( \{\alpha, \beta, E(N_0), St\ Dev(N_0)\} = \{6, 5, 14.97, 6.17\} \) for site 2. Rule of thumb 1 is to search the site where the most plants have already been found. Rule of thumb 2 is to search the site where the most plants have been found per minute searched.
Figure D3. The benefit of each strategy over uniform allocation of search effort, in terms of the expected number of individuals found over ten surveys. Detection rate in both sites is estimated for *Lomandra longifolia*. Prior belief in plant abundance is discrete Uniform[0, 30] in site 1 and has parameters $\{\alpha, \beta, E(N_0), \text{St Dev}(N_0)\} = \{0, 2, 5.96, 5.97\}$ for site 2. Rule of thumb 1 is to search the site where the most plants have already been found. Rule of thumb 2 is to search the site where the most plants have been found per minute searched.
Author/s:
Rout, TM; Hauser, CE; McCarthy, MA; Moore, JL

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Adaptive management improves decisions about where to search for invasive species

Date:
2017-08-01

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