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PERSPECTIVE

SPECIAL ISSUE ON INVASIVE MAMMAL SPECIES

Using and communicating uncertainty for the effective control of invasive non-native species

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ABSTRACT

Estimates of quantities needed to plan invasive species control, such as population size, are always uncertain; this is an issue that can become a problem when mishandled in ecological science and its communication. The complexities of incorporating uncertainty into sophisticated decision-support tools may be a barrier to their use by decision-makers, leading to decisions being made without due regard to uncertainty and risking mis-placed certainty of predicted outcomes. We summarise ways in which uncertainty has been incorporated into and used to advise decisions on the management of invasive non-native species and other problem species, and offer a simple conceptual model for accommodating and using uncertainty at the planning stage. We also demonstrate how frequently uncertainty has been mis-used and mis-communicated in the wildlife management literature. We contend that uncertainty in estimates of natural quantities must be acknowledged, can inform decisions and can be made to derive decisions, and should not be ignored if invasive species policy is to be delivered effectively. Uncertainty must be communicated thoroughly and correctly by scientists if decision-makers are to understand its consequences for planning and resourcing control programmes.

Keywords: confidence interval, decision-making, error, invasive non-native mammals, probability, wildlife management

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INTRODUCTION

Decisions regarding responses to invasive non-native species (hereafter referred to as invasives) are fraught with uncertainty. During the early stages of invasion, detection probability is likely to be low due to the species' very limited spatial range and low abundance (Mehta et al. 2007), leading to highly uncertain estimates of these quantities (Wenger & Freeman 2008). As the range expands and the population grows, the species may be detected more frequently. However, estimates remain uncertain, as evinced by the broad confidence intervals that typically define population estimates of new invaders and other low-density populations (Miller et al. 2005), with consequent uncertainty regarding the effort required to control them (Johnson et al. 2017). Even when widely established and highly abundant, estimation of a species' range, population size, and population growth to magnitudes of accuracy and precision that can be accommodated by traditional approaches to management planning can be challenging due to large uncertainties associated with limited sampling (Mackenzie 2005). This is problematic because comprehensive information on populations is required to improve the likelihood of success of management campaigns against invasives (Simberloff 2003). Policy-makers often seek certainty and simplicity from those experts chosen to provide policy-relevant evidence (Hammersely 2013). However, uncertainty in natural quantities, such as range and abundance, which can be used to inform management decisions can present significant challenges for decision-makers, because uncertainty makes the prediction of the outcomes, for a given investment, uncertain and imprecise (Nair & Howlett 2017). In consequence, decision-makers may ignore uncertainty, dismissing it as an inconvenient impediment to necessary action (Hammersely 2013), choosing instead to rely on subjective judgement (Regan et al. 2005). Many experts, including applied ecologists, who may advise decision-makers also have a history of mishandling uncertainty (Milner-Gulland & Shea 2017), which may compound this problem. A wide range of quantitative tools has been developed to incorporate uncertainty into decisions, including those pertaining to the control of invasives, yet uptake of these has typically been very low (Addison et al. 2013). A substantial number of campaigns against invasives have either failed (Pluess et al. 2012, Capizzi et al. 2020) or cost much more than originally anticipated (see Parkes et al. 2010, Mill et al. 2020), possibly due to a failure to incorporate uncertainty into management decisions adequately. While decision-makers may view uncertainty and complexity in estimates of natural quantities as unhelpful and indicative of the low quality or incredibility of available information (Hammersely 2013), we contend that the appropriate management of uncertainty can help inform campaigns against invasives better than if uncertainty was ignored (Funtowicz & Ravetz 1990).

AIMS

In this article, we sought to summarise what uncertainty is with respect to estimates of natural populations and processes, evaluate how uncertainty has been used and communicated in the wildlife management literature, and synthesise some simple principles for using and reporting uncertainty during the planning stage of campaigns against invasives and other wildlife species that people wish to control. There are many ways in which uncertainty can be incorporated into decision-making; the list of approaches described below is not exhaustive, and those that are advocated are simply those that we have found helpful when planning wildlife management programmes and communicating those plans with decision-makers and other stakeholders.

DEFINING UNCERTAINTY

The many sources of uncertainty in biological systems and models of them have long been recognised and incorporated into decision-making processes by fisheries scientists (see Hilborn & Walters 1992), and are increasingly considered within literature on the management of terrestrial vertebrates (Milner-Gulland & Shea 2017, Nichols 2019). In their seminal review, Regan et al. (2002) classified two main branches in the taxonomy of uncertainty as it arises in ecology and conservation biology: epistemic and linguistic uncertainty.

Epistemic uncertainty refers to the state of a system, and is due to the limitations of measuring instruments, natural variability within the system, inadequate sampling, and extrapolation and interpolation. Thus, epistemic uncertainty encompasses the accuracy and precision of inputs or measurements, and outputs or estimates (Nichols 2019). It can be characterised by describing measurement precision and sample size, quantifying measurement variability (see Box), stating and evaluating the assumptions underpinning calculations, interpolations or extrapolations, and by bias-correction when appropriate. It can be quantified (e.g. as confidence intervals) or described as a probability (i.e. of the null hypothesis being incorrect; Regan et al. 2002). The former is perhaps the most traditional approach employed widely in ecology, whereas uptake of the latter has perhaps been more recent, increasing particularly with the incorporation of Bayesian statistics into ecological studies.

Linguistic uncertainty arises from poor communication; language can be unspecific, ambiguous, vague and context-dependent. Borrowing from Regan et al. (2002), the importance of good communication for the minimisation of uncertainty is evident when considering the aim of an invasives control programme. If we wish to eradicate all invasives from an area, we must define precisely a) what invasives are so that we can determine which species to focus on, and b) what the area is.

Epistemic and linguistic uncertainty, alone and acting together, can result in model or outcome uncertainty, whereby the consequences of an action can be quite different to what was predicted due to complexities within the system (Regan et al 2002, Artelle et al. 2013).

COMMUNICATING UNCERTAINTY

It is important that uncertainty is communicated well by scientists to decision-makers so that management decisions can be more fully informed, but its reporting in the applied ecology literature is inconsistent. This failure to report uncertainty correctly is an important additional aspect of linguistic uncertainty to those described by Regan et al. (2002). Standard statistical terms used to evaluate different components or characteristics of uncertainty, such as the standard deviation of a sample mean and the standard error of a parameter estimate, may be reported in ways that are inconsistent with definitions given in basic statistical text books. To test this statement we evaluated the reporting of uncertainty in 98 published scientific papers on adaptive wildlife management (see Appendices S1 and S2). Among 65 articles reporting estimates, 17% did not report averages and 35% did not report measurement variability or estimate uncertainty. Instead of averages, other less useful metrics, such as minimum count, which does not account for detection probability, were reported. Among 63 of these articles, 35% should have used an average descriptor other than the mean because data were not normally distributed or sample sizes were small. Among these 63 articles, 43% reported the correct descriptor of measurement variability or estimate uncertainty, but only 17% sought to interpret the effect of estimated uncertainty quantitatively, and 29% qualitatively. Milner-Gulland and Shea (2017) stated that applied ecologists have often been guilty of ignorance, disregard and hubris in relation to uncertainty, and our results are consistent with this view. It should be no surprise that policy-makers, politicians and other decision-makers misunderstand and miscommunicate uncertainty when their expert advisors are equally guilty. We recommend that applied ecologists should adhere to the definitions of measures of uncertainty described in standard statistical text books (see Box), and should use them correctly in all communications.

UNCERTAINTY IN DECISION-MAKING

Many approaches exist for incorporating uncertainty into model outputs in applied ecology (Nichols 2019), and yet its importance for decision-making can be over-looked (Milner-Gulland & Shea 2017). For example, Wäber et al. (2013) estimated that, despite culling, a mean of 1103 Reeves' muntjac *Muntiacus reevesi* was recruited to an English plantation forest during 2008/2009 and 1287 during 2009/2010. A traditional approach to cull target setting might therefore have recommended removal of approximately 1100-1300 extra muntjac per year in order to halt population growth and prevent emigration. However, the 95% confidence interval for estimated recruitment was 21 to 2284 and 238 to 1783 muntjac in each year, respectively. Consequently, and accepting the validity of the assumptions underpinning the calculations, forest managers would have had to remove somewhere between these ranges of values to achieve their objective. The immediate problem is understanding where, within those ranges, the true number of muntjac that needed to be removed lies. The simple and unsatisfactory answer is that it is impossible to know. However, appropriate handling of estimate uncertainty can enable such decisions by reducing the risk of objective failure.

Milner Gulland and Shea (2017) and Nichols (2019) summarised a range of methodological options for minimising and incorporating uncertainty in scientific and modelling exercises, and reviewed a number of approaches to including uncertainty in management and decision-making. These included stochastic dynamic programming and partially observable Markov decision processes. We do not dispute the suitability of the solutions described by these authors, who provided examples of conservation and wildlife management interventions where they have usefully been employed, but we do question the extent of their utility. Artelle et al. (2018) found that the hallmarks of quality science were absent from the majority of 667 wildlife management approaches adopted in North America.

This is likely to be due to the complexity of biological systems and the way in which scientists describe them, resulting in decision-makers avoiding the use of robust scientific approaches for decision-making (Addison et al. 2013, Hammersley 2013). Indeed, the approach adopted by the UK government for the prioritisation of invasives for eradication under uncertainty is intuitive, qualitative and based on expert opinion (Booy et al. 2017), and does not incorporate quantitative models of ecological processes. Consequently, while we endorse the recommendations of Addison et al. (2013) for improving the uptake of ecological models for applied decision-making (see also Richardson et al. 2020, Bertolino et al. 2020), we nevertheless recommend simpler approaches for the inclusion, reporting and use of uncertainty to address perhaps the most simple and, in our experience, most frequently asked questions at the outset of invasives control programmes: how should we prioritise potential invasives prior to their arrival, is a priority species present, how is it distributed, how abundant is it, how many must be removed to control it and how much will a control programme cost? These questions, unsurprisingly, relate directly to the established approaches to controlling invasives, which are, in order of priority: prevention of invasion, rapid response to prevent establishment, eradication to reverse an invasion, and ongoing control of established populations (Simberloff 2003; Table 1).

Uncertainty in species prioritisation prior to invasion

In advance of invasion, knowledge of the risks that might be posed to anthropocentric or biodiversity interests will be limited to that available for a species' existing range. Consequently, extrapolation of the likely risks to the country to be invaded will result in uncertainty in outputs for that country. The requirement for horizon-scanning to enable evaluation of the likely risks posed (Roy et al. 2014) has led to the use of expert elicitation to populate risk assessments, with uncertainty characterised subjectively as an uncertainty score (Mumford et al. 2010). This can result in bias and mis-representation of uncertainty (Kynn 2008), but has been used to prioritise potential invaders according to the relative risks they may pose (Mumford et al. 2010) and the relative feasibility of control methods for eradicating them should they invade (Booy et al. 2017).

Uncertainty in species presence and distribution

Once prioritised for action, early detection of an invasive is necessary in order to prevent its establishment (Simberloff 2003). However, surveys designed to detect an invasion with a high probability have hitherto been extremely costly, since the invasives are likely to be highly geographically constrained and at low density during the early stages, leading to the conundrum of whether to invest more in detection or control (Mehta et al. 2007). The advent of novel detection techniques such as environmental DNA metabarcoding may reduce these costs substantially (Browett et al. 2020). Nevertheless, while the detection of a single individual or population may confirm that an invasion is underway, it does not explain the geographical extent of the invasion, and hence the area over which control is required. In contrast, the failure to detect an individual or population makes the conclusion of presence or absence highly uncertain, since surveys may suffer an inadequate detection probability (Christy et al. 2010). Occupancy estimation and modelling, which adopts the probabilistic approach to uncertainty characterisation (Mackenzie et al. 2017) can be used to address some of these problems. The underlying principles of occupancy estimation are that the probability of detecting a species increases with survey effort, and the detection probability for a single survey can be estimated. The probability of failing to detect a species, if it is present, decreases as the number of surveys increases such that, with sufficient surveys, this probability crosses a threshold (traditionally 0.95) that can be set by the user according to their attitude towards risk. Thus, with sufficient surveys (as defined by the detection probability and the threshold), failure to detect a species can be interpreted as likely absence, with a given probability defining the uncertainty. The same approach can be used in multiple locations to estimate the proportion of sites likely to be occupied and hence the area over which control may be required (Mackenzie et al. 2017). The concept of occupancy estimation is straight-forward, and the principle of characterising uncertainty probabilistically is intuitive, and hence may be easy to convey to decision-makers. However, the calculations are rather more complicated and so employment of this approach may be best suited to technical specialists.

Uncertainty in species abundance

Where eradication or ongoing management of populations are the selected approaches, estimates of management effort are usually required (McCann & Garcelon 2008); for medium to large mammals, these often require estimates of the number of animals to be removed and the proportion of the population that this target represents. Numerous methods for abundance estimation are available (for carnivores, see Wilson & Delahay 2001), but particularly for an eradication campaign during a single year, total population size should be estimated, since it equates to the number that must be removed in advance of the birthing season.

Regardless of the method chosen, and in addition to the assumptions on which calculations are based, uncertainty in population size can be quantified probabilistically or as a range of values. The probabilistic approach can be followed to evaluate whether uncertainty is tolerable. For example, if a requirement is to be 90% certain that a species' population is above a certain size, then a probability of 0.9 or more that the population estimate is correct, or conversely, a probability of 0.1 or less that it is incorrect, is sufficient to evaluate whether a policy objective is likely to be met. However, this approach cannot inform us how to use the uncertainty to set targets. To use uncertainty to reduce the risk of failing to achieve a management objective for invasives at the planning stage, uncertainty is best described as the confidence interval defining the estimated outputs (see below).

Uncertainty in cost of species control

Arguably, the most important component of an invasives management plan is an estimate of the likely financial cost of control, since this facilitates evaluation of the cost-effectiveness of the options available (Buhle et al. 2004). The costs of control relate to the size of the population, the species' life history (particularly as it relates to the population growth rate), the proportion of the population removed per unit effort and the cost per unit effort (Buhle et al. 2004, Ward & Lees 2011).

Uncertainty in the number to remove

Assuming that doing nothing is not an option if the objective is control of an invasive, the remaining options are to prevent population growth and spread, to reduce the population size, or to eradicate the species. The containment or eradication of an invasive (or any species) requires the removal of at least the number of females that is recruited to the population each year (Fryxell et al. 2014). For animals, the number to be removed has been calculated as the product of female population size at a point in time and female recruitment rate (the number of female offspring produced per female during the season), assuming that the mean of each of these values (the thin dashed lines A and B respectively in Fig. 1) offers an approximate estimate of the minimum number that must be taken (Buckland et al. 1996, Wäber et al. 2013). However, this approach suffers a high risk of failure because it ignores uncertainty in parameter estimates. Estimates of both quantities are uncertain, characterised as confidence intervals (the range between the thick dashed lines either side of A and B, Fig. 1). Line C is midway among the combined uncertainties; products of population size and recruitment rate point estimates along this line are equal to the value derived from the means of these variables (point d). Assuming an unbiased distribution of values around the mean, it should be clear that very nearly 50% of credible values of the number of females recruited lie to the left of line C, nearly 50% lie to the right of it and very few lie along it. Removal of the mean number of females recruited as a management objective has an approximately 50% chance of being too few, and a vanishingly small chance of being correct. Consequently, to be confident of removing at least the number of females recruited to the population, minimum cull targets should be set conceptually at point e, the product of the upper confidence limits of female population size and female recruitment rate estimates. The degree of confidence that must be afforded to the calculation of this value, i.e. the proportion of values likely to be contained within the interval, must be determined by the decision-maker's acceptance of the risk of failing to at least prevent population growth. For example, using 80% confidence intervals, and assuming an unbiased distribution, 10% of credible values will be to the left of the lower limit, and 10% will be to the right of the upper limit. Thus, risk-accepting decision-makers may choose a smaller confidence interval and risk-averse decision-makers may choose a larger one. This approach does not guarantee that the population will decline if the target is achieved, but, as long as the assumptions underpinning the calculations are correct, it substantially reduces the risk of under-culling from 50:50.

The opposite application of this approach is for the sustainable harvesting of a species. To ensure that populations persist, the maximum number of females that should be harvested is conceptually set at point f, i.e. the product of the lower confidence limits of female population size and female recruitment rate. This should ensure that no more than the number of females recruited to the population is removed during a single harvesting season (see Artelle et al. 2013).

Estimate uncertainties cannot simply be multiplied in the way implied by this concept since it will lead to over-estimation of uncertainty, instead they must be combined into a single estimate. This can be achieved by a number of methods (Nichols 2019) including Monte Carlo simulation: a single value is drawn at random from the confidence interval of female population size, and multiplied by a single value drawn at random from the confidence interval of the female recruitment rate, and the process is repeated a large number of times. The mean and standard deviation of the large number of outputs are used to calculate the confidence interval in the normal way. The upper limit of this interval corresponds to point e and the lower limit to point f on Fig. 1.

Johnson et al. (2017) developed a multi-step modelling approach to estimate the effort and hence costs of invasive non-native tegu lizard *Salvator merianae* control in Florida, USA. Demographic rates were summarised by repeatedly sampling point estimates derived by expert elicitation, to build population matrices that were scenario-tested for the likely cost and effectiveness of different control strategies. Scenario planning is an informative way of planning control campaigns against invasives at the outset, when planners are information-poor, and can help improve prioritisation of parameters for uncertainty reduction (Peterson et al. 2003). Moreover, the utility of this approach can be complemented by including consideration of uncertainty, not just when deriving parameter estimates, but when interpreting model outputs too.

An example is provided by the ongoing control of feral wild boar *Sus scrofa* in western England, for which the objective has been the prevention of population growth. Boar density, total abundance and population growth rate have been estimated annually since 2013, in order to advise single-year cull targets to prevent population growth (Table 2). A cull of 56.5% of the population was estimated to be required to prevent growth during 2015 and 2016 (Gill & Ferryman 2015, Gill & Waeber 2016). The method for calculating this cull target was not reported, but targets can be calculated from the average of the estimated female recruitment rate and female population size during each year. As argued above, we suggest that this approach has a high risk of under-culling during a given year, and hence might have contributed to the sustained trend of population growth.

Following the approach that we have advocated (Fig. 1), and accepting all assumptions underpinning calculations of wild boar population size, structure and productivity as correct, we combined estimates of female population sizes (values in Table 2 divided by two, to reflect the reasonable assumption of a 1:1 sex ratio; Keuling et al. 2003) with estimates of female recruitment rates (which were not reported for this population, and hence were summarised from other European populations as varying from 0.85 to 1.63; Bieber & Ruff 2005). Assuming a uniform distribution for both parameters, and with 1000 iterations in the Monte Carlo simulation, we estimate that female cull targets should have been much higher. During 2014, the number of females recruited was between 560 and 585 (95% confidence interval), so a risk-averse minimum cull target would have been 585 female wild boar. During 2015, recruitment of 657-680 required a minimum target of 680, and during 2016 and 2018, recruitment of 1040-1073 during both years required a minimum target of 1073. Of course, these values might be biased high or low if the assumption of a 1:1 sex ratio was incorrect or if any of the other assumptions underpinning the calculations were violated. These cull targets either exceed or are very close to the lower confidence limit of the population size estimate, and so might be impossible or extremely challenging to achieve. Achievement of our revised target during 2014 might have caused the eradication of the population. This would not be a problem if sufficient resources had been made available to remove those numbers from a population of invasives; it may in fact have been a benefit.

Uncertainty in the costs of removal

Estimating the costs of control according to worst-case scenarios should ensure that management campaigns are not under-resourced. In a modelling study of a range of hypothetical population sizes, Ward and Lees (2011) estimated that the eradication of populations of 200 Reeves' muntjac from Scotland, should they become established (which they are not, despite being widely established in England and Wales; Ward 2005), was likely to cost an average of GB£24050, but might cost as much as GB£60625, and advocated budgeting according to the latter figure. While this might be viewed as inefficient and risking resource not be available for other campaigns, it is likely to be more cost-effective than budgeting on averages, which, all else being equal, should result in their main objective not being met approximately 50% of the time, and may require additional resource to respond to population growth during subsequent years (see Parkes et al. 2010; Mill et al 2020). Indeed, under-resourcing has been one of the main factors associated with the failure of invasives control in New Zealand (Brown et al. 2015). However, risks associated with this approach include forecasting such high estimated costs that decision-makers decide that doing nothing or some lesser intervention is preferable, undermining the morale of operatives controlling populations of invasives as they toil towards an unattainable target.

SOLUTIONS TO UNCERTAINTY FOR THE CONTROL OF INVASIVES

Solutions to the issue of uncertainty in ecological science and decision-making have been summarised by several authors (including Regan et al. 2002, Milner-Gulland & Shea 2017, Nichols 2019), but have rarely been adopted for the control of invasives. We should accept that all of our estimates and hence predicted management outcomes are, under nearly all circumstances and particularly at the start of a management campaign, highly uncertain, and should respond accordingly. This requires working with uncertainty at all levels:

1) Researchers who estimate quantities should calculate, interpret and communicate uncertainty as fully and as simply as possible, and always accurately, so that decision-makers can respond appropriately.
2) Decision-makers should understand uncertainty, how to ensure it is included in decision-making processes, and how to work with it or use it to define desirable (and undesirable) outcomes.
3) Managers should incorporate uncertainty into management objectives, including targets, and should communicate this uncertainty to operatives, in order to manage expectations with regards to delivery.
4) Finally, operatives need to understand what uncertainty is and what its implications are for management, so that they can help managers evaluate outcomes, and so that they can manage their own expectations with regards to target achievement.

There is no single approach for incorporating uncertainty into decision-making that is universally applicable to all stages of the invasion process, and different approaches may be demanded to inform effective action at each stage. We advocate the following:

1) Prior to invasions, existing information can be used to inform risk assessments (Mumford et al. 2010) and risk management evaluations (Booy et al 2017), and uncertainty should be semi-quantified into confidence scores by expert opinion in order to prioritise potential invasives for eradication. These processes have been specifically designed to facilitate decision-making by non-specialists.
2) When an invasion is suspected, or if confirmation of the likely absence of a potential invader is required, occupancy estimation can be used to quantify the probability of absence and likely geographic range of the invasive, with uncertainty estimated probabilistically (Mackenzie et al. 2017). The principles of this approach are intuitive, but the complexities of its deployment mean that its use is probably best-suited to specialists who advise decision-makers.

3) To inform plans to eradicate an invasive, estimates of population size and geographical range will be required to estimate the management effort required and hence the total cost of control. We recommend a precautionary approach such that the upper limits of population size and range are used to estimate costs, with the limits defined by the decision-maker's attitude to risk.
4) For the ongoing control of established invasives, we recommend combining the upper limits of estimated female population size and female recruitment rate to derive minimum female cull targets, with limits defined by the decision-maker's attitude to risk. This precautionary approach is simple and intuitive, but it risks over-budgeting and hence culling more than is strictly necessary to prevent population growth or spread.

CONCLUSION

There has been a tendency for applied ecologists to mis-handle uncertainty when advocating or planning management action, and uncertainty has rarely been incorporated adequately into management campaigns against invasives. It is clear that point estimates, including averages of estimates, are very nearly always wrong, and using average point estimates to set management objectives for the control of invasives poses a high risk of failure. It is also clear that the approach that we recommend for using uncertainty to plan campaigns against invasives assumes the worst case, and hence is likely to produce targets that might be unattainable. Nevertheless, we argue that this approach offers a helpful first step for planning management campaigns, because it should ensure that sufficient resource is available at the outset to deliver the management objective. However, funding sources are always finite (Mill et al. 2020), and pressure is likely to be exerted on campaign managers to find cost savings as campaigns progress (Carrion et al. 2011); such cost savings could be driven by reducing the uncertainty of the scale of the problem being addressed (Milner-Gulland & Shea 2017).
Uncertainty can be reduced by collecting information on management inputs and outcomes as a campaign progresses, such that estimates of resource requirements and hence definitions of objectives can be refined. The cyclical process of setting objectives, predicting outcomes, delivering management action, simultaneously undertaking monitoring, evaluating inputs and outputs, learning

about the system under management and hence refining objectives and actions sequentially is termed adaptive natural resource management (Williams 2011). This approach has been adopted by many people intending to manage invasives, with varying degrees of diligence (Richardson et al. 2020). The concept of acknowledging and using uncertainty that we advocate for decision-making, applied to the principles of incorporating uncertainty into estimates of natural quantities summarised by Regan et al. (2002) and Nichols (2019) offers the ability to set clear, unambiguous, evidence-based management targets at the very start of campaigns against invasives, and at every stage at which new information arises and hence at which uncertainty is reduced.

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Table 1. Some major sources of uncertainty and ways in which they can be incorporated into decisions regarding the control of invasive non-native species during each stage of the invasion process.

Stage	Input uncertainties		Output uncertainties		References
	Source	***How to incorporate***	***How to report***	***How to use***	
Prior to invasion	List of risks. Factors contributing to likelihood and severity of risk. Feasibility of control.	Synthesis of existing information.	Risk score. Qualitative assessment of confidence in risk score.	Prioritisation of species by risk and feasibility of control. Identification of areas for further research to reduce uncertainty.	Mumford et al. 2010 Booy et al. 2017
Suspected invasion	Presence/absence.	Occupancy analysis of surveillance data.	Presence (if detected) or probability of absence.	Confirmation of presence. Acceptance of absence probability. Confirmation of requirement for further surveillance if probability of absence is below the acceptable threshold.	Mackenzie et al. 2017
Confirmed invasion (early)	Distribution.	Occupancy analysis of surveillance data.	Proportion of locations likely to be occupied with a given probability.	Map likely distribution to prioritise surveillance and control.	Mackenzie et al. 2017
	Population size.	Sampling error (mean and standard deviation of sample).	Confidence interval of population size estimate.	Assume worst case: population defined by upper confidence limits.	Ward & Lees 2011
	Number to remove.	Combine abundance with recruitment rate.	Confidence interval of number of recruits.	Set cull target according to worst case: Minimum target = upper limit of number of recruits.	
Established population	Population size.	Sampling error (mean and standard deviation of sample).	Confidence interval of population size estimate.	Assume worst case: population defined by upper confidence limit.	
	Number to remove.	Combine abundance with recruitment rate.	Confidence interval of number of recruits.	Set cull target according to worst case: Minimum target = upper limit of number of recruits.	Ward & Lees 2011

Table 2. Feral wild boar population size estimates, cull targets and cull returns for the Forest of Dean, western England.

Year	Mean population estimate	95% confidence interval	Advised cull target	Cull achieved	Sources
2014	819	506-1325		361	Gill 2014 *
2015	1081	696-1486	460	543	Gill & Ferryman 2015, Gill & Waeber 2016 *
2016	1562	1095-2296	712	492	Gill & Waeber 2016 *
2017				477	*
2018	1635	1200-2228			Gill & Waeber 2018

* In 2014-2017, sources also included: https://www.forestryengland.uk/article/more-information-about-wild-boar

Fig. 1. Conceptual model of female cull target setting given estimates of female population size and female recruitment rate. A is the mean of the female population size estimate, B is the mean of the female recruitment rate estimate. Heavy dashed lines are the confidence limits of these estimates. Line C describes products of values for population size and recruitment rate that yield the same value as the product of the means (d). Point e is the intersection of upper confidence limits, which conceptually defines the lowest cull target to be sufficiently confident that at least the number of females recruited to the population will be removed, if it is achieved. Point f is the intersection of the lower confidence limits, which conceptually defines the highest cull target to be sufficiently confident that no more than the number of females recruited to the population will be removed, if it is achieved.

Box. Measures of quantities and uncertainty

Box. Measures of quantities and uncertainty

Fowler et al. (1998), in their standard undergraduate text book on statistics for biologists, describe the following measures of uncertainty that have commonly been used in applied ecology for normally distributed data. Our interpretation is included in italics:

Arithmetic mean or mean – the sum of a set of observations divided by the number of observations.

Standard deviation – a measure of the degree of variability within a sample.

Standard error – the standard deviation of a set of sample means. The standard error is an indication of how close the sample mean is likely to be to the population mean. *Thus, the standard error is an appropriate measure of uncertainty of an estimated parameter, but should not be used to describe variability in a sample.*

Relative standard error (also known as the **relative standard deviation, relative standard uncertainty** or **coefficient of variation)** – the ratio of the standard deviation to the mean.

Confidence interval – The likely interval for the true population mean. *If all possible 95% confidence intervals are calculated from un-biased samples taken from a population, the true value of the mean will be within the interval of 95% of them (Neyman 1937).*

The corresponding values reported for non-normally distributed data are the **median** and **some proportion of the range** (typically the 2.5th and 97.5th percentiles, or the full range of values measured).

References

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Methods for the review of adaptive management literature.

Appendix S2. Data from the review of adaptive management literature.

Text box 1. Measures of quantities and uncertainty

Fowler et al. (1998), in their standard undergraduate text book on statistics for biologists described the following measures of uncertainty that have commonly been used in applied ecology. Our interpretation is included in italics:

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References

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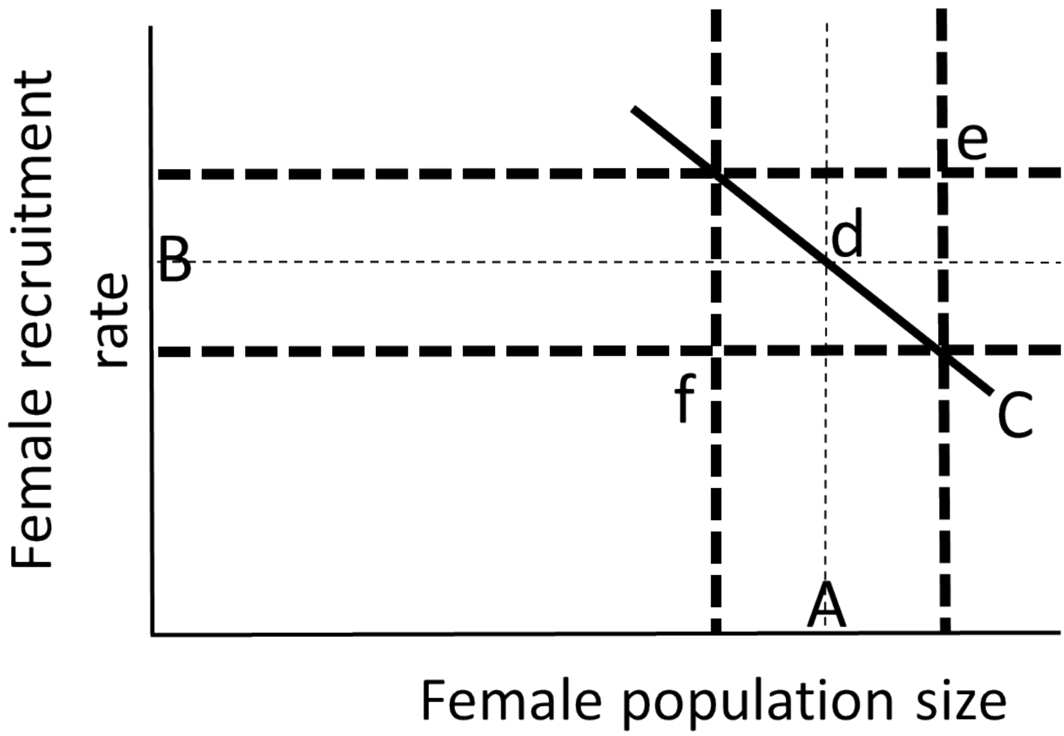
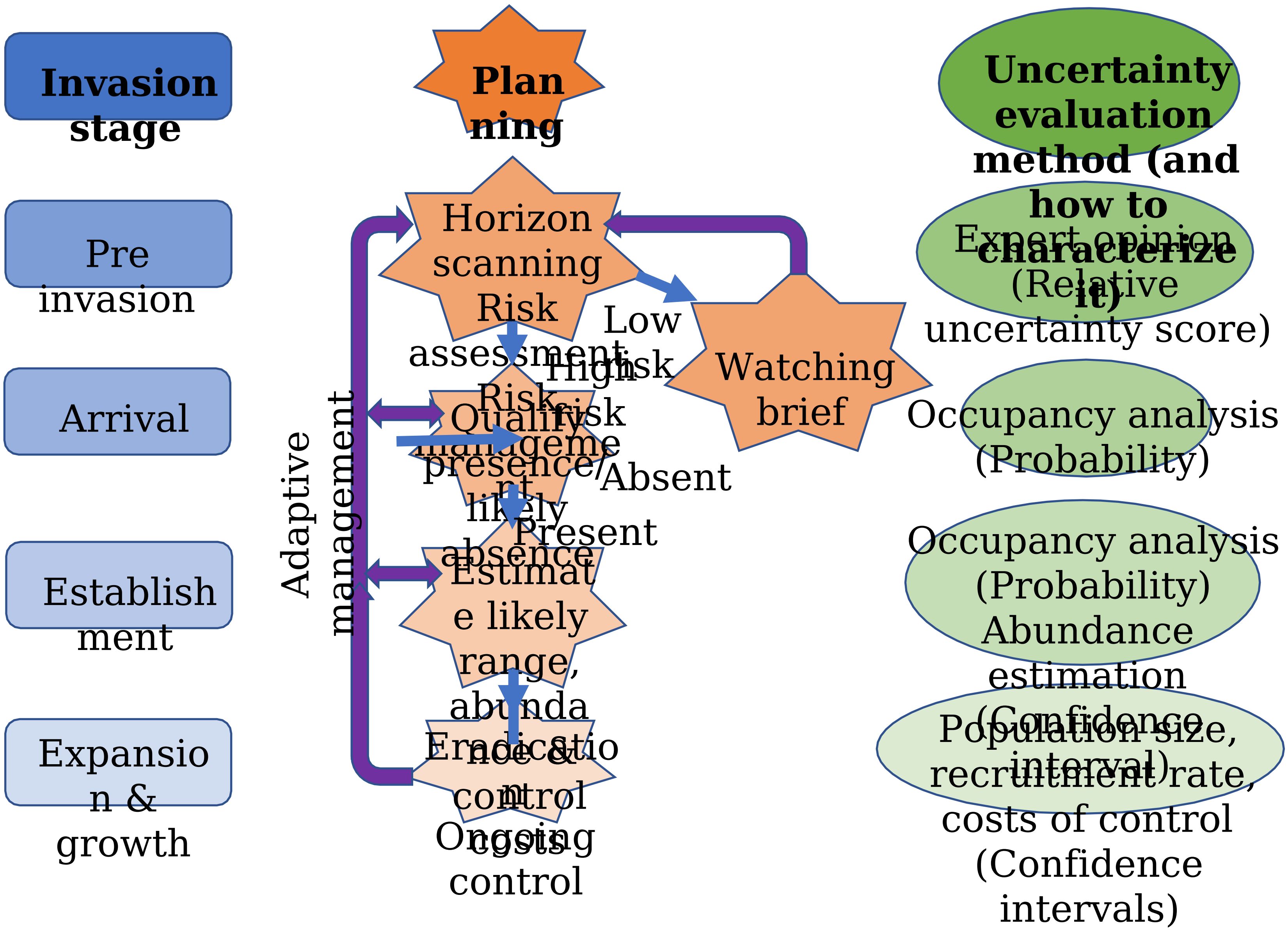


Fig. 1. Conceptual model of female cull target setting given estimates of female population size and female recruitment rate. A is the mean of the female population size estimate, B is the mean of the female recruitment rate estimate. Heavy dashed lines are the confidence limits of these estimates. Line C describes products of values for population size and recruitment rate that yield the same value as the product of the means (d). Point e is the intersection of upper confidence limits, which conceptually defines the lowest cull target to be sufficiently confident that at least the number of females recruited to the population will be removed, if it is achieved. Point f is the intersection of the lower confidence limits, which conceptually defines the highest cull target to be sufficiently confident that no more than the number of females recruited to the population will be removed, if it is achieved.



Invasion stage
Pre invasion
Arrival
Establishment
Expansion & growth
Planning
Horizon scanning Risk assessment
Low risk
Watching brief
High risk
Qualify presence/likely absence
Absent
Present
Estimate likely range, abundance
Adaptive management
Uncertainty evaluation method (and how to characterize it)
Expert opinion (Relative uncertainty score)
Occupancy analysis (Probability)
Occupancy analysis (Probability) Abundance estimation (Confidence interval)
Population size, recruitment rate, costs of control (Confidence intervals)

Reliable information is key to evidence-based decision-making and good decisions rely on a high degree of certainty. In advance of an invasion by a non-native species, we are very uncertain about their likely future distributio abundance, impacts and costs of control, so we may need to rely on the structured evaluation of expert opinion to prioritise invasive species for actio As an invasion progresses (invasion stages are represented here in blue boxes), more information is generated, reducing uncertainty, so it is possible to make better-informed decisions about control (planning actions corresponding to each stage are represented in orange stars, with informatio flows [purple arrows] and decision points [blue arrows]). These decisions anc predictions of their likely outcomes can be improved by including evaluations of uncertainty into the decision-making process (methods for capturing and characterizing uncertainty at each invasion stage are represented in green ovals). Ultimately, uncertainty cannot be completely eliminated, but it can be reduced via a process of learning-by-doing, termed adaptive wildlife management.