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Directions in reintroduction biology

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Reintroductions are attempts to return species to parts of their historical ranges where they were extirpated, and might involve release of either captive-bred or wild-caught individuals. The poor success rate of reintroductions worldwide has led to frequent calls for greater monitoring, and since 1990 there has been an exponential increase in the number of peer-reviewed publications related to reintroduction. However, these publications have largely been descriptive accounts or have addressed questions retrospectively based on the available data. Here, we advocate a more strategic approach where research and monitoring targets questions that are identified *a priori*. We propose ten key questions for reintroduction biology, with different questions focusing at the population, metapopulation and ecosystem level. We explain the conceptual framework behind each question, provide suggestions for the best methods to address them, and identify links with the related disciplines of restoration ecology and invasion biology. We conclude by showing how the framework of questions can be used to encourage a more integrated approach to reintroduction biology.

Introduction

The term 'reintroduction biology' refers to research undertaken to improve the outcomes of reintroductions and other translocations (Box 1) carried out for conservation purposes. Reintroduction attempts have occurred for at least 100 years [1], but the field of reintroduction biology was born much later in response to the poor success of reintroduction programmes. Although there have been some spectacular success stories (e.g. Ref. [2]), it became clear during the 1980s that most reintroduction attempts were failing and that little was being learned in the process [3–6]. This situation led to the formation of the International Union for Conservation of Nature and Natural Resources Species Survival Commission (IUCN/SSC) reintroduction specialist group (RSG; http://www.iucnsscrsg.org/) in 1988, and to numerous calls for greater monitoring (e.g. Refs [7–9]). The past 20 years have seen not only a substantial increase in monitoring, but also an explosion in the number of reintroduction-related papers in peer-reviewed journals, from <5 per year during the early 1990s to >50 per year currently [10].

Although the growing reintroduction literature is a valuable source of information, it largely consists of descriptive accounts of reintroduction programmes or retrospective analyses [10]. Therefore, the research questions addressed have largely been driven by the monitoring data available rather than the monitoring being driven by the questions. Although any monitoring will produce useful information, unfocused monitoring is an inefficient use of conservation funds in comparison to monitoring designed to address questions identified *a priori* [11]. Unfocused monitoring often leads to conclusions being derived solely by induction (i.e. from *post hoc* detection of patterns in data), which is notorious for leading to poor management of wildlife [12]. Failure to identify questions *a priori* might also result in the most important data not being collected or might result in monitoring effort not being allocated to the projects where it is most needed.

Our agenda here is to promote a more strategic approach to reintroduction biology. Although progress in this field depends partly on the adoption of stronger modes of inference, this point has been made previously [10,13,14] and we do not want to labour it here. Our point is that reintroduction biology will progress faster if researchers focus on the questions that need to be answered to improve species recovery and ecosystem restoration. That is, reintroduction biologists should nominate the key research questions then use the best methods available to answer them, rather than addressing the questions that are most easily answered or that lend themselves to the most rigorous science.

We propose ten key questions for reintroduction biologists to address, with different questions focusing on the population level, metapopulation level and ecosystem level (Figure 1). We explain the conceptual framework behind the questions, provide suggestions for methods to address them, and point to links with the related disciplines of restoration ecology and invasion biology. We conclude by showing how the framework of questions can be used to encourage a more integrated approach to reintroduction biology.

Key questions at the population level

Reintroduction biology has traditionally focused on the factors determining whether reintroductions are successful or not. These factors can be divided into those affecting establishment and spread of populations, following the division often made in invasion biology [15], but we suggest that distinguishing between establishment and persistence is more appropriate for reintroduction (Figure 1). Persistence is more general, because it applies to populations that are geographically bounded, and which therefore grow through increasing density rather than

increasing range, and also to populations that have reached carrying capacity. The dichotomy is useful because reintroduced populations can fail to survive the establishment phase in conditions that would enable long-term persistence once established.

Population establishment
Small release groups can fail to establish populations owing to either chance fates of those individuals (demographic stochasticity), or to low reproduction or survival rates at low densities (Allee effects) [16]. Therefore, the first key question (Q1) is: 'how is establishment probability affected by the size and composition of the release group?' (Figure 1). Populations might also fail to establish owing to high post-release dispersal, or to low survival or reproduction rates while organisms recover from translocation stress or acclimatise to the release site. These factors are related, because high post-release dispersal and

mortality creates a large disparity between the release group size and the effective initial population size. This disparity can be reduced through pre- and/or post-release management, so the second key question (Q2) is: 'how are post-release survival and dispersal affected by pre- and post-release management?' (Figure 1). This can, in turn, be subdivided into questions about effects of specific management practices. Release strategies intended to facilitate acclimatisation are often termed soft release [5], but it cannot be assumed that the strategies used will have the desired effect. For example, although it is often believed that dispersal and/or mortality can be reduced by holding animals at the release site for some period, the experiments conducted have not generally supported this notion (e.g. Refs [17–19]).

Questions about factors affecting post-release survival and dispersal lend themselves to experimental investigation (e.g. Refs [17–21]). It is also possible to experimentally manipulate the size of the release group [22], but such experiments require multiple reintroduction attempts and are unlikely to be feasible with threatened species. A better approach is usually to model the relationship based on the available data on survival, reproduction and dispersal rates for the species and system in question [23–25]. We caution that comparative analyses of reintroduction success rates for multiple species and systems (e.g. Ref [6]) probably give a misleading indication of the relationship between release group size and establishment success. This is because low numbers are generally released when reintroductions are perceived to have low probability of success or if the reintroduction programmes are poorly resourced, creating a bias toward success with large release groups. Where post-release dispersal and mortality are low, populations can potentially establish successfully from <10 released individuals [26].

Habitat effects on population persistence
Regardless of the strategy used to establish a population, a reintroduction will fail if the habitat (Box 2) at the release site cannot support the species. Consequently, the first key question about population persistence (Q3) is: 'what habitat
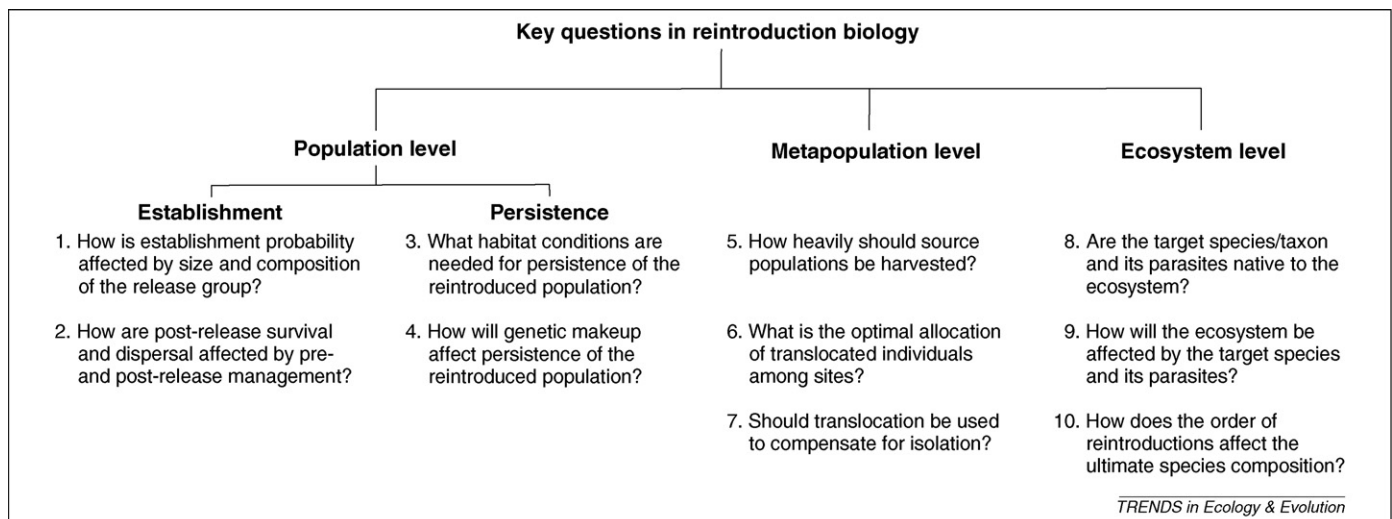

Figure 1. Ten key questions for reintroduction biology, divided into questions at the population, metapopulation and ecosystem level. Population-level questions are divided into questions about establishment and persistence of reintroduced populations.

Box 2. The habitat concept in reintroduction biology

Although habitat is a central concept in ecology and wildlife management, 'habitat' and related terms are used inconsistently in the literature, and usually incorrectly with respect to their original meanings [50]. Hall *et al.* [50] observed that 'habitat quality' should refer to the ability of the environment to provide conditions appropriate for individual and population persistence. They also observed that habitat quality should be explicitly linked to survival and reproduction rates of the species in question, and should not be equated with vegetation features. Consequently, when we refer to 'habitat conditions' needed for persistence of a reintroduced population (Figure 1), we refer to all aspects of the environment, including food, predators and parasites. This traditional use of the habitat concept should encourage reintroduction biologists to carefully consider the biological requirements of species rather than focusing on rapidly assessable features such as vegetation, and to measure habitat quality directly using post-release data on survival and reproduction. Although sophisticated analyses can be used to predict habitat quality before release (e.g. Ref [51]), it is essential to consider whether the data capture the features that are most relevant to the species, especially when the analyses rely on rapid acquisition of data from geographical information systems.

conditions are needed for persistence of the reintroduced population?' (Figure 1). Assuming the number of organisms released is below carrying capacity, the essential pre-requisite for persistence is positive growth and this should be the main target of reintroduction programmes. The IUCN reintroduction guidelines [9] emphasize that the original cause of decline must be identified and eliminated before a species can be reintroduced to a site. Although this sounds simple, assessing the conditions needed for growth is seldom trivial, particularly when assessing reintroduction sites before release (Box 2) given that no data are usually available for the species at the site. Invasion biologists face the same challenge when trying to predict habitats that can be invaded (e.g. Ref [27]), thus similar habitat modelling methods can be applied to projecting fates of invasions and reintroductions. After release, modelling of data on survival, reproduction and dispersal rates can be used to estimate the rate of population growth, and to quantify uncertainty in this relationship.

It might also be possible to use an adaptive management approach whereby habitat conditions are manipulated over time and/or space to determine requirements for population growth. For example, the failure of New Zealand hihi (*Notiomystis cincta*) reintroductions to islands with regenerating forest was suspected to be a result of insufficient food availability, so a series of food supplementation experiments were performed at a release site to estimate the effects of presence, quality and distribution of supplementary food on the growth rate of the reintroduced population [28]. Such adaptive management could be used to develop criteria for future reintroduction sites, as well as for protocols for the population under management.

Genetic effects on population persistence
Although habitat conditions will be the main drivers of population growth, it will also be affected by the intrinsic nature of the organisms. Therefore, the next key question (Q4) is: 'how will genetic makeup affect persistence of the reintroduced population?' (Figure 1). A population could

fail to grow from the outset if the founder group were highly inbred or of inappropriate provenance (i.e. genetically adapted to conditions different from those at the release site). However, a more probable problem is reduction in genetic diversity over time, potentially resulting in inbreeding depression and declining immunocompetence. Such effects are probable if populations remain small, hence ongoing management might be needed. For example, individuals are periodically translocated among reintroduced populations of some New Zealand bird species to reduce inbreeding. Although such management will be necessary in some instances, it can potentially have negative impacts by preventing local adaptation or by wasting resources that could be invested elsewhere [29]. Research is needed in this area, not only to predict how management will affect genetic diversity of reintroduced populations (e.g. Ref [30]), but also to predict effects on population growth and persistence. Making such predictions requires estimating the effects of genetic diversity on survival and reproduction of reintroduced populations, then projecting the impacts using population modelling. We are not aware of any study that has done this as yet.

A conceptual framework for population establishment and persistence
Graeme Caughley [16] noted that strategies for conserving populations tend to follow either the small population paradigm, which deals with the effect of smallness on populations, or the declining population paradigm, which deals with causes of decline and its reversal. Strategies for establishing reintroduced populations (Q1, Q2) ultimately boil down to ensuring that the effective initial population size is sufficient, so fall into the small population paradigm, and strategies for ensuring that persistence is not compromised by genetic makeup (Q4) also largely fall under this paradigm. However, strategies for ensuring that habitat conditions enable persistence (Q3) are within the declining population paradigm, because the key issue is ensuring that the conditions causing the previous decline have been reversed. Following Caughley's lead, we encourage reintroduction biologists to consider both paradigms but to particularly ensure that they incorporate the declining population paradigm in their research programmes by assessing the habitat conditions needed for persistence of populations. Although questions about establishment are usually easier to answer, in our experience the key factors ultimately found to determine whether reintroductions succeed have been habitat factors (e.g. food availability and exotic predators).

Key questions at the metapopulation level
When strategies are extended to multiple populations of a species, the resulting questions can be considered to be at the metapopulation level. The term metapopulation is traditionally used to describe networks of semi-isolated populations connected by natural dispersal [31]. However, conservation managers also use the term to describe networks of populations that can be connected by translocation [29], and any translocation involves at least a simple metapopulation consisting of the source population and recipient population.

Impact on source populations

Although reintroduction biology has traditionally focused on the fates of the reintroduced populations, the potential benefits of establishing these populations need to be balanced against the impact to source populations regardless of whether they are captive [32] or wild [33]. Therefore, the first key question at the metapopulation level (Q5) is: 'how heavily should source populations be harvested?' (Figure 1). This can be addressed through population modelling, but accurate projections require a good understanding of populations' regulatory mechanisms (i.e. the compensatory increases in survival and/or reproduction following density reduction). Harvesting provides density manipulations that are invaluable for understanding these mechanisms, so lends itself to adaptive management. For example, the North Island robin (*Petroica longipes*) population on Tiritiri Matangi Island is being repeatedly harvested for reintroduction to other sites, and the information gained from each density manipulation is used to refine the model used to recommend the size and frequency of subsequent harvests [33].

Allocation of translocated individuals among sites

Moving beyond a single source and recipient population, species recovery programmes often involve multiple reintroductions and many potential reintroduction sites. Therefore, another key question (Q6) is: 'what is the optimal allocation of translocated individuals among sites?' (Figure 1). In our experience such allocations are decided on an *ad hoc* basis during recovery group meetings, but they could potentially be decided using theoretically derived optimisation strategies [34]. Similar methods could also potentially be used to decide the optimal allocation of management effort among sites.

Using translocation to compensate for isolation

The final key question at the metapopulation level (Q7) is: 'should translocation be used to compensate for isolation?' (Figure 1). This is always considered, at least implicitly, because reintroduction is unnecessary if the species is likely to recolonise the site naturally. What is rarely considered is the fact that some local extinctions could be owing primarily to metapopulation dynamics following habitat fragmentation, meaning that translocation could be used to restore distributions without management of habitat. However, if the local extinctions were owing to local declines in habitat quality, this strategy would be disastrous. Addressing this issue requires methods for resolving the roles of habitat quality and metapopulation dynamics in species declines, an endeavour that is by no means trivial [35].

Key questions at the ecosystem level

Although the goal of reintroduction has traditionally been species recovery, reintroductions increasingly occur within the context of ecosystem restoration programmes. Despite this, there has been surprisingly little overlap between the disciplines of reintroduction biology and restoration ecology [36]. The reintroduction literature has taken a single-species perspective and focused on animals [37], whereas the restoration literature has focused on abiotic factors and vegetation [38,39]. We suggest that there are three key questions for reintroduction biology at the ecosystem level, and all of these bridge the two disciplines.

Historic range of target species and its parasites

The first key question at the ecosystem level (Q8) is: 'are the target species/taxon and its parasites native to the ecosystem?' (Figure 1). The IUCN reintroduction guidelines [9] stress that the organisms used for reintroduction should be as close as possible genetically to those originally found in the area, and that introducing (Box 1) a species outside its historic range should be considered only if there is no suitable habitat available within that range. Assessing the historic ranges and genetic provenances of species proposed for translocation is, therefore, a fundamental part of reintroduction biology. However, the parasites carried by a species are considered from a veterinary perspective, usually with no consideration as to whether those parasites already occur at the release site [40] or occurred there historically. The key foci of disease-screening procedures should be to restore host–parasite relationships and prevent introduction of non-native parasites, so need to be accompanied by research designed to reconstruct historic distributions of parasites.

These issues are likely to become increasingly complex in the future, given that global climate change is shifting the distributions of suitable habitat for many species [41]. At least some programmes will have to focus less on restoring what was originally found at a site and instead foucs on facilitating development of ecosystems suitable for new climatic regimes.

Ecosystem effects of releases

The next key question (Q9) is: 'how will the ecosystem be affected by the target species and its parasites?' (Figure 1). This is closely related to Q8, because it can be argued that the primary goal of translocations should be to restore ecosystem function rather than species composition. Although the IUCN reintroduction guidelines [9] make provision for introducing species to new areas to satisfy species recovery goals (see above), a better justification might be to restore the functional roles of extinct species [42]. Research designed to project impacts of translocated species is needed to justify such introductions, to determine which parasites it is most important to screen for, and to prioritise reintroduction of ecosystem engineers [43] and other species crucial to ecosystem function. Studies documenting previous ecosystem-level impacts of reintroductions [44,45] are relevant here, as are methods developed by invasion biologists for projecting impacts of new species on ecosystems [46].

Order of reintroductions

The final key question (Q10) is: 'how does the order of reintroductions affect the ultimate species composition?' (Figure 1). This question comes up frequently in the course of restoration programmes conducted in New Zealand, but decisions are currently made based on intuition. Because the question often concerns species at different trophic levels, one promising area for research is the functional responses between predator and prey species that are

likely to be reintroduced [47], because these responses could determine the ability of the predator and prey to coexist in relation to their initial densities.

The future of reintroduction biology

Reintroduction biology will always have a strong emphasis on case studies because there is no substitute for local knowledge of species and systems. Although meta-analyses might have a greater role in future research, useful meta-analyses depend on good data from individual case studies, and comparative analyses of simple statistics – such as success rates – will produce misleading or trivial results in the absence of such data. Our agenda here is to promote a more strategic approach so that the maximum value can be derived from the case studies being conducted. We envision five ways in which a more strategic approach can be developed using our proposed framework of questions.

First, as we emphasized at the outset, designing monitoring to address questions identified *a priori* will increase the amount of useful knowledge obtained from limited conservation funds.

Second, if researchers consider our full framework of questions, the scope of reintroduction research will increase dramatically. Reintroduction research [10] has so far focused on only four of the ten key questions we propose (Q1–Q3, Q5), with little attention given to meta-population- and ecosystem-level questions.

Third, the framework of questions can be used to improve communication between reintroduction researchers and practitioners. For example, the standard operating procedures for New Zealand translocations are currently being revised to ensure that practitioners consider the questions suggested here. Practitioners might be able to answer most of the questions based on prior expert knowledge and then to seek research support to address questions where the greatest uncertainty exists.

Fourth, the framework of questions will encourage researchers and practitioners to think beyond their own projects. That is, monitoring programmes can be designed not just to address the key questions identified for the current reintroduction, but to address questions of interest to other projects throughout the world. Some reintroductions provide ideal model systems to address general questions and it is important to take advantage of these systems.

Fifth, the framework of questions will encourage researchers and practitioners to build on the previous research. Consideration of questions to address will lead to consultation of previous research results, and those results can be taken into account when designing both management and monitoring strategies. Prior data could also be incorporated into subsequent analysis, and recent developments in Bayesian analysis [48] provide a promising methodology for doing this. For example, population growth rates (Q3, Q4) under a particular management regime could be estimated not just from monitoring data for the current reintroduction, but also incorporating prior estimates, potentially improving the precision of the estimates.

A common thread in our suggestions for a strategic approach to reintroduction biology is greater integration through communication between people and projects. Reintroduction is a challenging endeavour in which difficult decisions often need to be made based on few data. The best response to this challenge is to make the best use of our research resources by working together.

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