

Developing the Science of Reintroduction Biology

PHILIP J. SEDDON,*† DOUG P. ARMSTRONG,‡** AND RICHARD F. MALONEY§

*Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand, email philip.seddon@stonebow.otago.ac.nz

‡Wildlife Ecology Group, Institute of Natural Resources, Massey University, Palmerston North, New Zealand

§Research, Development and Improvement Division, Department of Conservation, P.O. Box 13049, Christchurch, New Zealand

Abstract: *With recent increases in the numbers of species reintroduction projects and reintroduction-related publications, there is now a recognizable field of reintroduction biology. Nevertheless, research thus far has been fragmented and ad hoc, rather than an organized attempt to gain reliable knowledge to improve reintroduction success. We reviewed 454 recent (1990–2005) peer-reviewed papers dealing with wildlife reintroductions from 101 journals. Most research has been retrospective, either opportunistic evaluations of techniques or general project summaries, and most inference is gained from post hoc interpretation of monitoring results on a species-by-species basis. Documentation of reintroduction outcomes has improved, however, and the derivation of more general principles via meta-analyses is expected to increase. The fragmentation of the reintroduction literature remains an obstacle. There is scope to improve reintroduction biology by greater application of the hypothetico-deductive method, particularly through the use of modeling approaches and well-designed experiments. Examples of fruitful approaches in reintroduction research include experimental studies to improve outcomes from the release of captive-bred animals, use of simulation modeling to identify factors affecting the viability of reintroduced populations, and the application of spatially explicit models to plan for and evaluate reintroductions. We recommend that researchers contemplating future reintroductions carefully determine a priori the specific goals, overall ecological purpose, and inherent technical and biological limitations of a given reintroduction and that evaluation processes incorporate both experimental and modeling approaches. We suggest that the best progress will be made when multidisciplinary teams of resource managers and scientists work in close collaboration and when results from comparative analyses, experiments, and modeling are combined within and among studies.*

Keywords: management, population restoration, reliable knowledge, reintroduction biology, species recovery, translocation

Desarrollando la Ciencia de Biología de la Reintroducción

Resumen: *Con el reciente incremento en el número de proyectos de reintroducción de especies y de publicaciones relacionadas con reintroducciones la biología de la reintroducción es un campo reconocible. Sin embargo, la investigación hasta ahora ha sido fragmentada y ad hoc, en vez de un intento organizado para obtener conocimiento confiable para mejorar el éxito de las reintroducciones. Revisamos 454 artículos recientes (1990–2005), revisados por pares, sobre reintroducciones de vida publicados en 101 revistas. La mayor parte de la investigación ha sido retrospectiva, ya sea evaluaciones oportunistas de técnicas o resúmenes de proyectos generales, y la mayoría de las inferencias se obtienen de la interpretación post hoc de resultados de monitoreo una base de especie por especie. Sin embargo, la documentación de los resultados de reintroducciones ha mejorado, y se espera que aumente la derivación de principios más generales por medio de meta análisis. La fragmentación de la literatura sobre reintroducción sigue siendo un obstáculo. Se tiene el propósito de mejorar la biología de la reintroducción con una mejor aplicación del método hipotético-deductivo, particularmente por medio del uso de métodos de modelado y experimentos bien diseñados. Entre los ejemplos de métodos*

†Additional affiliation: Bird Section, World Conservation Union, Species Survival Commission, Reintroduction Specialist Group

**Additional affiliation: Oceania Section, World Conservation, Species Survival Commission, Reintroduction Specialist Group
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fructíferos en la investigación sobre reintroducción se incluyen estudios experimentales para mejorar los resultados de la liberación de animales criados en cautiverio, el uso de modelos de simulación para identificar factores que afectan la viabilidad de poblaciones reintroducidas y la aplicación de modelos espacialmente explícitos para planificar y evaluar reintroducciones. Recomendamos a los investigadores que contemplen llevar a cabo reintroducciones en el futuro que a priori determinen cuidadosamente las metas específicas, el objetivo ecológico general y las limitaciones técnicas y biológicas inherentes de una reintroducción y que los procesos de evaluación incorporen tanto métodos experimentales como de modelado. Sugerimos que el progreso será mejor cuando equipos multidisciplinarios de gestores de recursos y cinéticos trabajen en colaboración cercana y cuando los resultados de análisis comparativos, experimentos y modelado sean combinados dentro y entre los estudios.

Palabras Clave: biología de la reintroducción, conocimiento confiable, gestión, recuperación de especies, restauración de la población, translocación

Introduction

Reintroduction projects attempt to reestablish species within their historical ranges through the release of wild or captive-bred individuals following extirpation or extinction in the wild (IUCN 1998). Such programs have traditionally been undertaken purely as management exercises and have seldom been designed to meet research objectives. During the 1990s, however, there have been frequent pleas in the literature for more monitoring of reintroductions, a greater focus on research, and the application of experimental approaches (Armstrong et al. 1994; Sarrazin & Barbault 1996; Seddon 1999). Since that time the level of monitoring of reintroduction projects has increased substantially, and several studies have been published testing hypotheses associated with reintroductions (e.g., Wolf et al. 1998; Armstrong & Perrot 2000; Bar-David et al. 2005; Bretagnolle & Inchesti 2005). There is therefore now a recognizable field of reintroduction biology. Nevertheless, reintroduction research so far has generally been fragmented and ad hoc, rather than an organized attempt to gain the knowledge needed to improve the success of reintroduction programs. We reviewed the recent animal reintroduction literature to provide a summary of the principal research topics and approaches to date. We then used our summary as a basis for outlining useful directions for reintroduction research and illustrated these by reviewing some examples of fruitful approaches in reintroduction studies.

A Brief History of Reintroductions

Humans have moved domesticated or captive animals from one place to another for millennia, and there is a well-documented history of wildlife releases to establish new food resources, for biological pest control, and for aesthetic reasons (Griffith et al. 1989; Green 1997), although these have frequently entailed release of species outside their natural ranges (Vitousek et al. 1997). Movement of native species may involve the release of animals

within their natural ranges to restock hunted populations, to solve human-wildlife conflicts (Fischer & Lindenmayer 2000), or to supply nonconsumptive industries such as nature-based tourism. The reintroduction of species to fulfill a biodiversity preservation or restoration objective is a relatively recent activity that has developed as a consequence of increasing global awareness of the need to conserve biological diversity in the face of species extinctions.

It is difficult to identify the first true reintroduction, but one candidate is the 1907 release of 15 American bison (*Bison bison*) into a newly established reserve in Oklahoma (Kleiman 1989), a project that anticipated the need for careful planning, prerelease health-risk assessment, strong local community support, and the use of corporate and media backing (Beck 2001). It was a model for reintroductions that was not often upheld in the decades to follow, where reintroductions frequently involved the release of animals with little planning and often no monitoring.

Increased awareness of reintroduction as a viable conservation option was enhanced by the high-profile reintroductions of a few charismatic vertebrates in the 1970s and 1980s, including the Arabian oryx (*Oryx leucoryx*) in Oman (Stanley Price 1989), golden lion tamarins (*Leontopithecus rosalia*) in Brazil (Kleiman & Mallinson 1998), and Peregrine Falcons (*Falco peregrinus*) in North America (Cade & Burnham 2003). Reintroductions are an attractive option for generating publicity, particularly because handling, transport, and release of animals are media-friendly events and show concrete action being taken by concerned authorities, whereas the subsequent fates of reintroduced populations attract little media attention. The available data for wildlife reintroductions in the 1970s and 1980s suggest the majority failed to establish viable populations (Griffith et al. 1989; Wolf et al. 1996).

It was a proliferation of ill-conceived releases that prompted the formation of the Reintroduction Specialist Group (RSG) under the auspices of the World Conservation Union's (IUCN) Species Survival Commission

Table 1. Trends in numbers of animal species that are the focus of known reintroduction projects from 1900.

Taxon	1900-1992	By 1998	By 2005
Invertebrates	2	19	65
Fish	9	11	20
Reptile & amphibians	22	42	94
Birds	54	69	138
Mammals	39	77	172
Total	126	218	489
References	Beck 1994*	Stanley Price & Soorae 2003	Seddon et al. 2005

*Includes only the reintroduction of captive-born animals and is therefore likely to be an underestimate of all animal reintroduction projects.

(SSC) (Stanley Price & Soorae 2003). The RSG was created in 1988 to provide guidance for increasing numbers of wildlife restoration projects globally. The RSG's first strategic planning workshop was held in 1992 and led to formulation of Reintroduction Guidelines (IUCN 1998). By early 2006 the RSG consisted of a volunteer network of over 300 practitioners and maintained a database of nearly 700 reintroduction projects. One of the resolutions of the second RSG Strategic Planning Workshop in 2002 was that it was insufficient to encourage monitoring and that the RSG should provide strategic research direction in reintroduction biology. This resolution led to a symposium (Developing the Science of Reintroduction Biology) at the Third International Wildlife Management Congress in 2003 and the production of this paper. Further information about RSG activities and publications is available from <http://www.iucnsscrs.org/>.

In addition, changing public attitudes toward captive wildlife have encouraged zoos to expand their activities to wider conservation measures including reintroductions. Furthermore, governments and private organizations have increasingly attempted reintroductions to reestablish or restock populations for conservation or hunting. The consequence has been a recent marked increase in the number of animal reintroduction programs, as indicated by increases in the number of species that are the focus of reintroduction attempts (Table 1).

Trends in Reintroduction Research

Reintroduction as a conservation tool seeks to restore viable populations of native species within their former ranges. The dichotomy between management and research is that wildlife managers manipulate systems to achieve management objectives rather than to discover more about how systems work (McNab 1983). Management manipulations typically lack controls, replicates, adequate monitoring, or even the guidance of explicit objectives, let alone hypotheses. In such cases nothing can be learned about what variables were important in a suc-

cessful manipulation, and even less knowledge is gained from failures, which tend to be undocumented.

In the early years many reintroduction projects were purely management manipulations, often doomed to failure due to poor planning, inappropriate founder animals (confiscations from illegal trade, surplus animals from captive breeding programs, or problem exotic pets), low sample sizes, and lack of resources. The attitude was largely "let's put some animals out there and see if they survive." Postrelease monitoring was negligible or absent so that causes or timing of failures were unknown, as were the processes by which reintroduced populations may have become established. In part through the efforts of the RSG and those of biologists associated with well-organized reintroduction projects, the prevalence of adequate postrelease monitoring increased and well-documented failures as well as successes found their way into the scientific literature.

To examine trends in reintroduction research we compiled a list of 515 reintroduction-related papers published since 1935 by combining the results of searches on Biblioline Wildlife and Ecology Studies (<http://biblioline.nisc.com>) and Web of Science (<http://isiknowledge.com>). We searched for the key term *reintroduction*. This excluded papers relating to releases of wildlife for other purposes, such as introductions of non-native species, supplementation of existing wild populations not previously established through reintroduction, and translocation of problem wildlife. We included only full papers published in peer-reviewed journals, excluding newsletter articles, published abstracts and papers only peripherally related to reintroductions. The resulting compilation is therefore not an exhaustive summary of reintroduction-related publications but is, we believe, indicative of longer-term trends in reintroduction publications (Fig. 1).

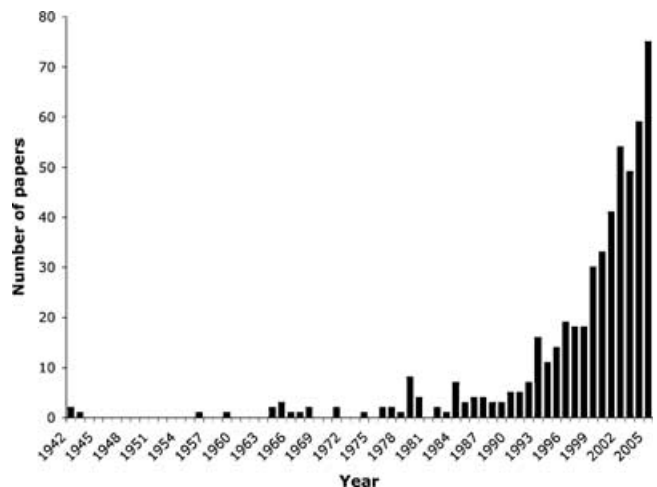


Figure 1. Number of reintroduction-related papers published in peer-reviewed journals by year since the first records located up to 2005.

Table 2. Proportions of reintroduction papers published between 1990 and 2005 by journal.*

Total papers/ journal (%)	Total overall (%)	Number of papers	Journal
>4	35	157	<i>Biological Conservation; Conservation Biology; Journal of Wildlife Management; Oryx</i>
1-4	36	165	<i>Animal Conservation; Journal of Zoo and Wildlife Medicine; Wildlife Society Bulletin; Zoo Biology; Biodiversity and Conservation; Molecular Ecology; Restoration Ecology; Canadian Field Naturalist; Conservation Genetics; Ecological Applications; Journal of Applied Ecology; Journal of Arid Environments; Journal of Mammalogy; Journal of Wildlife Disease; Journal of Zoology; Mammal Review; South African Journal of Wildlife Research; Wildlife Research</i>
<1	29	132	<i>American Journal of Primatology; Auk; Condor; Ecological Modelling; Ibis; International Journal of Primatology; Journal of Animal Ecology; Journal of Avian Medical Surgery; Journal of Raptor Research; Northwestern Naturalist; Proceedings of the Royal Society of London—Biological Sciences; Western North American Naturalist, plus 68 other titles available from corresponding author</i>

*Each journal is ranked according to the proportion of the total papers published in them and placed in one of three groups, each comprising approximately one-third of the total number of papers. Each journal in a category contains that category's proportion of papers (e.g., *Biological Conservation, Conservation Biology, the Journal of Wildlife Management, and Oryx, each have >4% of the total of 454 papers and overall account for 35% of all papers*).

The trend has been few publications between 1942 and the late 1970s, followed by modest but increasing numbers of papers through the late 1990s, and a relatively recent marked increase from 2000. So what are reintroduction biologists studying and reporting? To assess recent trends in reintroduction research, we examined more closely a subset of 454 journal articles published from 1990 to 2005 inclusive.

Location of Research

The 454 papers relating to wildlife reintroductions were scattered over 101 journals. Although the premier conservation journals *Conservation Biology* and *Biological Conservation* were well represented, papers in these two journals constituted <0.25 of all papers. Approximately two-thirds of the papers were in only 22 journals that contained 17–78 papers each, but the remaining one-third of papers were scattered over 79 journals and some of these

journals are obscure (Table 2). This summary does not include books, book chapters, technical reports or other gray literature. This fragmentation of outputs may hamper reintroduction biologists' efforts to access, cite, and build on the work of others.

Topic of Research

We placed papers into one of nine categories, depending on the principal topic being addressed: (1) captive management, (2) veterinary management, (3) general accounts, (4) population dynamics, (5) genetics, (6) social factors, (7) habitat, (8) ecosystem effects, and (9) behavior of released animals. See Table 3 for a full description of each category.

The best-represented categories (Table 3) were general accounts (category 3) and population dynamics (category 4), reflecting an emphasis on documentation of reintroduction outcomes and explicit assessment of the

Table 3. Proportions of the 454 reintroduction papers published between 1990 and 2005 within each of nine topic categories.

Topic category	Description	Papers (%)
Captive management	captive breeding and care, handling, transport, prerelease behavioral training, release methods	10
Veterinary management	diagnosis and treatment of disease, trauma in both captive and released animals, postrelease disease-related risk assessment	6
General accounts	status (numbers, range, threats) of species being reintroduced, including feasibility of planned releases	21
Population dynamics	estimation of vital rates (survival, productivity), documentation of dispersal, factors affecting these parameters	21
Genetics	taxonomic status of proposed founder animals and retrospective evaluations of the origins of poorly documented releases	15
Social factors	e.g., local attitudes to proposed or ongoing releases	4
Habitat	release-site suitability, habitat requirements for viable populations, habitat preparation and restoration, habitat selection by released animals	11
Ecosystem effects	predator-prey interactions, effects and interactions between released animals and other elements	7
Behavior	e.g., social behavior or foraging	5

status and viability of released populations, respectively. Investigations of genetics and habitat requirements were increasingly prevalent, particularly as part of preproject feasibility studies and preparation. There were relatively few studies on human dimensions (dominated by studies of human attitudes to proposed reintroductions of large carnivores), behavior, and veterinary aspects.

Research and Nonresearch Approaches

We also classified each of the 454 papers into one of six categories according to their primary approach. Research papers were divided into three approaches: (A) retrospective evaluation of specific parameters in an opportunistic or a posteriori fashion, including both statistical and anecdotal evaluations; (B) experimental approaches designed to test hypotheses about reintroduction strategies; (C) use of population modeling to project growth, expansion, and/or viability of reintroduced populations. Non-research papers were divided into three additional categories: (D) papers relating to general planning and discussion of implications for future releases; (E) progress or status reports, project evaluations, summaries, and descriptions of general results; (F) discussions of general principles and development of general guidelines.

Most reintroduction publications (59%) were retrospective studies, either opportunistic evaluations of techniques or investigations of specific parameters (category A, 41%) or general project summaries or progress reports (category E, 18%). Experimental (category B) and modeling (category C) approaches were used in 8% and 15% of studies, respectively, whereas general planning (category D) was a focus of 13% of papers. The least-common papers discussed or developed the application to reintroductions of general principles from other disciplines such as population ecology (category F, 5%).

Of the research approaches taken (i.e., excluding categories D, E, and F), 65% of the 291 papers in categories A, B, or C were category A, opportunistic evaluations of specific parameters; 23% involved application of modeling techniques to guide future work (category C); and 12% could be classified as experimental (category B). Clearly, over the last 15 years opportunistic a posteriori evaluations have continued to dominate the literature, and although there has been a rise in the application of modeling approaches that inform future reintroductions, there are still relatively few examples in the reintroduction literature of rigorous experimental tests of explicit hypotheses.

Reintroduction Biology: Gaining Reliable Knowledge

Williams (1997) suggests that the maturation of a scientific discipline can be divided into three stages: (1) ob-

servations guided by intuition, tradition, and guesswork; (2) organization of those observations into coherent categories, the exploration of observations for patterns, and the clear description of patterns; and (3) recognition of the underlying causes of patterns and formulation of theories that lead to testing of predictions deduced from these.

So how mature is reintroduction biology as a discipline? Reintroduction practitioners and biologists have largely progressed beyond stage 1—advances gained solely through intuition and guesswork—and have gone some way to categorizing observations, although the exploration of observations for patterns still appears to be in its infancy.

Platt (1964) argues that some fields of scientific endeavor advance more rapidly than others due to application of a process he calls “strong inference,” whereby alternative hypotheses are put forward to explain some observed phenomena and crucial experiments are used to eliminate alternatives and thereby lead to the formulation of general conclusions. Romesburg (1981) makes a similar argument to explain what he perceives as the poor performance of wildlife science. He notes that wildlife scientists worked largely through induction, whereby general conclusions are drawn from a set of premises derived from observations, and that induction is an unreliable mode of inference when used alone. He advocates that wildlife scientists should make greater use of the hypothetico-deductive method, whereby general postulates (model, explanation, or theory) are used to deduce hypotheses that can be tested experimentally.

Reintroduction biology as a scientific discipline is still largely in a phase of inductive inference, involving the compilation and organization of observations relating to certain taxa to derive patterns of association and explore the causes of such patterns. Consequently, much of the focus to date has been on components of the reintroduction process that are accessible and easily measured, such as release techniques, rather than on factors that may be more critical to the successful establishment and long-term persistence of a new population. The process of deduction will necessarily require specific knowledge of species and systems, but must also involve more general theory if reintroduction is to advance as a discipline. This theory need not spring de novo out of the reintroduction discipline, but should draw on theory from population ecology, ethology, genetics, and other disciplines. In turn, reintroductions can potentially provide opportunities for tests of fundamental theory (Sarrazin & Barbault 1996).

Although we advocate greater emphasis on explicit development and testing of theory in reintroduction biology, we do not necessarily advocate Platt's (1964) narrow vision of strong inference. Platt's argument has been criticized for its assumption that there is only one effective scientific method and his failure to identify other cases of important scientific progress that did not use this method

(O'Donohue & Buchanan 2001). It is difficult, if not impossible, to perform replicated, controlled experiments to address many ecological questions (Bennett & Adams (2004), and it is usually least feasible when working with threatened species. Therefore, although we advocate the use of experiments when they can be feasibly used to address questions in reintroduction biology, alternative or complementary approaches will be needed in many cases. One approach is the replication of entire studies (i.e., metareplication), whereby conclusions derived from separate studies of the same process provide a more powerful test of the generality of findings than could any single study (Johnson 2002). Another approach is adaptive management, whereby management actions are "experiments" in the sense that they are designed to gain information (Holling 1978), but management decisions are reviewed continually rather than following a rigid experimental protocol (Lee 1999). Recent statistical advances in information-theoretic inference (Burnham & Anderson 1998) and Bayesian inference (Ellison 1996) have facilitated powerful analyses of data that were not collected in classic experimental designs (Holl et al. 2003).

Examples of Research Approaches in Reintroduction Biology

Below are some selected examples of recent reintroduction-related research that we believe illustrate the types of benefits to be gained from a scientific approach. We examined three areas: application of an experimental approach to improve outcomes from the release of captive-bred animals, use of population modeling to evaluate the factors limiting population establishment, and the recent application of geographical information systems and spatially explicit models to plan for reintroduction projects.

Experiments to Mitigate the Effects of Captivity in Reintroductions

A large and growing number of reintroduction projects entail the release of captive-bred animals, but with the apparently greater success of reintroductions involving wild-to-wild translocations (Griffith et al. 1989; Wolf et al. 1996), there are concerns that captivity may decrease the ability of individuals to survive in the wild (Kleiman et al. 1994; Snyder et al. 1996). Captive animals could potentially have poor health, due either to captive conditions (Mathews et al. 2005) or stress during the release process (Hartup et al. 2005), and captivity may result in the inadvertent selection of individuals lacking key traits, such as fearfulness (McPhee 2003), or present a lack of opportunities for animals to acquire essential learned behaviors,

such as predator recognition (Kleiman 1989; Griffin et al. 2000). Understanding and mitigating these factors is essential for ethical reasons and for ensuring successful reintroduction.

Although some form of prerelease conditioning is widely believed to be beneficial, the benefits have been described as more a matter of faith than of science (Dobson & Lyles 2000). For example, hand rearing of captive animals has been criticized for the likelihood that abnormal behaviors will occur after release; however, the perception that parent-rearing methods will always be superior is being challenged by the results of a number of well-designed experimental studies (Kreger et al. 2005). For example, hand rearing with puppets results in increased vigilance and possibly contributes to increased survival of the Common Raven (*Corvus corax*), used as a model for the Hawaiian Crow (*C. hawaiiensis*) and the Mariana Crow (*C. kubaryi*) (Valutis & Marzluff 1999). Results of a 4-year experiment comparing hand-reared and parent-reared Mississippi Sandhill Cranes (*Grus canadensis pulla*) demonstrated that hand-reared cranes had better postrelease survival (Ellis et al. 2000).

Experiments with other forms of prerelease conditioning have also been used to revise and improve management procedures. In 1991, 49 captive-bred black-footed ferrets (*Mustela nigripes*) were released in Wyoming. Unfortunately, all the ferrets had been raised in cages and all released with the same postrelease support; thus, no comparative evaluation was possible (Biggins et al. 1999). Subsequent releases experimentally compared the effect of three alternative rearing strategies on behavior and survival and determined that ferrets reared in quasi-natural outdoor pens placed over prairie dog (*Cynomys leucurus*) burrows had better prey-catching skills and higher survival (Biggins et al. 1999). As a result of this work, the use of such on-site preconditioning pens became standard practice in Colorado, Montana, and New Mexico (Dobson & Lyles 2000).

Mortality caused by predation is a significant factor limiting the survival of released captive-bred animals, and interest has grown in the possibility of teaching naïve animals to recognize predators (e.g., Maloney & McLean 1995). Nevertheless, in the absence of evidence, the idea of teaching animals about predators may be viewed skeptically by wildlife managers (Griffin et al. 2000). High postrelease mortality of reintroduced Houbara Bustards (*Chlamydotis* spp.) was due to predation by red foxes (*Vulpes vulpes*) (Combreau & Smith 1998). The initial management response of translocating red foxes away from the Houbara release site was halted after it was found that foxes quickly returned to the area (Lenain & Warrington 2001). Experimental cohorts of bustards were matched by age and released under identical conditions to assess the efficacy of alternative forms of prerelease training (van Heezik et al. 1999). Birds were divided into prerelease treatment groups exposed to either a model

or a live predator under standardized conditions and a predator-naïve control group. Contrary to expectations, use of a model predator was not an effective conditioning stimulus, but prerelease training with a live predator significantly improved postrelease survival (van Heezik et al. 1999). These results provide evidence of the type and intensity of prerelease training necessary to improve postrelease survival.

In general an experimental approach is most productively applied to evaluate management options and to test assumptions relating to factors within management control. Without such explicit tests of assumptions, in which potentially confounding variables are accounted for, there is a danger that untested ideas enter management lore and are applied uncritically at some cost and with no benefit.

Population Modeling to Evaluate Reintroductions

The application of computer simulation models is now a standard approach to project the trajectory of populations of conservation concern. Population viability analysis (PVA) is used to predict the likely future status of a population (Morris & Doak 2002) and thus provides a quantitative basis for evaluating alternative management strategies. The availability of commercial programs such as VORTEX has facilitated the application of population modeling in reintroduction planning (e.g., Bustamante 1998) and postrelease evaluation (e.g., Slotta-Bachmayr et al. 2004). With improvements in the quality of data derived from carefully designed postrelease monitoring and awareness of the potential pitfalls of uncritical use of commercial software packages (Morris & Doak 2002), recent reintroduction-related population assessments have used custom-built models (e.g., Schaub et al. 2004; Armstrong et al. 2006).

The direct benefits of PVA for management are evident in a number of studies. Simulations of Bearded Vulture (*Gypaetus barbatus*) populations determined that plans to expand reintroductions would dangerously deplete the captive source population (Bustamante 1996). Population modeling highlighted the need to establish a second population to ensure the viability of beaver (*Castor fiber*) reintroduced in the Netherlands (Nolet & Bavoco 1996). A deterministic population model indicated that the high mortality of released California Condors (*Gymnogyps californianus*) exceeded the levels necessary for projected population stability and focused management attention on the need to address sources of lead contamination before establishment of a viable wild population was possible (Meretsky et al. 2000).

Simulation models were used to identify the factors affecting survival of reintroduced passerines in New Zealand, with a focus on population dynamics in relation to habitat. New Zealand Robins (*Petroica longipes*)

were released onto a predator-free island with only small amounts of fragmented habitat, and simulations suggested that the small population was viable and could be harvested by managers to use for other translocations (Armstrong & Ewen 2002). A population model for a reintroduced island population of Saddlebacks (*Philesturnus carunculatus*) indicated that proposed future releases on mainland sites would not be viable because animals would be killed if aerial poison drops were used to control mammalian predators, but that the alternative use of permanent poison bait stations should reduce mortality to acceptable levels (Davidson & Armstrong 2002). The failure of early attempts to reintroduce Stitchbirds (*Notiomystis cincta*) on predator-free islands was hypothesized to be due to food limitation. This idea was tested with experimental on-off provision of supplementary food at a new reintroduction site (Armstrong & Perrott 2000), and population-simulation modeling was used to confirm the value of this management intervention. More important, the simulations showed project managers the need for sustained control of nest mites and the likely existence of one or more additional limiting factors (Armstrong et al. 2002).

Some form of population modeling should be part of every reintroduction evaluation to explore the possible short-term consequences of management strategies, identify key vital rates, provide information on uncertainty of population persistence, and assess longer-term viability. PVA is acknowledged, however, to be more than an attempt to model a probability of extinction because the need to synthesize information about a species entails close collaboration between managers and scientists to develop a long-term process of modeling and research to refine models and explore management options. In this way PVA can be, as the above studies illustrate, a powerful example of adaptive management (Boyce 1992).

Geographic Information Systems and Spatially Explicit Models

The IUCN reintroduction guidelines emphasize the need for an assessment of the availability of suitable habitat as a key component of reintroduction planning (IUCN 1998). Sophisticated tools have been applied to the identification of suitable release sites, particularly geographic information systems (GIS) to model the distribution of available habitat (e.g., Li et al. 2002; Hirzel et al. 2004; McShea et al. 2005). Increasingly, however, such assessments have been extended beyond the derivation of habitat maps that can assist in the selection of future release sites to consideration of patch-specific characteristics as the basis for the development of spatially explicit models. The combination of the power of GIS with the flexibility of PVA in recent work has set new standards for reintroduction planning. Suitable release sites for the reintroduction of

wild boar (*Sus scrofa*) were identified in Scotland with GIS, and the PVA program RAMAS was used to calculate the necessary size of a founder population (Leaper et al. 1999). The two tools were more closely linked, for the first time in reintroduction planning, in the evaluation of reintroduction strategies for beavers (*Castor fiber*) in Scotland, where GIS was used to identify available habitat. This information was then used to construct a custom-built GIS-based model of population dynamics and dispersal (MacDonald et al. 2000; South et al. 2000).

Most recently work toward the reintroduction of Eurasian lynx (*Lynx lynx*) has fully integrated the evaluation of habitat suitability and distribution (Kramer-Schadt et al. 2002) with the development of GIS-based statistical models to quantify characteristics of lynx home range in fragmented landscapes (Schadt et al. 2002). This information was used within a spatially explicit dispersal model to assess the probability of a dispersing lynx reaching a suitable habitat patch (Kramer-Schadt et al. 2004). The ultimate product was an individually based spatially explicit model that could simulate potential spatiotemporal population dynamics and thereby test the viability of a reintroduced population under different scenarios (Kramer-Schadt et al. 2005).

Conclusions

Over the last 15 years most reintroduction research could be classified as descriptive (i.e., studies that anecdotally or statistically evaluate parameters in an opportunistic or a posteriori fashion). Far less common have been experimental approaches specifically designed to test hypotheses rigorously or scientifically evaluate reintroduction techniques. Most inference in reintroduction biology takes place by induction, gained from post hoc interpretation of monitoring results or through exploratory comparative analyses. There is scope to improve reintroduction biology by greater application of the hypothetico-deductive method, where models derived from careful observation and theory are subject to testing. Factors likely responsible for the dominance of descriptive studies over experimental and modeling approaches include greater technical ease (i.e., measuring things that are most easily measured), inadequate planning, lack of financial resources, small sample sizes associated with most reintroduction efforts, and frequent lack of statistical controls. Nevertheless, rigorous experimental or adaptive management approaches can yield reliable knowledge when correctly applied to reintroductions. We recommend that researchers contemplating future reintroductions carefully evaluate a priori the specific goals, overall ecological purpose, and inherent technical and biological limitations of a given reintroduction, and that planning and evaluation processes incorporate both experimental and modeling approaches. We recognize that any reintroduction

attempt will benefit from both good management and good research, and we suggest that the best progress will be made by multidisciplinary teams of resource managers and scientists working in close collaboration and when results from comparative analyses, experiments, and modeling are combined within and among studies.

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Literature Cited

- Armstrong, D. P., and J. K. Perrott. 2000. An experiment testing whether condition and survival are limited by food supply in a reintroduced Hibi population. *Conservation Biology* **14**:1171–1181.
- Armstrong, D. P., et al. 2002. Population dynamics of reintroduced forest birds on New Zealand islands. *Journal of Biogeography* **29**:609–621.
- Armstrong, D. P., and J. G. Ewen. 2002. Dynamics and viability of a New Zealand Robin population reintroduced to regenerating fragmented habitat. *Conservation Biology* **16**:1074–1085.
- Armstrong, D. P., T. Soderquist, and R. Southgate. 1994. Designing experimental reintroductions as experiments. Pages 27–29 in M. Serena, editor. *Reintroduction biology of Australian and New Zealand Fauna*. Surrey Beatty & Sons, Chipping Norton, New South Wales.
- Armstrong, D. P., E. H. Raeburn, R. M. Lewis, and D. Ravine. 2006. Estimating the viability of a reintroduced New Zealand Robin population as a function of predator control. *Journal of Wildlife Management* **70**:1020–1027.
- Bar-David, S., D. Saltz, T. Dayan, A. Perelberg, and A. Dolev. 2005. Demographic models and reality in reintroductions: Persian fallow deer in Israel. *Conservation Biology* **19**:131–138.
- Beck, B. B. 1994. Reintroduction of captive-born animals. Pages 265–286 in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner, editors. *Creative conservation: interactive management of wild and captive animals*. Chapman & Hall, London.
- Beck, B. B. 2001. A vision for reintroduction. *Communiqué* September 2001: 20–21. American Zoo and Aquarium Association, Silver Spring, Maryland.
- Bennett, L. T., and M. A. Adams. 2004. Assessment of ecological effects due to forest harvesting: approaches and statistical issues. *Journal of Applied Ecology* **41**:585–598.
- Biggins, D. E., A. Vargas, J. L. Godbey, and S. H. Anderson. 1999. Influence of prerelease experience in reintroduced black-footed ferrets (*Mustela nigripes*). *Biological Conservation* **89**:121–129.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* **23**:481–506.
- Bretagnolle, V., and P. Inchausti. 2005. Modelling population reinforcement at a large spatial scale as a conservation strategy for the declining little bustard (*Tetrax tetrax*) in agricultural habitats. *Animal Conservation* **8**:59–68.
- Burnham, K. P., and D. R. Anderson. 1998. *Model selection and inference*. Springer, New York.
- Bustamante, J. 1996. Population viability analysis of captive and released Bearded Vulture populations. *Conservation Biology* **10**:822–831.
- Bustamante, J. 1998. Use of simulation models to plan species

- reintroductions: the case of the bearded vulture in southern Spain. *Animal Conservation* **1**:229–238.
- Cade, T. J., and W. Burnham. 2003. Return of the Peregrine. The Peregrine Fund, Boise, Idaho.
- Combreau, O., and T. R. Smith. 1998. Release techniques and predation in the introduction of houbara bustards in Saudi Arabia. *Biological Conservation* **84**:147–155.
- Davidson, R. S., and D. P. Armstrong. 2002. Estimating impacts of poison operations on nontarget species using mark-recapture analysis and simulation modeling: an example with saddlebacks. *Biological Conservation* **105**:375–381.
- Dobson, A., and A. Lyles. 2000. Black-footed ferret recovery. *Science* **288**:985–988.
- Ellis, D. H., et al. 2000. Postrelease survival of hand-reared and parent-reared Mississippi Sandhill Cranes. *The Condor* **102**:104–112.
- Ellison, A. M. 1996. An introduction to Bayesian inference for ecological research and environmental decision-making. *Ecological Applications* **6**:1036–1046.
- Fischer, J., and D. B. Lindenmayer. 2000. An assessment of the published results of animal relocations. *Biological Conservation* **96**:1–11.
- Green, R. E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *Journal of Animal Ecology* **66**:25–35.
- Griffin, A. S., D. T. Blumstein, and C. Evans. 2000. Training captive-bred or translocated animals to avoid predators. *Conservation Biology* **14**:1317–1326.
- Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* **245**:477–480.
- Hartup, B. K., G. H. Olsen, and N. M. Czekala. 2005. Fecal corticoid monitoring in Whooping Cranes (*Grus maricana*) undergoing reintroduction. *Zoo Biology* **24**:15–28.
- Hirzel, A. E., B. Posse, P. A. Oggier, Y. Crettenand, C. Glenz, and R. Arlettaz. 2004. Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. *Journal of Applied Ecology* **41**:1103–1116.
- Holl, K. D., et al. 2003. Landscape restoration: moving from generalities to methodologies. *BioScience* **53**:491–500.
- Holling, C. S. 1978. Adaptive environmental assessment and management. John Wiley and Sons, Chichester, United Kingdom.
- IUCN (World Conservation Union). 1998. Guidelines for reintroductions. IUCN/SSC Re-introduction Specialist Group, IUCN, Gland, Switzerland, and Cambridge, United Kingdom.
- Johnson, D. H. 2002. The importance of replication in wildlife research. *Journal of Wildlife Management* **66**:919.
- Kleiman, D. G. 1989. Reintroduction of captive mammals for conservation. *BioScience* **39**:152–161.
- Kleiman, D. G., and J. J. C. Mallinson. 1998. Recovery and management committees for lion tamarins: partnerships in conservation planning and implementation. *Conservation Biology* **12**:27–38.
- Kleiman, D. G., M. R. Stanley Price, and B. B. Beck. 1994. Criteria for reintroductions. Pages 287–303 in P. J. S. Olney, G. M. Mace, and A. T. C. Feistener, editors. *Creative conservation: interactive management of wild and captive animals*. Chapman and Hall, New York.
- Kramer-Schadt, S., F. Knauer, P. Kaczensky, E. Revilla, T. Weigand, and L. Trepl. 2002. Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. *Ecological Applications* **12**:1469–1483.
- Kramer-Schadt, S., E. Revilla, T. Wiegand, and U. Breitenmoser. 2004. Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. *Journal of Applied Ecology* **41**:711–723.
- Kramer-Schadt, S., E. Revilla, and T. Wiegand. 2005. Lynx reintroduction in fragmented landscapes of Germany: projects with a future or misunderstood wildlife conservation? *Biological Conservation* **125**:169–182.
- Kreger, M. D., J. S. Hatfield, I. Estevez, G. F. Gee, and D. A. Clugston. 2005. The effects of captive rearing on the behavior of newly-released Whooping Cranes (*Grus americana*). *Applied Animal Behaviour Science* **93**:165–178.
- Leeper, R., G. Massei, M. L. Gorman, and R. Aspinall. 1999. The feasibility of reintroducing wild boar (*Sus scrofa*) to Scotland. *Mammal Review* **29**:239–259.
- Lee, K. 1999. Appraising adaptive management. *Conservation Ecology* **3**: <http://www.consecol.org/vol3/iss2/art3/>.
- Lenain, D. M., and S. Warrington. 2001. Is translocation an effective tool to remove predatory foxes from a desert protected area? *Journal of Arid Environments* **48**:205–209.
- Li, X., D. Li, Y. Li, Z. Ma, and T. Zhai. 2002. Habitat evaluation for crested ibis: a GIS-based approach. *Ecological Research* **17**:565–573.
- Macdonald, D. W., F. H. Tattersal, S. Ruston, A. B. South, S. Rao, P. Maitland, and R. Strachan. 2000. Reintroducing the beaver (*Castor fiber*) to Scotland: a protocol for identifying and assessing suitable release sites. *Animal Conservation* **3**:125–133.
- Maloney, R. E., and I. G. McLean. 1995. Historical and experimental learned predator recognition in free-living New Zealand Robins. *Animal Behaviour* **50**:1193–1201.
- Mathews, F., M. Orros, G. McLaren, M. Gelling, and R. Foster. 2005. Keeping fit on the ark: assessing the suitability of captive-bred animals for release. *Biological Conservation* **121**:569–577.
- McNab, J. 1983. Wildlife management as scientific experimentation. *Wildlife Society Bulletin* **11**:397–401.
- McPhee, M. E. 2003. Generations in captivity increases behavioural variance: considerations for captive breeding and reintroduction programmes. *Biological Conservation* **115**:71–77.
- McShea, W. J., K. Koy, T. Clements, A. Johnson, C. Vongkhamheng, and M. Aung. 2005. Finding a needle in the haystack: regional analysis of suitable Eld's deer (*Cervus eldi*) forest in Southeast Asia. *Biological Conservation* **125**:101–111.
- Meretsky, V. J., N. F. R. Snyder, S. R. Beissinger, D. A. Clendenen, and J. W. Wiley. 2000. Demography of the California Condor: implications for reestablishment. *Conservation Biology* **14**:957–967.
- Morris, W. F., and D. F. Doak. 2002. *Quantitative conservation biology*. Sinauer Associates, Sunderland, Massachusetts.
- Nolet, B. A., and J. M. Baveco. 1996. Development and viability of a translocated beaver *Castor fiber* population in the Netherlands. *Biological Conservation* **75**:125–137.
- O'Donohue, W. J. A., and Buchanan. 2001. The weaknesses of strong inference. *Behavior and Philosophy* **29**:1–20.
- Platt, J. R. 1964. Strong inference. *Science* **146**:347–353.
- Romesburg, C. H. 1981. Wildlife science: gaining reliable knowledge. *Journal of Wildlife Management* **45**:293–313.
- Sarrazin, F., and R. Barbault. 1996. Reintroduction: challenges and lessons for basic ecology. *Trends in Ecology & Evolution* **11**:474–478.
- Schadt, S., et al. 2002. Assessing the suitability of central European landscapes for the reintroduction of Eurasian lynx. *Journal of Applied Ecology* **39**:189–203.
- Schaub, M., R. Pradel, and J.-D. Lebreton. 2004. Is the reintroduced white stork (*Ciconia ciconia*) population in Switzerland self-sustainable? *Biological Conservation* **119**:105–114.
- Seddon, P. J. 1999. Persistence without intervention: assessing success in wildlife re-introductions. *Trends in Ecology & Evolution* **14**:503.
- Seddon, P. J., P. S. Soorae, and E. Launay. 2005. Taxonomic bias in reintroduction projects. *Animal Conservation* **8**:51–58.
- Slotta-Bachmayr, L., R. Boegel, P. Kaczensky, C. Stauffer, and C. Walzer. 2004. Use of population viability analysis to identify management priorities and success in reintroducing Przewalski's horses to southwester Mongolia. *Journal of Wildlife Management* **68**:790–798.
- Snyder, N. F. R., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, S. B. Smith, W. D. Toone, and B. Miller. 1996. Limitations of captive breeding in endangered species recovery. *Conservation Biology* **10**:338–348.

- South, A., S. Ruston, and D. Macdonald. 2000. Simulating the proposed reintroduction of the European beaver (*Castor fiber*) to Scotland. *Biological Conservation* **93**:103-116.
- Stanley Price, M. R. 1989. *Animal re-introductions: the Arabian oryx in Oman*. Cambridge University Press, Cambridge, United Kingdom.
- Stanley Price, M. R., and P. S. Soorae. 2003. Reintroductions: whence and whither? *International Zoo Yearbook* **38**:61-75.
- Valutis, L. L., and J. M. Marzluff. 1999. The appropriateness of puppet-rearing birds for reintroduction. *Conservation Biology* **13**:584-591.
- van Heezik, Y., P. J. Seddon, and R. F. Maloney. 1999. Helping reintroduced houbara bustards avoid predation: effective anti-predator training and the predictive value of pre-release behaviour. *Animal Conservation* **2**:155-163.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-induced global change. *New Zealand Journal of Ecology* **21**:1-16.
- Williams, B. K. 1997. Logic and science in wildlife biology. *Journal of Wildlife Management* **61**:1007-1015.
- Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation Biology* **10**:1142-1154.
- Wolf, C. M., T. Garland, and B. Griffith. 1998. Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. *Biological Conservation* **86**:243-255.

