

## Reintroduction: challenges and lessons for basic ecology

François Sarrazin  
Robert Barbault

**Ecology is a subject where theoretical predictions are often difficult to test experimentally in the field. To address this challenge, the Ecological Society of America suggested exploiting large-scale environmental management decisions in a scientific way. This 'adaptive management' constitutes one of the purposes of the Sustainable Biosphere Initiative. Meanwhile, in the current context of the biodiversity crisis, translocations and particularly reintroductions of threatened species are becoming more numerous. It is time for ecologists and wildlife managers to collaborate on these unique opportunities for large-scale studies.**

François Sarrazin and Robert Barbault are at l'Université Pierre et Marie Curie, Laboratoire d'Ecologie, URA 258 CNRS, Bât A. 7ème étage, 7 Quai Saint Bernard, BP 237, 75252 Paris Cedex 05, France (Fsarrazi@snnv.jussieu.fr).

The threats to biodiversity resulting from human activities, and the understandable reluctance to perturb their study subject, often prevent ecologists from developing their own large-scale experiments. Therefore, long-term monitoring or experiments on model species are often used, but this may limit the range of testable hypotheses<sup>1-3</sup>. Meanwhile, faced with the increasing numbers of translocations<sup>4,5</sup>, the International Union for Conservation of Nature (now IUCN – The World Conservation Union) proposed in 1987 to define reintroduction as the introduction of a species in a previously occupied area in order to improve the conservation of the species. Reintroduced individuals may come from captive breeding programs or be translocated from natural populations. The IUCN also recommended that reintroduction programmes incorporate feasibility studies and preparatory, introduction and monitoring periods<sup>6</sup>. Moreover, restoration of the original habitat and amelioration of causes of extinction were considered as essential conditions for these projects. Unfortunately, the monitoring period that should follow reintroductions often remains neglected<sup>4,7,8</sup> or is documented only in 'grey' literature.

Our purpose is to show that, in order to combine the recommendations of the IUCN and the Sustainable Biosphere Initiative<sup>9</sup>, reintroduction programs should systematically include ecologists who are proficient in population biology and genetics, behavioural ecology and evolution. They could then generate a fruitful approach for testing hypotheses in basic ecology, and particularly in population biology (Box 1). Without overlooking conservation issues, reintroduction programs could provide important opportunities for

real-scale hypothetico-deductive experiments in ecology.

### The mutual scepticism of field conservationists and population biologists

Despite the recent development of conservation biology as a science<sup>10-12</sup>, the gap between field conservationists and scientists persists. Caughley<sup>12</sup> distinguished two approaches in conservation biology: the declining population paradigm and the small population paradigm. The first investigates extinction processes empirically case by case, and the second theoretically considers the consequences of smallness on population viability. In restoration ecology<sup>13,14</sup>, reintroduction suffers from the same discrepancy between practical works published in grey literature (see Ref. 15) and a comparatively poor theoretical background.

Practical reasons explain this situation. Non-governmental organizations, which usually initiate reintroduction programs, are supported by sponsors requiring maximum efficiency in terms of time and cost. They aim at protecting and restoring biodiversity, but the understanding of the mechanisms of population extinction and growth is not their first priority. Moreover, Kleiman *et al.*<sup>6</sup> suggested that reintroduction success seemed more linked to biopolitical conditions and long-term funding than to scientific rigour. Obviously reintroduction in a hostile human context<sup>16</sup>, and with low funding, would be very unlikely to succeed whatever the biological background, but once funding and local agreement are obtained, the success of reintroduction remains a question of population viability involving demographic, genetic, behavioural and ecological processes.

This kind of misunderstanding probably explains the poor level of involvement by ecologists, and particularly population biologists, in reintroduction programs – only slightly more than half of the reintroductions involve professional biologists<sup>7</sup>. Academic laboratories generally face constraints preventing them from sustaining long-term and costly applied projects on their own. On the other hand, as Lindburg<sup>17</sup> emphasized, many biologists 'outside the community of zoo professionals' argue that the large amount of money necessary for single species reintroduction could be spent far more usefully to protect whole ecosystems from destruction. They also underline that environmental conditions at the time of release are rarely exactly the same as those prevailing before extinction, and the extinction causes are often difficult to determine and to quantify<sup>18</sup>. Furthermore, reintroductions in developed countries – particularly reintroductions of large vertebrates – generally suppose that the future population will be artificially maintained at least for some time because of continuing human impact on the ecosystem<sup>18</sup>. This is against the IUCN recommendations, but often remains difficult to prevent. In many cases, the reintroduced populations contain few individuals, at least during the first years, and they may be difficult to observe<sup>7</sup>. Moreover, some behavioural traits exhibited by these individuals can be altered by captivity or human imprinting, or by low density of conspecifics. These negative effects may vanish in the first wild-born generation, at least for species in which social learning and cultural transmission are low. However, demographic and even behavioural studies require long-term effort, to achieve sufficient sample sizes and relevant observations in the second generation. The possibility of controlling and replicating should also be considered. To assess the particular effect of population foundation on any biological trait, it is desirable to study a control sample in natural conditions. This is possible in the case of local reintroduction – that is, where remnant populations persist in other areas – but not when reintroduction constitutes the only way to restore a species that is extinct in the wild.

Overall, the scepticism of scientists results from the basic problem of reintroduction: the initial decision concerning reintroduction is usually a pragmatic choice and not a scientific one. Indeed, even when the IUCN conditions are respected, the decision of release remains a political one. Because the role of biodiversity in general, and of one species in particular, is often hard to establish from a strictly scientific point of view, philosophical, aesthetic or more economic reasons usually

lead to such projects. Therefore, ecologists generally have fewer arguments in favour of reintroduction than against it. We want to show that the planning and monitoring of reintroduced populations may be relevant for both conservationists and ecologists provided that they work together<sup>6,19</sup>.

### Reintroduction preparation and knowledge of species biology

Whenever reintroduction managers use scientific tools, the questions they aim to answer are generally focused on the preparation phase of translocations. The challenge of captive breeding<sup>20</sup> requires studies of the genetic consequences of inbreeding<sup>21</sup>, behavioural consequences of captivity<sup>22</sup>, and population consequences of infectious diseases<sup>18</sup>, involving mainly veterinary and zoo biologists. Many efforts are dedicated to the maintenance of high levels of genetic variation in captive-bred and reintroduced populations. This may be achieved by selecting individuals with known pedigrees<sup>23</sup>, individuals with high allozyme heterozygosity or individuals coming from geographically separated populations<sup>24</sup>. However, in the last case, the consequences of outbreeding depression must be considered<sup>25</sup>. Moreover, reintroduced individuals lack locally selected traits that are likely to have existed in the extinct populations<sup>18</sup>. In the case of population reinforcement, the impact of releases on the residual population implies caution regarding the origin of translocated individuals (e.g. Ref. 26).

This bias towards genetics should not mask the need for a priori knowledge about life history traits of reintroduced species<sup>4,6</sup>. Caughley<sup>12</sup> underlined that endangered species, which should be the primary target of translocations, are also among the least understood. He also argued that half the books on conservation biology published in the 1980s were about genetics. However, demographic and environmental stochasticity are also likely to have a short-term impact on very small<sup>11,18,27</sup> and reintroduced populations. Moreover, all biological factors able to play a role in population viability do so by acting on survival and fecundity rates, whatever their genetic, behavioural or environmental origin. Therefore, a good knowledge of the demography of a species is crucial to assessing the possible effects of all factors affecting reintroduction success. In that way, comparative studies in population biology can provide useful information.

### Reintroduction monitoring as an assessment of reintroduction methods

Monitoring of reintroduced populations after releases provides an assess-

ment of reintroduction methods, which can be useful in other projects<sup>50</sup>. Recently, Cade and Temple<sup>15</sup> reviewed the success of numerous bird reintroduction programs according to the methods involved. It appeared, however, that even the success criterion was not clearly defined among authors. For example, Craig and Reed (in Ref. 15) think that a three-year breeding population with a recruitment rate that is higher than the death rate of adults describes successful reintroduction. According to Minimum Viable Population studies, Beck *et al.*<sup>7</sup> consider 500 free-living individuals as representing good success and regret the low availability of published results using this criterion. However, without taking into account life history traits, habitat quality or the eventual metapopulation structure (which varies widely between reintroduced populations), this threshold of 500 individuals seems relatively arbitrary<sup>18</sup>. Since the settlement of a self-sustaining population corresponds to a dynamic process, extinction probability estimates that combine population size, growth rate and growth rate variance<sup>28</sup> should be the main criteria for assessing this success. This necessitates the accurate estimate of demographic parameters such as survival rates<sup>29</sup> and the modelling of various dynamics scenarios, including unexpected catastrophic events. A shorter term criterion to assess this success could be the breeding of the first wild-born generation in the release area<sup>30</sup>. Clearly, elaborating success criteria for reintroduction, at least similar to Mace's<sup>31</sup> criteria for threatened species, is an urgent challenge for theoretical population biology.

Results from already reintroduced populations can also be important for further project preparation. By recording as much relevant information as possible on potential release candidates (such as origin, sex, age, breeding status), it becomes possible to model the efficiency of different release strategies using simulations with various survival and reproductive rates obtained from the monitoring of reintroduced populations<sup>32,33</sup>. Similarly, surrogates have already been used to improve release strategies of the Californian condor (*Gymnogyps californianus*)<sup>34</sup> and black-footed ferrets (*Mustela nigripes*)<sup>35</sup>. Outside the conservation area, numerous game species translocations<sup>4</sup> could be exploited as experiments in order to improve our understanding of reintroduction requirements.

Moreover, once the new population is settled, wildlife managers have to judge the feasibility of further releases, the relaxation of help for already released individuals, and the long-term viability of the population. In that way, in stage or age-structured population models, the analyses of growth rate sensitivity<sup>28,36</sup> to

demographic parameters can be used to determine what kind of individuals should be protected or which measures should be adopted to maintain and encourage the expansion of a population.

Again, population dynamics models that integrate demographic parameters and behavioural data recorded in the field can lead to simulations and tests of a priori hypotheses. The use of previous results to design further decisions is a central concept of adaptive management, that is, learning by doing<sup>2</sup>. In that purely applied context, population ecologists should therefore collaborate on reintroduction programs.

Some projects on Arabian oryx (*Oryx leucoryx*)<sup>23</sup>, black-footed ferrets (*Mustela nigripes*)<sup>16,35</sup> or golden lion tamarin (*Leontopithecus rosalia*)<sup>30</sup> are now recognized for having been precisely designed and well documented and many others are just too recent to give relevant results. For both preparation and monitoring of reintroductions, increasing contacts between academic population biologists and wildlife managers is encouraged within the Survival Species Commission (SSC, IUCN), especially the Conservation Breeding Specialist Group (CBSG) and the Reintroduction Specialist Group (RSG) (Ref. 37). Such forums, including Conservation Assessment and Management Plans (CAMPs), Global Captive Action Plans (GCAPs) and Population and Habitat Viability Assessment (PHVA), have already covered various aspects of status assessment, captive breeding, and reintroduction opportunities and organization for more than 2100 taxa<sup>38</sup>. They are often dedicated to whole groups of endangered species with international involvement, but they constitute good examples for more permanent scientific collaborations at the local scale.

### Reintroduction as a way to experiment in ecology

The two previous points concern what ecologists can contribute to reintroductions. However, reintroduction monitoring can also constitute a framework for more-theoretical ecological studies in an extended view of 'adaptive management'.

First, restoration has already been identified as an 'acid test for ecology' since its success checks our understanding of ecosystems<sup>39</sup>. Reintroduction could therefore become an 'acid test for population biology'.

Second, reintroduction monitoring could be a good opportunity for evolutionary biologists to complement their knowledge of processes among the wide range of plant and animal models. Indeed, the characteristics that lead some species to be reintroduced make them interesting models for biologists. Reintroduction concerns

species that disappeared recently under human impact on the environment. In many cases, extinctions are due to the disturbance of whole habitats – particularly isolated island habitats. Although knowledge of species status varies among taxa<sup>40</sup>, it appears that extinction rates resulting from interactions between environment and species characteristics are higher for habitat specialists or long-lived species exhibiting extreme life history traits<sup>11,41</sup>. Moreover, whatever the motivations of their choice, conservationists often choose flagship species to be reintroduced. Despite the warnings of taxonomists<sup>42</sup> that many invertebrates are disappearing each year, most reintroduction efforts concern 'charismatic' megafauna: for example,

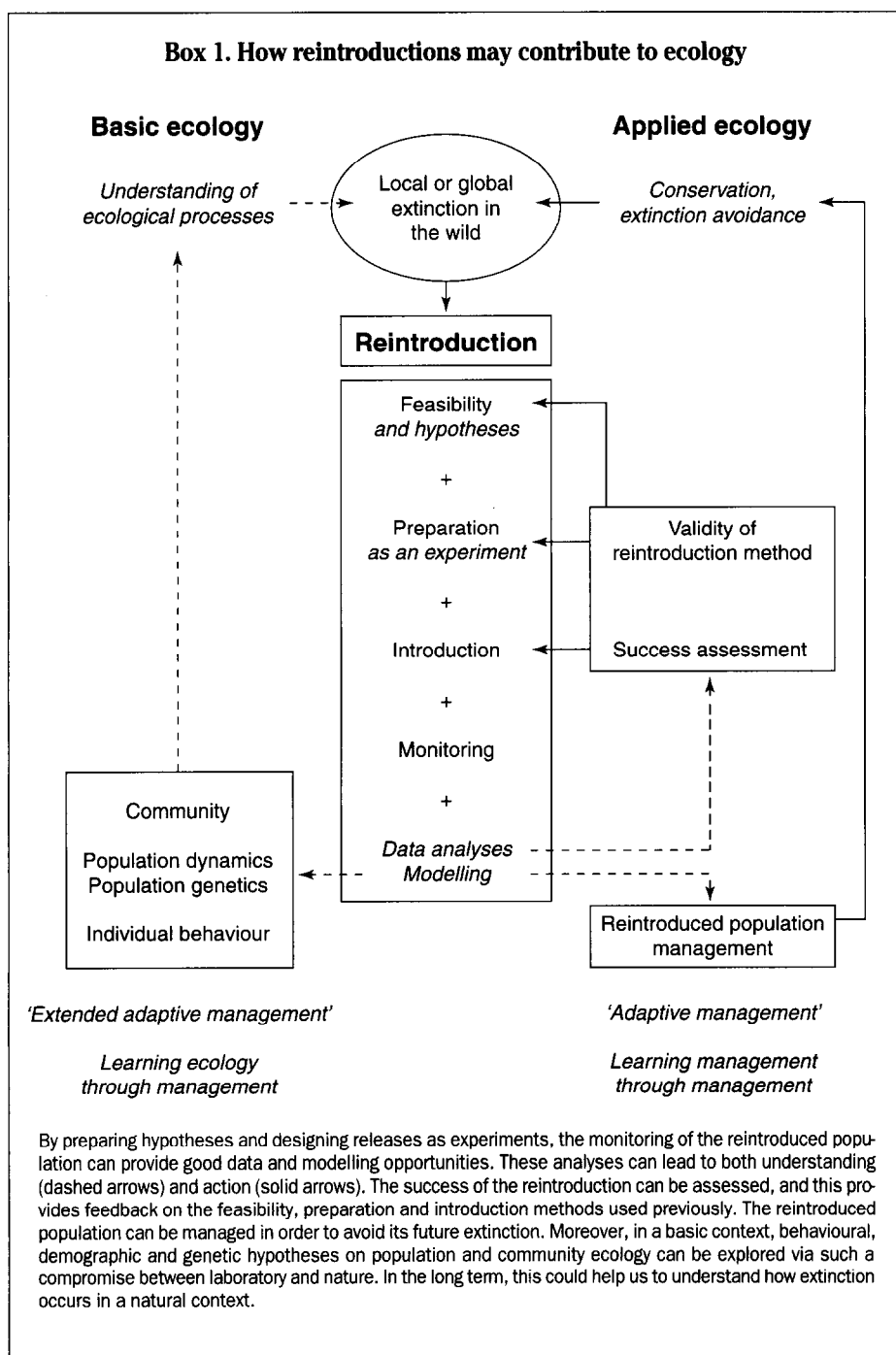
Californian condor (*Gymnogyps californianus*), white-tailed sea eagle (*Haliaeetus albicilla*), griffon vulture (*Gyps fulvus*), Przewalski's horse (*Equus przewalskii*), white rhinoceros (*Ceratotherium simum*) or orang-utan (*Pongo pygmaeus*)<sup>4,5,15</sup>. These large species often display the most extreme life history traits among the pool of endangered species such as low reproductive rate, late age at maturation, long generation times, low density, and so on. Because of these characteristics, they cannot be studied in the laboratory and natural populations cannot easily be manipulated and studied considering their endangered status. Consequently, reintroduction programs constitute unique opportunities for experimental work

concerning their behavioural, population and community ecology.

Third, behavioural ecologists may use reintroductions to study newly founded populations in which the origin of each individual is known. They can be aged, sexed and individually identified by genetic methods of fingerprinting, which allow, for example, studies of mating strategies. Morton<sup>43</sup> planned experimental introductions of wrens (*Cyphorhinus phaeocephalus* and *Henicorhina leucosticta*) to study the settlement abilities, habitat selection and vital requirements of these species at an individual level. Komdeur<sup>44</sup> assessed the role of habitat saturation and territory quality in the evolution of cooperative breeding by translocating Seychelles warblers (*Acrocephalus sechellensis*) in a recovery context. Release strategies can allow the comparison of groups coming from different environments<sup>35</sup>. The study of the appearance of social transmission in newly founded groups may also be considered.

Fourth, reintroduced populations may show many characteristics induced by colonization and founder effects that remain rarely studied in the wild, although being strongly emphasized in metapopulation studies<sup>45</sup>. To mimic the natural colonization that is likely to occur in metapopulation, three conditions should be fulfilled: (1) the biology of released individuals should not be altered by captivity or translocation; (2) the released individuals should mimic propagules (age and sex of dispersers); and (3) their number should be likely to occur in nature. The impact of translocation on the biology of propagules may be assessed by comparison with second generation individuals<sup>29,46,50</sup>, and amelioration of translocation effects remains one of the challenges of reintroductions. Similarly, the intrinsic value of individuals as dispersers can be discussed – introduction experiments only test settlement ability not dispersal<sup>47</sup>. Furthermore, numbers of releases are often maximized in order to increase reintroduction success inducing a breach of the third point. However, assuming these conditions, the a priori constitution of future released cohorts permits tests of different hypotheses concerning settlement mechanisms, such as the importance of conspecific attraction<sup>48</sup>. Moreover, demographic and genetic monitoring of the reintroduced population may provide potential assessments of bottleneck and founder effects. In the same way, the appearance of density-dependent processes resulting from increasing intra-specific or interspecific competition, and the revision of the controversial carrying capacity concept could be assessed by monitoring reintroduced populations.

Finally, reintroduction programmes may facilitate studies of the role of



keystone species in community ecology. Rosenzweig<sup>49</sup> argued that it is generally impossible to study community ecology by looking at small perturbations. Only removing or adding species in the wild would be likely to give significant patterns. Obvious ethical arguments usually prevent ecologists from doing this outright, but reintroductions provide a way. By monitoring ecosystems during the feasibility and preparatory periods advised by the IUCN, and considering, for example, disturbance in food webs or competition in any niche dimensions induced by the reintroduced species, it seems possible to assess the role of these species at the community and perhaps the ecosystem level.

Deliberate or accidental invasions have already constituted opportunities for ecological studies<sup>18</sup>. However, all individuals of a reintroduced population may be of known origin. The size of the original population is known exactly and this allows predicted models of population dynamics and genetics to be tested. Moreover, demographic parameters can be estimated, at least during the first years, for the overall population and not only for an indeterminate part of it.

### What timing for reintroduction studies?

It is quite clear that the timescale involved in these different approaches varies strongly (Box 1). The preparation of reintroduction, including a priori knowledge of reintroduced species and the reintroduction success assessment, is a matter of urgency because of the increasing number of reintroduction projects. The management of reintroduced populations implies long-term monitoring with direct interactions between ecologists and managers. The theoretical use of reintroduction, as basic experiments, must, by definition, not be constrained by time, although it will eventually lead back to microconservation biology<sup>42</sup> by allowing a better knowledge of metapopulation functioning and extinction mechanisms and finally limiting the need for reintroductions.

Restoration must remain the main aim of reintroductions. Nevertheless, reintroductions offer a unique opportunity for experimental studies on ecological processes. It behoves us as ecologists and conservationists not to let this opportunity pass.

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## Sewall Wright meets Artificial Life: the origin and maintenance of evolutionary novelty

Yukihiko Toquenaga  
Michael J. Wade

**A decade ago, Langton coined the term Artificial Life (A-Life) to identify the new field of research that is attempting to create and characterize open-ended evolving systems using diverse computer-based methods. Fruitful interactions between A-Life research and that of conventional biological sciences (B-Life) are rare. Using the framework of molecular and evolutionary genetics, we discuss some of the reasons for this lack of conceptual cross-pollination between the disciplines and we identify some potential areas for interdisciplinary collaboration.**

Yukihiko Toquenaga is at the Institute of Biological Sciences, University of Tsukuba, Japan (toque@biol.tsukuba.ac.jp); Michael Wade is at the Dept of Ecology and Evolution, University of Chicago, 1103 E. 57th Street, Chicago, IL 60637, USA (mwade@pondside.uchicago.edu).

‘What is life?’ and ‘what could life be?’ are central questions in the interdisciplinary field of Artificial Life (A-Life). It tries to subsume all of the conventional domain of the biological sciences (B-Life) and it can make fundamental contributions to our understanding of B-Life processes<sup>1,2</sup>. However, a decade after the birth of A-Life, there are few reciprocal contributions between the A-Life and B-Life sciences. These two sciences converge most conspicuously in the development of genetic algorithms, which are computer-based models for creating open-ended evolving systems in A-Life in addition to solving complex problems in

engineering. Modern texts in evolutionary genetics rarely cite any A-Life publications<sup>3–5</sup> and some biologists have considered these genetic algorithms as computer exercises in pseudo-genetics: *ad hoc* treatments with a fragmentary theoretical basis of B-life genetics. Computer scientists, on the other hand, have found few if any useful theorems in evolutionary genetics that improve the adaptive performance of genetic algorithms or that permit the solution of complex problems (cf. Ref. 6).

We discuss the general structure and findings of genetic algorithms (see definition in Box 1) in the context of classical

evolutionary and population genetics. The lack of reciprocal exchange between the fields results from the different questions each is trying to address. These differences in central questions lead the fields to differ in the emphasis placed upon the evolutionary forces that consume or generate genetic and phenotypic variations. Finally, we discuss the conceptual convergence between some A-Life models and the evolutionary genetic theories of Sewall Wright, and indicate some unexplored avenues for two-way interactions between genetic algorithms and population genetics.

### Evolutionary and population genetics

The goal of population genetics theory is to characterize and to discriminate among the several evolutionary forces that operate simultaneously in natural populations. The mathematical tools of the theory vary from simple linear algebra to statistical and stochastic diffusion models. A major focus is the balance among evolutionary forces that maintains genetic variation in natural populations. The signature of natural selection is detected by comparison with the predictions of null models where only the neutral forces (mutation and random drift) are operating. Two extreme views coexist within formal evolutionary theory<sup>7</sup>.

#### The fisherian worldview

R.A. Fisher proposed that adaptation typically takes place in large and randomly mating populations<sup>3–5,7,8</sup>. Random drift is negligible in this context and mutation and selection are sufficient to explain patterns of genetic variation. Fisher’s fundamental theorem of natural selection (FFT)<sup>8</sup> predicts that the rate of adaptive evolution of a population is determined