Old wine, new bottles? Using history to inform the assisted colonization debate

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Abstract Assisted colonization, or the translocation of species threatened with extinction to habitats outside their indigenous range (usually as a response to predicted climate shifts), is a divisive issue for conservationists. Yet, history shows that wildlife scientists were discussing the trade-offs and challenges of translocating species for conservation purposes, including introducing them to new habitats, long before anthropogenic climate change was recognized as posing a conservation problem. Here we examine a case of the scientific and policy deliberations of a high profile group of scientists and policy advisers from the 1960s (the U.S. Bureau of Sport Fisheries and Wildlife's Committee on Rare and Endangered Wildlife Species) to provide a useful historical context for assessing current debates on assisted colonization. The Committee's attempt to produce a consistent policy for the 'transplantation' of threatened species illustrates how translocation debates have long hinged on an unresolved set of scientific and conceptual concerns, including the relative value of individual species and historically intact ecosystems and the philosophical status of human-assisted movement of wildlife. Bringing the Committee's deliberations to light places contemporary debates over assisted colonization in the USA in their historical context and illustrates how what often appear to be highly technical and scientific disagreements over conservation translocations are ultimately driven by deeper conceptual issues about the means and ends of conservation.

Keywords Climate change, conservation history, conservation policy, threatened species, translocation

Introduction: the assisted colonization debate in historical context

A ssisted colonization (also known as managed relocation or assisted migration) is the practice of translocating species, threatened with extinction by local and/or global environmental change, outside their

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Received 14 July 2012. Revision requested 19 October 2012. Accepted 31 October 2012. First published online 21 November 2013. indigenous range (Ricciardi & Simberloff, 2009a). It has proved to be a controversial idea, eliciting sharp disagreements in the scientific community over its potential risks and rewards (e.g. McLachlan et al., 2007; Davidson & Simkanin (2008); Hoegh-Guldberg et al., 2008; Ricciardi & Simberloff, 2009a, b; Richardson et al., 2009; Seddon, 2010; Thomas, 2011; Webber et al., 2011). Much of this discussion derives from the uncertainty over whether assisted colonization will exacerbate or avert ecological destruction. From one viewpoint, assisted colonization is not an acceptable conservation option because its potential for causing significant ecological harm is seen as too high (Ricciardi & Simberloff, 2009a; Sandler, 2010). From another, however, the extinction risk posed by multi-dimensional threats such as climate change forces us to consider assisted colonization and other interventions if we wish to save species vulnerable to changes over the coming decades (Minteer & Collins, 2010). Conservation translocation is not a novel development: for example, the U.S. Fish and Wildlife Service has often engaged in translocation of threatened species to recover declining populations (e.g. Benz, 1989). Such translocations, however, have typically been conservation reintroductions rather than conservation introductions, given that the movement of individuals was within the species' historical range. Assisted colonization, however, is a potentially more contentious form of translocation in that it entails the release of organisms outside their indigenous range (Seddon et al., 2012).

An analysis of the historical context of conservation translocations (including reintroductions and introductions) is useful for understanding and informing the current debate over assisted colonization as a conservation response to anthropogenic climate change and other threats. Here we examine a controversial case of the movement of bird species in Hawaii in the 1960s, a case that revolved around establishing a scientifically coherent and consistent policy for what was then called 'species transplantation'. At the time scientists and policy advisers argued over issues that would resonate today: the ecological consequences of translocating species to new habitats (including outside their historical ranges), the relative value of species vs ecosystems, and the past failures of species translocations. Although global climate change is a catalyst for the contemporary discussion about assisted colonization, our research shows that today's debate resurrects decades-old issues in conservation practice. In particular, the modern assisted colonization debate circles back to concerns about species protection and ecosystem integrity that were never

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resolved by U.S. scientists and policy advisers in the late 1960s and early 1970s (and thus did not inform subsequent conservation policy). We believe that these issues remain unsettled at the international level, although organizations such as IUCN are now clarifying the terminology, techniques and motivations underlying discussions of such conservation translocations. Our analysis illustrates how science-based determinations regarding what species are to be conserved, and how this should be done, must be made within a broader decision environment informed by both ecological and value-based commitments, including those of the public.

The case we studied is that of the Committee on Rare and Endangered Wildlife Species, scientists and wildlife managers within the U.S. Bureau of Sport Fisheries and Wildlife who were chosen in 1964 to offer advice for developing a federal policy on threatened species. In the late 1960s and early 1970s the Committee's scientists sought an intellectually consistent scientific position regarding the translocation of threatened species within and outside historical habitats. The discussions among these committee members anticipate many of the current disagreements over the risks and benefits of assisted colonization as an acceptable conservation tactic, including the tension between species-centred and ecosystem-centred approaches to conservation, and the distinction between human-assisted movement of populations and natural dispersal.

In reviewing this case we demonstrate the parallels between current deliberations over species translocations under climate change and earlier concerns over species vulnerability and ecosystem integrity that prompted U.S. wildlife scientists and policy advisers in the 1960s and 1970s to consider moving species to new habitats. Our analysis also helps to explain the divisiveness apparent in many of today's scientific exchanges. Present-day arguments over assisted colonization, despite their link to contemporary concerns about global climate change, are in many ways a rehashing of deeper and older debates that predate the 1973 U.S. Endangered Species Act—issues that continue to polarize conservation scientists.

What to do with threatened Hawaiian birds?

In 1956 the Fish and Wildlife Act established, within the U.S. Department of the Interior, the Bureau of Sport Fisheries and Wildlife, the predecessor of the modern U.S. Fish and Wildlife Service (Aldrich, undated). Eight years later, the Committee on Rare and Endangered Wildlife Species was formed within the Bureau to advise on creating a federal endangered species programme (Barrow, 2009; Winston, 2011). In the decade before the Endangered Species Act was signed into law the Bureau, and especially the Committee, was at the centre of sweeping changes in U.S. wildlife

conservation policy that continue to shape the conservation of threatened species.

The Committee on Rare and Endangered Wildlife Species was tasked with advising the Director of the Bureau on 'Rare and Endangered Species of birds, mammals, fish (including mollusks and crustacea), reptiles, amphibians, and biotic communities of the United States, including: [the] official designation of rare and endangered species and biotic communities (sic)' (U.S. Department of the Interior, 1964). For nearly a decade the Committee contributed to U.S. federal endangered species policy, culminating with passage of the Endangered Species Act in 1973 (Winston, 2011). Most of the conceptual work leading to the Act, such as identifying biological targets of conservation and establishing a captive-breeding programme at the Patuxent Wildlife Research Center in Laurel, Maryland, was carried out by Committee members from the Bureau's Division of Wildlife Research, especially from the Division's Bird and Mammal Laboratories (Winston, 2011). The Smithsonian Institution Archives in Washington, DC, hold an extensive record of the Laboratories' activities, including the scientific and policy debates surrounding species transplantations in the context of saving threatened wildlife.

By 1967 the Committee had been meeting for 3 years, the threatened species research programme at the Patuxent Wildlife Research Center had been operating for 2 years, and the Office of Endangered Species of the Bureau of Sport Fisheries and Wildlife would celebrate its first anniversary. In this year Winston Banko, the first federal field biologist assigned exclusively to the study of threatened wildlife on the Hawaiian Islands, wrote a memorandum to the Director of Patuxent regarding the possibility of moving individuals of threatened species in the islands. Banko's comments were directed at a few points that seemed 'important to the subject but, so far as [he was] informed, may not have been considered' (Banko, 1967). Banko was wrestling with many of the same concerns that weigh on today's deliberations over assisted colonization as a conservation tactic.

Conservation on the Hawaiian Islands, according to Banko, 'calls for recognition of certain facts which may not always be apparent under more general conditions prevailing on the mainland' (Banko, 1967). The small islands of Hawaii, Banko noted, are home to a number of equally small populations of species, many of which are found nowhere else (Table 1). By the mid 20th century increasing human activity on the islands threatened to shrink the already limited ranges of many of these species. Even species on more isolated islands were of concern to the Committee and the Bureau for fear that a natural disaster or a new pathogen or predator would eradicate the populations. The Committee's concern for the special case of Hawaii is evident in its 1964 draft of the Red Book (the first U.S. federal list of endangered species). Of the 62 endangered TABLE 1 Hawaiian species* listed in the 1964 Draft of the Red Book.

Nene Branta sandvicensis Laysan duck Anas wyvilliana laysanensis Hawaiian duck Anas wyvilliana wyvilliana Hawaiian gallinule Gallinula chloropus sandvicensis Hawaiian stilt Himantopus himantopus knudseni Hawaiian crow Corvus tropicus Puaiohi Phaeornis palmeri Nihoa millerbird Acrocephalus kingi Kauai oo Moho braccatus Kauai akialoa Hemignathus proceru Kauai nukupuu Hemignathus lucidus hanapepe Maui parrotbill Pseudonestor xanthophrys Ou Psittirosta psittacea Palila Psittirostra bailleui Nihoa finch Psittirostra cantans ultima Crested honeycreeper Palmeria dolei

*Species names reflect those listed in Committee on Rare and Endangered Wildlife Species (1964)

species listed, 16 (c. 25%) were Hawaiian (Table 1; United States, 1964). The Bureau put forward a proposal to 'transplant' breeding pairs of threatened Hawaiian species to neighbouring islands to create additional populations to protect against catastrophic loss. These translocations included moving species to other Hawaiian or Pacific islands with 'suitable habitat,' and included historical and new habitats (Panel Discussion, 1972). Banko had a number of concerns about an aspect of what was becoming accepted practice in federal threatened species conservation. His first concern was that an overemphasis on individual species or populations was causing researchers to lose sight of the selective pressures in their environments, pressures that favoured adaptations defining the species in question. "No species can be 'preserved' outside its natural range for any extended period of time, the role of natural selection in the evolutionary process being what it is" (Banko, 1967). Relying on Ernst Mayr's biological species concept, Banko infused an evolutionary perspective into the transplantation debate and raised several seminal questions. What exactly was the critical distinction between active conservation management, including transplanting animals, and preservation in a natural state? If transplantation to 'suitable habitat' on adjacent islands was a means of preserving threatened species, what exactly was being preserved in this process? For Banko, changes in selection pressures as a result of changing the habitat of a transplanted species (no matter how subtle that change) made it more likely that a new species, or at least subspecies, would be created than an old one preserved. "Any attempt to 'preserve' species via the technique of establishing isolated breeding populations outside natural ranges is therefore (sic) unrealistic-in fact, impossible" (Banko, 1967).

Banko also sought to temper an overenthusiastic commitment to species introductions by placing these in the context of global historical records, which indicated more failures than conservation successes. Influenced by these data, available from the Smithsonian Institution and Bureau of Sport Fisheries and Wildlife (Bump, 1963; Agreement Between the Smithsonian Institution and Department of the Interior, 1967), Banko supported conservation introductions only after conducting a thorough ecological analysis, by 'qualified biologists,' to determine the suitability of the new habitat for transplantation. Decisions to introduce or not introduce species for conservation purposes were thus clearly to be made by scientific experts rather than the public.

Banko's third point referenced a significant divide in 20th century North American conservation: the preservation of ecological systems vs the conservation of individual species. Any proposal to save threatened species by introducing them into Hawaiian wildlife refuges set these two conservation practices on a collision course: 'The successful introduction of a species into an area outside its native range unavoidably alters the existing ecology—often to a degree unforeseeable at the time of introduction. There is wide agreement both in and outside the Bureau that the natural ecology of islands in the National Wildlife Refuges should be preserved insofar as possible' (Banko, 1967).

A choice had to be made: was the conservation emphasis to be placed on the protection of individual species (in which case they could be translocated outside their native ranges to conserve them) or on preservation of communities and their historical assemblages of species? Science alone could not tell conservationists which to prefer; i.e. which 'conservation target' was the right one for policy makers and managers to support. Banko had identified a fundamental conflict in the practice of conservation that bedevils scientists and policy makers to this day.

The Bureau of Sport Fisheries and Wildlife was predisposed to a single-species approach to conservation and ecology and so favoured 'transplants' (including introductions) over preservation of ecosystems in any unaltered state. Banko was aware of the Bureau's general position and simply wanted to encourage everyone to consider all aspects before proceeding with 'inadequate or unenlightened management'. His fourth and final point was thus to make clear that aggressively pursuing a policy of introductions would at some level alter the ecology of the islands. It would be naïve to introduce species without acknowledging that fact, and it would be reckless to be aware of these inevitable alterations and still introduce new species without deliberate care and planning.

Banko concluded his memo with a summary judgement that transplantation could carry more risk than reward as a species protection strategy: "[E]ach of the foregoing points seems to point toward a negative, or at least a very

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conservative policy of introducing species of threatened wildlife on islands outside their natural range with the objective of 'preserving' the species" (Banko, 1967). Yet Banko was aware that species introductions had wide support within the Bureau of Sport Fisheries and Wildlife. He therefore set forth criteria for determining when introduction was warranted and recommended that the Bureau establish a transplantation policy, reviewed and approved by the Committee On Rare and Endangered Wildlife Species on a case-by-case basis. In his criteria he conceded that introductions were warranted 'when there is a clear danger that the species will be lost in its natural habitat' (Banko, 1967).

Banko was not the first among his colleagues in the Bureau to raise the issue of transplanting Hawaiian species but his memo offered a coherent synthesis of growing concerns among those responsible for advising on U.S. conservation policy. In responding to several memos on the subject of Hawaiian species transplantation, Banko argued for more thought regarding the consequences of ensuring the welfare of single species over ecosystem integrity as well as establishing a Bureau-wide policy that set an important new line of inquiry in motion. Banko's scepticism towards those transplantations that entailed conservation introductions would soon be challenged within the Committee, most notably by the ornithologist John Aldrich, who took a more positive position than Banko on species introductions.

Establishing guidelines for transplantation

Aldrich produced a draft document on guidelines for transplanting threatened species less than a year after Banko's memo circulated. The debates and negotiations over the Bureau of Sport Fisheries and Wildlife policy, captured in the Bureau's records, represent a philosophically and scientifically rich discussion of the problems and possibilities of species transplantation as a tool for conserving rare and threatened species.

In April 1968 Aldrich circulated his document *Philosophy* and *Guidelines for Transplanting Insular Species and Subspecies.* The draft was a direct response to Banko, providing a paragraph-by-paragraph rebuttal. Although Aldrich agreed with Banko that extreme care and oversight should be part of any transplant programme, he did not seem to share the latter's pessimistic evaluation of transplantation as a means for saving threatened species.

Philosophy and Guidelines began by framing a conflict between two conservation approaches. One was the singlespecies approach that involved practices such as introducing individual threatened species and subspecies to new habitats to maintain population viability. The other was what might be described as the ecosystem integrity approach. In the latter, potential transplantation sites were 'relatively unspoiled examples of rare ecosystems' the protection of which was at least as important as preserving threatened species (Aldrich, 1968). This single-species/ecosystem integrity distinction was more of a continuum than a dichotomy within the Bureau. Banko sided with preservation of the historical integrity of undisturbed areas, allowing transplants only in the most extreme cases. Aldrich was more focused on preserving species and populations, and more open to transplantation as a means to that end.

Aldrich began to dig even deeper into the philosophical issues underpinning the transplantation question. Having distinguished between the two conservation approaches, he attempted to unravel the concept of so-called natural areas. Citing John Sincock, a Bureau of Sport Fisheries and Wildlife ornithologist assigned to Hawaii just months after Banko submitted his 1967 memo, Aldrich pointed out that such areas were inherently human constructs, thus anticipating the philosophical debates over wilderness that would ripple through the conservation community more than a quarter of a century later (e.g. Callicot & Nelson, 1998). "All 'natural' communities have been affected to some degree by the activities of man" (Aldrich, 1968). Aldrich suggested that the establishment of species through natural immigration into new areas possessing habitat suitable for them was simply one means by which these communities change.

Aldrich's willingness to advocate the preservation of natural communities in the Pacific Islands was contingent on his interpretation of the boundaries of those communities: 'We suggest that a particular ecosystem if it is defined as a specific type of ecological community, together with its entire environment, usually is not confined to a single island any more than a particular type of subalpine forest is confined to a single mountain peak. Therefore, these similar communities on different islands as well as on different mountain peaks might be considered parts of the same ecosystem even though widely separated and not quite the same in their species composition' (Aldrich, 1968). By being more inclusive in defining what counts as the entire ecosystem, Aldrich envisioned the different islands as simply parts of a fragmented whole; therefore, movement of species from one part to another within that whole was unlikely to cause significant disruption to the system.

But Aldrich went further by suggesting that transplants are only speeding up a process that is likely to take place naturally. In his analysis Aldrich stops short of asking what seems to be a key philosophical question surrounding the acceptability of transplantation (and later, debates over assisted colonization): what is the difference between natural movement of species and careful, scientifically guided, human-assisted transplantation of species into new (but suitable) habitat? He did not appear to draw a sharp distinction between natural and human-assisted dispersal of populations to new systems.

The next section of the Aldrich draft guidelines addressed Banko point-for-point in an attempt to move the debate towards a more pro-transplantation position. Taking on Banko's claim that from an evolutionary standpoint no species can be preserved outside its natural range, Aldrich responded by creating a distinction between 'geographic range' and 'required environment' (Aldrich, 1968). Species adapt to niches, he explained, and if suitable habitat exists in a geographical area other than that of the species' current range, the species in question will occupy the new habitat if and when it is able to reach the new area. It follows that human-assisted dispersal is just one means of moving a species into a niche in which it is already adapted to thrive. Such translocations therefore cannot be dismissed a priori as inherently harmful interventions in ecosystems.

Aldrich continued to address concerns of evolutionary change in transplanted species. Banko worried that a small number of transplanted individuals did not represent adequately the genetic composition of the population from which individuals were selected and that the new environment would produce further genetic separation between the source population and newly established populations. Aldrich again brushed aside the perceived problem by asserting that if the target habitats are chosen carefully by qualified experts to be as similar as possible to the historical habitat, then any differences in selection pressures on the two populations will be negligible. Even if genetic differences emerge, the related populations will be similar enough, and 'it would seem preferable to preserve a type very closely related to the original form than to lose an endangered gene pool entirely' (Aldrich, 1968). Changes caused by human-assisted colonizations are therefore not different in kind from natural shifts in genetic composition of a population over time.

Aldrich came closest to agreeing with Banko on the point that any successful introduction of a species to a new environment unavoidably alters the existing ecology, often in unforeseen ways. Aldrich conceded the historical record of unfortunate experiences on this matter and agreed that Banko's principle of ecological alteration should be carefully considered in each proposed case of transplantation. Potential ecological disruptions should, he believed, be weighed against the value of saving threatened forms, although Aldrich did not provide an account of how these values should be traded off in conservation planning and decision-making. This issue continues to challenge conservationists debating the acceptability of assisted colonization, although decision-making models promise to help managers and the public make more informed choices in assisted colonization contexts (e.g. Hoegh-Guldberg et al., 2008; Richardson et al., 2009).

Not surprisingly, Aldrich's analysis led him to establish a fairly liberal transplant policy. He advocated for transplanting threatened forms to establish new populations outside current or historical ranges under a set of scientific and management conditions. Specifically, (1) the existing population must be large enough to permit removal of individuals for transplant, (2) competent biologists must deem the habitat into which the new population is being introduced to be sufficiently similar to the species' current habitat, (3) the new habitat must not possess endemic species or subspecies closely related to the transplant species, and (4) expert research personnel must oversee the entire transplant process and conduct follow-up studies (Aldrich, 1968).

Aldrich concluded his position statement with a brief discussion of the conditions under which wildlife managers may alter a habitat receiving transplants to make it more suitable. It is clear that he supported a significant role for ecological modification and intensive management for conservation purposes. Such alterations, Aldrich wrote, included removal of possible predators and introduction of 'good' plants. According to the proposed guidelines, however, removal should not be permitted when the predators were themselves threatened or if the new habitat is 'considered by competent ecologists to represent a unique and relatively undisturbed ecosystem' (Aldrich, 1968).

The position statement was circulated throughout the Division of Wildlife Research, and the Bird and Mammal Laboratories. Additionally, Aldrich received counsel from the renowned ecologist Charles Elton. In a letter dated 23 April 1968 Aldrich drew praise from the British ecologist for his claim that saving a closely related form was good enough, with Elton stating that '[i]f you have a good phenotype, why worry too much about gene details?' (Elton, 1968). Elton also suggested that the Bureau of Sport Fisheries and Wildlife set up a number of reserves to experiment with forms of habitat management, predator control and other practices. In this way the Bureau could hone its management techniques, and if initiated on 'one or two fairly dull islands' resistance from proponents of the historical integrity of ecosystems would be less likely (Elton, 1968).

Richard Banks, Director of the Bird and Mammal Laboratories in 1968, also made extensive comments on Aldrich's draft document. Banks worried about labelling the island species 'endangered' as their populations were not undergoing any significant change in numbers or density. They were 'vulnerable' because their limited habitat meant the populations were, and probably had always been, small. He also took exception to Aldrich's liberal interpretation of the distinction between natural immigration and humanassisted introductions, claiming that there indeed exists a significant conceptual and ecological difference between the two. Aldrich's 'broad view of ecosystems' was also problematic: 'An ecosystem may not be confined to a single island, but each island is a particular and distinct ecological situation' (Banks, undated).

In his comments on the Aldrich draft Banks was questioning Aldrich's philosophy of dividing the natural world. For example, later in his memo Banks continues his critique of Aldrich on the issue of preserving closely related forms as preferable to losing entire gene pools. "Does not introduction merely provide additional 'endangered' populations?" he asked (Banks, undated). This last point was in line with Aldrich's approach to identifying objects of conservation to be catalogued in the U.S. endangered species list (the identification and listing of all distinct, evolutionarily significant populations considered to be endangered; Winston, 2011). In summary, Aldrich's (1968) draft generated significant discussion on the topic of island transplants but did not produce a consistent or acceptable policy. By 1968 a number of Hawaiian transplant projects (which involved translocation outside their historical range) were already underway, including those for Nihoa finches Telespiza ultima, Laysan ducks Anas laysanensis, Nihoa millerbirds Acrocephalus familiaris, and others (Banko, 1972; Morin & Conant, 1990). On the mainland, active transplant programmes, usually reintroductions, were being carried out, including those involving sandhill cranes Grus canadensis, trumpeter swans Cygnus buccinator, and red wolves Canis lupus rufus (National Fish and Wildlife Laboratory (U.S.) 1933-1979 & undated).

There was no apparent change in the direction of any of these projects in the months following the debates over Aldrich's draft guidelines. These two sets of transplant programmes, island and mainland, were not taken by the U.S. Fish and Wildlife Service biologists to be in the same class; in particular, the mainland projects were not taken to be problematic in the same way as the island translocations. As Banko's memo put it, endangered species management on the Hawaiian Islands called for considerations not always apparent under mainland conditions.

Uncovering the contested values of the transplanting endangered species argument

The Patuxent Wildlife Research Center was the site for the U.S. Fish and Wildlife Service Panel Discussion on Philosophical Guidelines for Re-establishment of Endangered Wildlife Populations, held on 16 February 1972. The panel included participants well acquainted with the translocation arguments: Chairman John Aldrich, Winston Banko, John Sincock, Richard Banks, Bureau of Sport Fisheries and Wildlife mammalogist Clyde J. Jones, and Bureau of Sport Fisheries and Wildlife ornithologist Paul W. Sykes. The meeting produced a seven-page transcript and in many ways rehashed the transplantation debates of 1968.

As Chair, Aldrich opened the discussion by limiting the panel to discussing 'the desirability and practicability of attempting to introduce endangered species outside their known ancestral range' (Panel Discussion, 1972). Aldrich continued with a brief history of the 1968 transplant debate, initiated when the U.S. Fish and Wildlife Service transplanted several Hawaiian birds (Laysan and Nihoa finches, and Laysan ducks, outside their native range) as recommended by the Bureau's Red Book and encouraged by highranking members of the International Council for Bird Preservation. In all such cases of transplanting species outside their historic range, Aldrich continued, 'the objective is to increase the geographic distribution of species that are confined to very limited and vulnerable habitat' (Panel Discussion, 1972). The opposing view he described was one in which the introduction of foreign species for any reason was biologically unsound. The same dichotomy frames modern assisted colonization debates.

The panel transcript then records the views of each member, beginning with Sykes who was 'opposed to any introduction of any species outside its natural range' (Panel Discussion, 1972). Sykes supported his position in two ways. Firstly, he made the familiar claim that introduced species had a suspect record of success. With few exceptions, he noted, 'introductions of alien species have either been dismal failures or many-headed monsters' (Panel Discussion, 1972). His second point was that any time and resources spent on complicated transplant programmes would be better used managing a threatened species in its natural range. If populations are large enough to remove individuals for introduction programmes, with uncertain chances for success, then there should be sufficient time to solve some of the problems facing threatened species in their current (i.e. historical) habitats. On the other hand, if a population was critically small, then any removal of individuals would have to be considered too risky.

Banko continued Sykes's sceptical appraisal of species introductions, listing the several Pacific island introduction projects then in progress and expressing concern that they were being carried out without sound 'biological or ecological guidelines' (Panel Discussion, 1972). He had made the same claim in his 1967 memo and in his opinion little had changed in the ensuing 5 years.

Richard Banks jumped in at this point and played the role of evolutionary sceptic. Banks restated the argument that a small segment of a species' gene pool introduced to a different environment (and therefore subjected to a different set of selection pressures) represented the establishment of a novel threatened population rather than protection of the original one. He also argued that if the protection of undisturbed ecosystems were to be of value to conservationists, then any introduction must be seen as fundamentally opposed to that goal.

Clyde Jones, who was at the time chief of the mammal section of the Bird and Mammal Laboratories, made a point that was not yet a part of the Bureau's discussion, expressing concern about the propensity for biologists to 'find themselves in some sort of philosophical rut' in such debates (Panel Discussion, 1972). He encouraged his fellow committee members to reassess the underlying assumptions that had become reified as part of the transplantation discussions by providing four examples of what he had in mind.

Firstly, Jones expressed concern that the catalogue of North American mammals relied on data collected around the turn of the 20th century, leaving it inaccurate and outof-date. Relying on this inadequate data set, Jones claimed, caused many to assume that threatened species were always found in optimal habitats. These species, however, might actually be clinging to existence in marginal habitats. This consideration was especially damaging to Aldrich's position; if Jones were right, new habitat selected to match one that is only marginal for the target species would not provide the kind of assurances Aldrich was promising (see also Seddon et al., 2012).

Next, Jones claimed that it is often assumed that increasing the size of a threatened population will promote recovery. This is not the case, however, when the current habitat cannot support an increased population, a condition that may lead to rapid decline and, ultimately, to extinction. He also challenged the view that threatened species recovery requires one or more interventionist programmes. '[I]n numerous cases, an endangered species might be managed best by leaving it as completely alone as possible' (Panel Discussion, 1972). Finally, Jones restated some previous concerns over the assumed static nature of species and ecosystems. Species and ecosystems undergo constant, and under certain conditions, rapid change. Conservation management of endangered species must therefore include conservation and management of habitats and ecosystems.

Following Jones' comments John Sincock brought the discussion back to the specific topic of island populations, explaining that in most cases what was being talked about were small populations restricted to single islands. Moving some of them outside their historical range (however vaguely defined this term was), he argued, provided insurance against catastrophic loss. In that respect, Sincock considered the value of such insurance to outweigh any disruption to the ecosystem of the transplantation sites. Sincock also expressed scepticism regarding claims that transplantation produced significantly different genetic populations. Any genetic differences between the transplanted and parent populations, in his mind, would be no different than genetic variation that naturally occurs within all species and even within populations.

Aldrich contributed to the pro-transplant position by restating the argument that natural colonization and human-assisted transplantation should not be viewed as different. As before, for Aldrich, human-assisted species translocations were simply a way of accelerating a potentially natural process in the interest of saving threatened wildlife. Unfortunately, the record is cut short at this point, stating that 'Considerable stimulating discussion followed' (Panel Discussion, 1972). The final conclusion reached by the panel, however, was similar to the summary remarks of Banko's 1967 memo. Most panellists expressed a strong sentiment against transplants of species outside their historical ranges. Yet the panel did not completely shut the door on the idea of transplanting some members of critically endangered species for conservation purposes. The panel conceded that in extreme circumstances, such as instances of highly restricted insular species, transplants might ultimately be necessary to save the species from extinction.

Conclusion: the legacy of the Committee on Rare and Endangered Wildlife Species debates

There is no record of what effect the 1968 memos or the 1972 panel discussion had on formal Bureau policy. Although the 1972 panel was conservative with respect to transplants, transplantation/translocation continued as cornerstones of Bureau policy after the passage of the Endangered Species Act in 1973 and continue to this day. Conservation-driven translocations of species have been performed for a variety of taxa elsewhere over several decades. For example, New Zealand wildlife managers have used translocations to protect vulnerable species, including moving them to predator-free islands, to establish new populations (Saunders & Norton, 2001; Seddon, 2010).

Despite the extensive and often scientifically justified tradition of translocating species for conservation purposes, including to habitats outside their indigenous range, it is apparent that the ecological, evolutionary, and conceptual arguments for or against this practice remain unclear. This is especially true in the case of climate change-driven translocations, such as assisted colonization. As our examination of the transplantation debate of the Committee on Rare and Endangered Wildlife Species reveals, U.S. conservation scientists and policy advisers have been grappling with the core issues surrounding species translocation (especially conservation introductions), ecological manipulation, and disruption since at least the late 1960s. Moreover, the Bureau of Sport Fisheries and Wildlife was proposing a justification for what today would be classified as assisted colonization well before the concept became more narrowly associated with reducing extinction risks posed by climate change.

In the 1960s and early 1970s the Committee's scientists were divided over the scientific, conceptual, and policy implications of species transplantations. Sceptics such as Banko emphasized their poor success record, their tendency to disturb native ecosystems, and the potential of transplantations to divert attention from in situ conservation.

A more tolerant view was taken by scientists such as Aldrich who argued that transplants could be an important tool to protect species from unavoidable habitat change and that there was no sharp distinction between human-assisted movement and the natural dispersal of wildlife populations. There are echoes of this debate in present exchanges over assisted colonization. Ricciardi & Simberloff (2009a,b) and Webber et al. (2011) have argued that climate-driven translocations are too risky ecologically and that they will draw scarce resources away from traditional conservation practices. Yet others have suggested that our commitment to conservation requires considering assisted colonization as an option and argue that we can make informed decisions by adopting scientific criteria reminiscent of Aldrich's (1968) guidelines and social criteria addressing relevant value/ethical considerations (e.g. Richardson et al., 2009; Minteer & Collins, 2010).

Among other lessons, the history of the debates of the Committee on Rare and Endangered Wildlife Species shows that we should not assume that science-based evidence alone will direct conservationists to privilege individual threatened species or the historical continuity of an ecosystem. Instead, we should assume that policy choice will turn on value-based commitments that involve weighing diverse conservation goals and priorities under rapid global change. This process, moreover, will not be driven solely by scientific experts (as the Committee's biologists envisioned); rather, we should expect it to be informed by a diversity of groups holding a pluralistic mix of values and preferences, including different moral, aesthetic, and cultural attitudes toward species and ecosystems (Camacho et al., 2010). The IUCN Guidelines for Reintroductions and Other Conservation Translocations (IUCN/SSC (2013), which highlights the significance of public values and attitudes to the translocation planning processes, will therefore be indispensable for making scientifically sound and socially acceptable decisions on conservation translocation.

We should also expect a significant commitment to context dependence. For example, in the debates of the Committee on Rare and Endangered Wildlife Species participants reached different conclusions for island vs continental species and habitats. Similarly, local, regional, and cultural circumstances will in many cases inform and shape a particular decision to privilege conserving a single species, even at the expense of an ecosystem's historical integrity.

Finally, this history reminds us that although the threat of global climate change to biodiversity is transforming conservation science and practice, many of the issues it raises are not novel. The same concerns that have animated current debates over assisted colonization were raised in the U.S. transplantation debates of the late 1960s and early 1970s, with similar discussions about ecosystem disruption, human intervention, and distraction from traditional in situ conservation. Although today's arguments over assisted colonization add new elements to this debate, the core issues reflect tensions and unresolved questions that have shaped scientific deliberations since the 1960s. Answering these questions, and fashioning a scientifically based and publicly acceptable policy for species translocations under global change, remains a significant challenge for conservation scientists and wildlife managers.

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