

NEW ZEALAND JOURNAL OF ECOLOGY

Conservation translocations of fauna in Aotearoa New Zealand: a review

Kevin A. Parker^{1*}, John G. Ewen², John Innes³, Emily L. Weiser⁴, Aisling Rayne⁵, Tammy E. Steeves⁵, Philip J. Seddon⁴, Lynn Adams⁶, Natalie Forsdick⁵, Matt Maitland⁷, Troy Makan⁶, Denise Martini⁴, Elizabeth Parlato⁸, Kate Richardson⁹, Zoe Stone⁸ and Doug P. Armstrong⁸

¹Parker Conservation Ltd, 3 Sowman Street, Nelson 7010, New Zealand

²Institute of Zoology, Zoological Society of London, Regent's Park, London, UK

³Manaaki Whenua-Landcare Research, Private Bag 3127, Hamilton 3240, New Zealand

⁴University of Otago, PO Box 56, Dunedin 9054, New Zealand

⁵University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand

⁶Department of Conservation, PO Box 10420, Wellington 6243, New Zealand

⁷Auckland Council, Private Bag 92300, Victoria Street West, Auckland, New Zealand

⁸Massey University, Private Bag 11222, Palmerston North 4442, New Zealand

⁹Waikato Regional Council, Private Bag 3038, Waikato Mail Centre, Hamilton 3240, New Zealand

*Author for correspondence (Email: k.parker@parkerconservation.co.nz)

Published online: 18 December 2023

Abstract: There have been numerous declines and extinctions of native fauna in Aotearoa New Zealand since human settlement. Against this background of loss there have been remarkable advances in conservation management, including the use of conservation translocations to reduce extinction risk and restore depauperate ecosystems. Here we review conservation translocations in Aotearoa New Zealand. Our review assembles knowledge from Aotearoa New Zealand's rich history of faunal translocations and describes six key considerations for successfully establishing translocated populations: (1) What values will be met by a translocation? (2) What is the natural and conservation history of the translocation candidate? (3) Does the release site habitat match that of the proposed source population, and if not, why is the release site considered appropriate and can management ameliorate differences? (4) Will dispersal be a problem? (5) Will genetic management be required and how realistic is it that this management will be implemented? (6) What do future developments mean for the management of translocated populations? We discourage a focus on any single element of translocation planning but rather encourage all people involved in translocations, particularly decision makers, to explicitly recognise that successful translocations typically have multiple, values-based objectives. We also support recommendations that the principles of good translocation decision-making are embedded in government policy.

Keywords: conservation translocation, decision making, reintroduction, restoration

Introduction

There have been numerous declines and extinctions of native fauna in Aotearoa New Zealand (hereafter Aotearoa) following human settlement (Caughley 1989; Holdaway 1989). For example c. 50% of all native bird and frog species have become extinct since the first humans arrived (Caughley 1989; Holdaway 1989), and remaining extant, native species show varying levels of vulnerability to exotic pests (Innes et al. 2010). This history of extinction and drastic reduction in population size and range is recounted in Māori whakataukī (proverbs) such as "Ko te huna i te moa - destroyed like the moa" (Wehi et al. 2018), and by Diamond (1984) who stated that "New Zealand doesn't have an avifauna, just the wreckage of one".

Despite these losses there have been remarkable advances in conservation management, including the use of conservation translocations, defined as the intentional movement of animals from one place to another for a conservation benefit (referred to as translocation hereafter). The increasing use of translocations in Aotearoa has been enabled by advances in large-scale pest eradication and control (pest primarily refers to exotic mammalian predators and competitors, but also includes other unwanted harmful vertebrates, invertebrates, plants, and pathogens). Multi-species eradications have been completed on large and small islands (Towns & Broome 2003). Fenced sanctuaries provide islands of habitat on the main islands of Aotearoa within which most significant pests are absent most of the time (Innes et al. 2019). Such sanctuaries are also often isolated from adjacent unmanaged habitat (Innes et al. 2019). The number of unfenced mainland sites under varying forms of protection is also increasing every year (Innes et al. 2019) and the Government's 2016 announcement of Predator

Free 2050 will likely lead to an increase in control of some pests, especially rats (*Rattus* spp.), stoats (*Mustela erminea*), and possums (*Trichosurus vulpecula*). This will result in a gradient of pest density from areas with complete eradication/ zero density, to areas with lower densities than are currently achievable. Surprisingly, there has been little detail about what a predator-free Aotearoa might look like, but implicit is the goal of exchanging pest biomass for native and endemic biomass. Translocations are an important tool for achieving this goal.

Aotearoa conservationists are very good at doing translocations to pest free islands. However, progress is also being made in the translocation of some forest birds to sites where community conservation initiatives have restored the available habitat through pest control, planting, and translocations. Many such projects have successfully re-established high-density populations of native wildlife, particularly forest birds. A critical limitation is that most of these sites are small (c.100-1000 ha), and mice (Mus musculus) have rarely been eradicated, or even effectively controlled, which is problematic for the recovery of endemic lizards, amphibians, invertebrates, bats, and some threatened plants. In contrast, the bulk of our biodiversity is contained within vast areas (1000s of hectares) of back country conservation estate which is both harder to protect and harder for the public to engage with. The Department of Conservation (DOC) Tiakina Ngā Manu/Battle for our Birds programme is achieving impressive conservation gains by controlling pests over huge areas of habitat (c. 500 000 ha in 2022), in conjunction with species-focussed mainland recovery programmes, e.g. kakī / black stilt (Himantopus novaezelandiae) and kākāriki karaka / orange-fronted parakeet (Cyanoramphus malherbi). Nevertheless, biodiversity continues to decline in vast tracts of land, especially non-forested habitats, that remain unprotected.

The current situation on the main islands of Aotearoa is neatly captured by Caughley's (1994) small population and declining population paradigms. Our small, protected populations, which by definition include all translocated populations, are subject to the risks of being small, including pest incursions, dispersal, extreme weather events, novel pathogens, and loss of genetic diversity. In contrast, many of our large mainland populations are declining because of the pervasive impacts of pests. The ongoing tension in conservation management in Aotearoa lies in deciding how to allocate resources to maintain small populations, because this seems generally easier and currently achievable, while also continuing to manage the large areas of habitat on the main islands that contain the bulk of our biodiversity, a much harder challenge largely dependent on the continued use of aerially applied toxins. Both approaches are necessary.

Small, intensively protected populations provide insurance against further declines and can serve as source populations for natural colonisation of, or translocation to, pest-free habitats when these become available. Such sites also provide a glimpse of what a predator-free Aotearoa might look like and are critical tools for engaging the general public in conservation management (Parker 2008). In contrast, ongoing pest control in large mainland areas is essential for protecting biodiversity not readily protected on islands, or in small intensively protected areas. When these large mainland areas are released from the pervasive effects of pests (primarily a question of social licence and technical advances) they will further buffer threatened species against the challenges of small population size.

In this paper we use our collective experience as practitioners and conservation scientists to focus on small population management in Aotearoa, specifically translocated populations that have been established following local extinction. The DOC translocation proposal document captures the principles of sound translocation practice, including those described in the IUCN "Guidelines for reintroductions and other conservation translocations" (IUCN 2013). However, these principles are not currently captured in DOC policy (Parliamentary Commissioner for the Environment 2017), which sometimes compromises the ability of DOC to assess and approve translocation proposals. This is important, especially as we move beyond translocations to typical sites (islands and relatively small protected mainland areas), towards release sites with much more uncertainty, e.g. very large areas (1000s of hectares) of contiguous habitat, and also urban (van Heezik & Seddon 2018), and rural landscapes.

We want more successful translocations and we think the best way to achieve this is to explicitly define a clear set of measurable, a priori, fundamental, values-based objectives at the outset of each translocation (Ewen et al. 2014, 2023). Common biological values include fundamental objectives such as reducing extinction risk and restoring depauperate ecosystems. However, mana whenua and local community values can be equally critical and central to translocation success. Therefore, achieving project objectives requires careful and measurable evaluation of all factors that might contribute to translocation success and an understanding of the species and people specific time scales over which such factors might act, rather than focussing on single factors and arbitrary timeframes. We also note the increasing demand for translocations and that some might proceed with different fundamental objectives to those posited above. However, a translocation cannot be considered successful if a population fails to establish, even though uncertainty means that this sometimes happens. Conservation translocations are not easy and many fail (Miskelly & Powlesland 2013) but these failures are informative for future efforts to establish populations.

We draw together knowledge that has been gained from the rich history of fauna translocations in Aotearoa and outline six key considerations for translocation decision-making:

(1) What values will be met by doing a translocation? All translocations are values based so these values should be explicitly stated (e.g. a translocation might reinstate rangatiratanga, kaitiakitanga or mauri, reduce extinction risk, restore a depauperate ecosystem or reconnect a local community with the target species).

(2) What is the natural and conservation history of the translocation candidate?

(3) Does the release site habitat (e.g. pests, vegetation associations, pathogens) match that of the proposed source population? If not, why is the release site considered appropriate? Can management ameliorate differences?

(4) Is dispersal likely to be an impediment to establishment and persistence?

(5) Will genetic management be required and how realistic is it that this will be implemented (e.g. increase the number of founders, conduct reinforcement translocations or increase the size of the management area)?

(6) What do future developments (e.g. improved pest control or emerging genomic tools) mean for the management of translocated populations?

These key considerations can be applied to most fauna and we apply them to several species and species groups that have **Table 1.** Five of the six key considerations for some terrestrial species/species groups that have been translocated in Aotearoa. We have not specified key consideration number one because values are project specific. However, for the species listed they usually include objectives such as minimise extinction risk, restore depauperate ecosystems, restore mauri and reconnect local communities with the translocated species. Knowledge is patchy, even for many bird species, and there is a lot of uncertainty to resolve, especially for herpetofauna and invertebrates. In particular other habitat variables, such as ideal vegetation associations, are often difficult to resolve until suitable pest control is in place. NI – North Island; SI – South Island.

Translocated species or species group	2. Pest thresholds based on extirpation and management history	3. Habitat match required?	4. Ability 1 High	to disperse when Medium	n connectivity is: Low	5. Will genetic management be required?	6. What future developments will assist translocation of this species?
Kiwi spp.	Key pest species controlled to low density, typically mustelids	Not necessarily: occupy a diverse range of habitats	High	High	?	Possibly: depending on the size of the recipient site, the number and source of founders and vital rates post release	Improved pest control Safe dispersal corridors
Weka spp., particularly NI and buff weka		Not necessarily: occupy a diverse range of habitats	High	High	?	Possibly: depending on the size of the recipient site, the number and source of founders and vital rates post release	Improved pest control Safe dispersal corridors Acceptance that weka are a natural, endemic predator that co-evolved with all other indigenous species and ecosystems.
Whio / blue duck		Unknown. Archaeological evidence suggests whio might have once used a more diverse range of habitats	High	High	?	Unknown?	Improved pest control Safe dispersal corridors Understanding dispersal behaviour Trial translocations to test habitat plasticity
Toutouwai / robin spp.	Multi-species pest control to low density, typically including ship rats, mustelids, possums, and cats, sometimes including ungulates and pigs. Mice usually present, sometimes at high density Control is sometimes delivered seasonally (e.g. over the bird breeding season)	No: but vital rates vary among sites, suggesting some, especially damp lowland forest with thick leaf litter, are better than others	High	?	Low	Possibly: depending on the size of the recipient site, the number and source of founders and vital rates post release	Improved pest control Safe dispersal corridors
Yellow crowned kākāriki		Not necessarily: occupy a diverse range of habitats	High	High	?	Possibly: depending on the size of the recipient site, the number and source of founders, vital rates post release and dispersal distance to other populations	Improved pest control Safe dispersal corridors Understanding dispersal behaviour
Popokōtea / whitehead		Not necessarily: occupy a diverse range of habitats	High	Moderate	Low	Unlikely, except at very small sites (<50ha)	Improved pest control Safe dispersal corridors
Mohua / yellowhead		Not necessarily - occupy a diverse range of habitats	High?	?	Low	Possibly: depending on the size of the recipient site, the number and source of founders, vital rates post release and dispersal distance to other populations	Improved pest control Safe dispersal corridors
Titipounamu / rifleman		Not necessarily: occupy a diverse range of habitats	?	?	Low	Unlikely, except at very small sites (<50ha)	Improved pest control Safe dispersal corridors
Kākā		Kākā are mobile and use a wide range of habitats but their core requirements are unclear	High ¹	High ¹	High	Possibly: depending on the size of the recipient site, the number and source of founders, vital rates post release, dispersal distance to other populations and propensity to mix with other populations	Improved pest control Safe dispersal corridors
North Island kōkako		Kōkako persist in a wide range of habitats but large (≥2000ha) diverse forested habitats are likely optimal habitats	High	?	Low	Possibly: depending on the size of the recipient site, the number and source of founders, vital rates post release and dispersal distance to other populations	Improved pest control Safe dispersal corridors
Pekapeka / Short-tailed bats		Short-tailed bats use a variety of habitats but the full extent of their habitat plasticity is unknown	High?	?	?	Unknown: no translocated populations have persisted	Development of successful translocation techniques
Mainland herpetofauna (e.g. Northern spotted skinks and the infrapunctatum complex, jewelled and forest geckos, Hochstetter's frog)		Unknown	?	?	?	Unknown: will depend on source populations, founder size and vital rates at new sites	Improved pest control, especially of mice Improved understanding of basic biology and ecology, including habitat plasticity Improved profile and funding by government and the broader community
Mainland invertebrates		Unknown	?	?	?	Unknown: will depend on source populations, founder size and vital rates at new sites	Improved pest control, especially of mice Improved understanding of basic biology and ecology, including habitat plasticity Improved profile and funding by government and the broader community

Table 1. Continued.

Translocated species or species group	2. Pest thresholds based on extirpation and management history	3. Habitat match required?	4. Ability to High	o disperse when Medium	n connectivity is: Low	5. Will genetic management be required?	6. What future developments will assist translocation of this species?
Tīeke / saddleback spp.	Multi-species pest control to eradication or zero density of all mammalian pests with the probable exception of mice (as is typical of all mainland fenced sanctuaries).	Not necessarily: occupy a diverse range of habitats	High	Low	Low	Unlikely with careful selection of founder populations but very small populations might benefit from periodic reinforcement translocations	Improved pest control Safe dispersal corridors
Hihi		Unknown: but large, intact and diverse forested habitats are likely optimal	High	Moderate?	Low	Possibly: depending on the size of the recipient site, the number and source of founders and vital rates post release	Improved pest control Improved understanding of habitat requirements Safe dispersal corridors
Kākāpō		Historically occupied a wide variety of habitats	High	?	?	Possibly: depending on the size of the recipient site, the number and source of founders and vital rates post release	Improved pest control, especially over very large landscapes
Highly threatened herpetofauna, e.g. McGregor's, robust, and Whitaker's skink, Duvaucel's gecko, tuatara	Multi-species pest control to eradication or zero density of all mammalian pests, including mice.	Unknown	?	?	?	Unknown: will depend on source populations, founder size and vital rates at new sites	Improved pest control, especially of mice Improved understanding of basic biology and ecology, including habitat plasticity Improved profile and funding by government and the broader community
NZ snipe		Unknown: but could likely persist in a wide range of habitats when key pests are absent	?	?	?	Possibly: depending on the size of the recipient site, the number and source of founders and vital rates post release	
Large native and endemic threatened invertebrates, e.g. giant wētā, weevils and beetles		Unknown	?	?	?	Unknown: will depend on source populations, founder size and vital rates at new sites	Improved pest control, especially of mice Improved understanding of basic biology and ecology, including habitat plasticity Improved profile and funding by government and the broader community

 1 Dispersal of translocated kākā has been moderated through the provision of supplemental food



Figure 1. Steps in the structured decision-making process for conservation translocations (adapted from Gregory et al. 2012). Note the double loop learning whereby monitoring might lead to a revision of management alternatives.

been translocated in Aotearoa (Table 1). The examples we use, and the perspectives we bring, mainly relate to terrestrial birds, simply because these have been translocated for conservation more frequently than other taxa (Miskelly & Powlesland 2013; Swan et al. 2016; Rayne et al. 2020). However, significant information gaps exist, even for bird translocations.

(1) What values will be met by doing a translocation?

Translocations are most frequently conducted on public land administered by national or local government and they usually involve the use of at least some public money. Accountability for the management of translocated species is vested in government, i.e. DOC, and is bound by a commitment to give effect to Te Tiriti o Waitangi/The Treaty of Waitangi. Therefore, at minimum, there is a legal requirement to consult with mana whenua (iwi, hapū, and whānau with customary authority over an identified area) about every translocation, including ongoing management of source populations, translocated populations, and release sites. However, engagement may extend far beyond economic and legal obligations, especially where translocations emerge from trusted relationships and recognise the deep connections that mana whenua and local communities share with populations and places (Bioethics Panel 2019). Translocations can therefore contribute to realising multiple fundamental objectives, including those that are responsive to the needs and aspirations of mana whenua and local communities (Parker 2008; McMurdo Hamilton et al. 2021; Fischer et al. 2023; Parker et al. 2023).

The challenge is that the values and objectives underlying translocations usually seem obvious to the project instigators, managers, and decision makers. However, they might overlook key fundamental objectives of mana whenua and local communities. For example, a manager trained in modern science might see a translocation as an opportunity to reduce extinction risk or restore a depauperate ecosystem. In contrast, mana whenua might see it as an expression of rangatiratanga (sovereignty, authority, self-determination), kaitiakitanga (guardianship), and the restoration of mauri (not easily defined but sometimes translated as life essence) (McMurdo Hamilton et al. 2021, Fischer et al. 2023; Parker et al. 2023). A community conservation group or private landowner might simply want a particular species living in their area. These objectives might seem similar, but this should not be assumed, nor will they necessarily be measured in the same way. This is critical because a review by Ewen et al. (2014) found that the setting, reporting and, measurement of objectives is highly variable among reintroduction programmes. Furthermore, most are rooted in Western science with little mention of other values. Ewen et al. (2014) also noted that fundamental objectives (the things we want, e.g. reduce extinction risk) were often mixed with means objectives (how we get what we want, e.g. do a translocation), and are not measured in an appropriate way, nor even explicitly stated. In the case of Predator Free NZ, the name states a means objective (and has led some to believe the project to be short-sighted), but the fundamental objective is clear: a landscape dominated by indigenous biodiversity (Department of Conservation 2020).

Given this complex decision environment, Ewen et al. (2014, 2023) characterise a conservation translocation as a sequence of decisions and argue that poor planning,

implementation, and monitoring is a consequence of not approaching the decision-making process in a deliberate and rational manner. They, along with several other authors, advocate a more structured approach to decision making (Maguire 1986; McCarthy et al. 2012; Converse et al. 2014). Structured decision making is an iterative process whereby uncertainty is addressed by (1) defining clear objectives and how they will be measured, (2) identifying a range of possible management alternatives, (3) predicting the outcomes of the chosen management alternatives relative to the stated objectives, (4) evaluating trade-offs and uncertainty, and (5) implementing the optimal management alternative and monitoring its results (Fig. 1; Gregory et al. 2012; Ewen et al. 2014, 2023). This approach to decision making has been characterised as "a formalisation of common sense for decision problems which are too complex for informal use of common sense" (Keeny 1982).

Structured decision making is useful only if all people with connections to, or who might be impacted by, a translocation are directly involved in setting fundamental and means objectives for the project and then deciding between management alternatives as to how these might be achieved. For example, translocation planning for pekapeka/short tailed bats (Mystacina tuberculata) was initiated at Te Kiri marae alongside Ngāti Manuhiri who led the korero on a mātauranga Māori (Māori knowledge, wisdom) fundamental objective for assessing translocation options (McMurdo Hamilton et al. 2021). Similarly, recovery planning for the kuaka / Whenua Hou diving petrel (Pelecanoides whenuahouensis) was initiated on Takutai o Te Tītī marae with Kāi Tahu seeing kuaka translocation as one means to express rangatiratanga and exercise kaitiakitanga (Fischer et al. 2023). On Rēkohu / Wharekauri / Chatham Islands the translocation of karure / kakaruia/black robins (Petroica traversi) to reduce extinction risk is viewed by Moriori as consistent with their principles and values. Black robin translocation also recognises Ngāti Mutunga o Wharekauri as Treaty Partners and provides a means for the broader Chatham's community to reconnect to black robins, a vital source of local identity (Parker et al. 2023).

Ultimately, meaningful engagement and decision sharing with mana whenua, and local communities, provides a means to deepen support, interest, and engagement in conservation. However, resourcing is often limited for genuine relationshipbuilding, given the substantive costs, time and energy needed, e.g. for hui (meetings) and site visits. Where translocations are initiated by DOC they might cover this cost (Fischer et al. 2023). But translocations initiated outside of DOC can result in poorly resourced community conservation groups asking poorly resourced mana whenua for time and energy. It is difficult to know how to resolve this, other than increasing funding bids to cover all translocation costs, although it could also be argued that these initiatives are contributing to national conservation objectives and might therefore deserve government assistance.

(2) What is the natural and conservation history of the translocation candidate?

One obvious starting point for setting biological objectives and informative performance measures is understanding the natural and conservation history of the candidate species (Ewen et al. 2023). For example, North Island (NI) toutouwai / NI robins (*Petroica longipes*) have persisted at sites on the main islands of Aotearoa with no predator management whereas NI tīeke / NI saddlebacks (*Philesturnus rufusater*) have been extinct on the mainland for > 120 years (Heather & Robertson 2015). These two species clearly differ in their ability to tolerate pests and therefore require different performance measures for pest control (a means objective), even though the fundamental biological objectives for translocating these species, typically to reduce extinction risk or restore a depauperate ecosystem, are often the same (Table 1).

However, it can be extremely difficult to determine why a translocation failed. One way is to model vital rates from another species to estimate the vulnerability of the focal species to pests. For example, Parlato and Armstrong (2018) used NI toutouwai data to predict rat-tracking indices that might correlate with NI tieke translocation success. Alternatively, factors other than pests might lead to translocation failure. For instance, of nine korimako / bellbird (Anthornis melanura) translocations only one appears to have been successful (Miskelly & Powlesland 2013). While several factors might have contributed to these failures it is unequivocal that dispersal from the release site has been a critical factor, even at sites where some breeding occurs. Given such low success it is questionable whether any further translocations of korimako are justified unless there is a significant change in methods or understanding, especially given their ability to naturally recolonise protected sites (Brunton et al. 2008). Clearly, if a species has rarely or never been translocated then the outcomes of previous translocations are not useful indicators of future outcomes. In these cases, the translocation of other species, along with the ecology and conservation history of the candidate species, will have to be assessed against extirpation history, vulnerability to pests, dispersal abilities, and other habitat requirements. However, there will naturally be a higher degree of uncertainty regarding establishment and persistence of the translocated population.

(3) Does the release site habitat match that of the proposed source population? If not, why is the release site considered appropriate and can management ameliorate differences?

Conservation translocations are typically, but not always, carried out within the former range of a species, i.e. are reintroductions (IUCN 2013), following local extirpation, and where natural recolonisation is unlikely on a time scale acceptable to site managers, mana whenua and local communities. Clearly, the conditions that we understand/ predict a species needs to persist must be present in the release area. However, these conditions might also be provided by management, for example the provision of supplementary food to translocated hihi (*Notiomystis cincta*) (Ewen et al. 2013).

Unfortunately, the concept of habitat is often misused and poorly defined in translocation planning (Stadtmann & Seddon 2018). Here, we use the definition of Hall et al. (1997), in describing habitat "...as the resources and conditions in an area that produce occupancy – including survival and reproduction–by a given organism." This includes all physical (e.g. climate, aspect) and biological (e.g. predators, vegetation associations, landscape connectivity) aspects of an area where a species lives. Habitat quality refers to "...the ability of the environment to provide conditions appropriate for individual and population persistence" specifically survival, reproduction, and population growth (Hall et al. 1997). Habitat quality is a continuous variable, ranging from low quality to high quality and can be very difficult to define explicitly, although there are useful proxies (Hall et al. 1997). The finite rate of increase (λ) is the most direct measure of habitat quality, assuming density dependence and genetic quality are accounted for. The most essential pre-requisite for translocation success is that λ is > 1 at low density as the population will otherwise decline to extinction. High quality habitat is typically perceived as places where animals formerly occurred. However, habitat conditions need not replicate past states if they are predicted to allow λ to be > 1 (Table 1).

Pests are nearly always considered in translocation planning but are rarely explicitly defined as a habitat variable in Aotearoa, where discussions of habitat quality have focussed on vegetation associations that animals are either known or assumed to rely on for survival, while recognising that remnant populations do not necessarily survive in high quality habitat (Griffith et al. 1989). However, any assessment of habitat quality in Aotearoa must consider the presence and density of pests because they have such a critical impact on the survival of so many native and endemic species (Table 1; Innes et al. 2010; Richardson et al. 2014). While other biological and physical habitat variables, especially vegetation associations, are clearly essential, effective pest control is almost always a prerequisite for translocated populations to establish and persist.

In Aotearoa, current management of mammalian pests includes three major regimes of control: (1) total eradication on offshore islands, (2) maintenance of pests at "zero density" within fenced mainland sites, i.e. key pests are absent most of the time but when present they are quickly detected and removed, and (3) suppression of pest densities in unfenced mainland areas relative to unmanaged sites (Byrom et al. 2016). These are not mutually exclusive and there is often overlap between them. For example, peninsula fences, such as at Tāwharanui Open Sanctuary are leaky but have extensive areas of pest control outside the fences. It is hoped that this reduces incursions while also providing some protection for animals that disperse outside the fence.

Pest densities at the release site must be within the tolerance of the translocated species (Table 1). For example, NI toutouwai can persist with moderate levels of ship rats (Rattus rattus) but will have higher survival and reproduction rates if rats are reduced to low levels (\leq 5% tracking tunnel indices) before each breeding season, with mustelid control also likely to be beneficial. NI toutouwai persist at some sites with ship rat tracking indices of > 25%, but female survival, reproductive output and ultimately population growth are reduced (Parlato & Armstrong 2012, 2013). As well as reducing the likelihood of population persistence, slow population growth and loss of founders will increase the loss of genetic diversity. In stark contrast, the current distribution of species such as tieke, hihi, and red-crowned kākāriki (Cyanoramphus novaezelandiae) indicates they are much more vulnerable to pests, as they currently persist only in sites where pests have either been eradicated or reduced to zero density. A further challenge when making translocation decisions is that the impact of varying densities of pests is well understood for only a few bird species, poorly predicted for many others, and virtually unknown for most invertebrates, lizards, amphibians, and bats (Table 1). For example, pest thresholds on the mainland, and population growth in response to pest control, have only been demonstrated for Otago skinks (Oligosoma otagense) and grand skinks (Oligosoma grande) (Reardon et al. 2012), just two of 106 endemic lizard species.

Further habitat variables, including climate, altitude, aspect, and soil type will be associated with vegetation and might shift habitat quality from high to low, i.e. decrease the probability of establishment and persistence, depending on the needs of the translocated species and their ability to adapt to variable conditions. This might be especially difficult at sites that experience climatic extremes relative to those with more benign conditions. Climate change might also cause high-quality habitat to become low quality in the future. Furthermore, the impact of these variables is not consistent across species. For example, NI toutouwai and NI mātātā / fernbird (Poodytes punctatus vealeae) are evidently flexible in their habitat requirements as they occupy a broad range of habitats and have been successfully translocated between very different habitats. Productivity and population growth has varied between sites, suggesting that some are better than others (Parlato & Armstrong 2012, 2013; KAP unpubl. data), but they clearly tolerate a range of habitats during establishment and persistence. In contrast, species such as hihi need protection from mammalian pests but the vital rates of translocated hihi populations, and the fact that most require supplementary food to establish and persist, indicate that there are also other currently unknown habitat requirements (Ewen et al. 2013).

Translocating animals to a habitat similar to their current habitat is likely to have a greater chance of success than translocating them to a different habitat. For instance, Parlato and Armstrong (2012, 2013) showed that translocation of NI toutouwai between habitats with similar pest assemblages and vegetation associations had a small advantage over translocations between contrasting habitats. The similarity of the source and release site, the objectives of the translocation, and the risk profile or level of uncertainty associated with the translocation will also influence decisions about health screening. For example, translocations between two mainland sites and/or relatively close inshore islands will have a relatively low disease risk because their pathogen communities are probably similar (Sainsbury & Carraro 2023). In contrast, translocations between distant sites with different habitats could be relatively high risk, especially if the recipient site has species that could be vulnerable to novel pathogens. Ideally, there should also be an understanding of potential pathogen impacts on the translocated species, and on conspecifics and heterospecifics at the release site, and/or a documented history of health screening to inform decisions about health management (Parker et al. 2006; Ewen et al. 2007; Ortiz-Catedral et al. 2011; Ewen et al. 2012; Massaro et al. 2012; Sainsbury & Carraro 2023). Unfortunately, this information is usually lacking or of poor quality.

(4) Is dispersal a likely impediment to establishment and persistence?

Individuals translocated to a managed site must stay there rather than dispersing into adjacent unmanaged habitat where their likelihood of persistence will be much lower, or, in many cases zero. Habitat connectivity, and the ability for species to disperse between habitat patches, is typically seen as a positive landscape feature and a desirable management objective. However, dispersal from managed release sites into adjacent unmanaged areas appears to be an important cause of failure for many translocations (Richardson et al. 2014). Dispersal generally affects population growth at two levels. First, post-release dispersal following the initial release can

thereby reducing the probability of establishment and persistence. For example, an analysis of 14 reintroduced NI toutouwai populations showed that habitat connectivity was a key factor determining individual establishment following translocation, with individuals released at highly connected sites having a lower establishment probability than those at less connected sites, such as islands or isolated forest patches (Parlato & Armstrong 2013). Second, natal dispersal, i.e. the loss of juveniles raised at the release site, can also reduce establishment and persistence if juveniles move from managed to unmanaged sites (Richardson et al. 2014). Critically, the interaction of post-release dispersal and natal dispersal can limit population growth, erode genetic diversity, and reduce the likelihood of the long-term persistence of a translocated population.

The dispersal of translocated species from release sites is highly variable and sometimes difficult to predict (Table 1; Richardson et al. 2014; Innes et al. 2022). For instance, some birds are very strong dispersers regardless of habitat connectivity. These include korimako, miromiro / tomtit (Petroica macrocephala), and red-crowned kākāriki (Table 1; Parker et al. 2004; Brunton et al. 2008; Ortiz-Catedral 2010) whereas others, such as NI toutouwai and NI tieke, are less likely to disperse from sites with low connectivity (Table 1; Newman 1980; Richard & Armstrong 2010). The connectivity of the release site to surrounding unprotected habitats therefore varies according to the dispersal ability of the species in question, making connectivity difficult to measure. The shape of the relationship between dispersal ability and connectivity is also unknown for all species. However, we hypothesise that it will show a similar shaped curve as seen for other sources of mortality or loss to a managed population, e.g. increasing predator density (Fig. 2). Many species, including some with relatively strong dispersal abilities, rarely leave isolated sites such as islands or forest patches surrounded by pasture (Table 1). In contrast, species with poor dispersal abilities can move out of protected areas if connected to habitat that the species will willingly move through (Table 1; Richard & Armstrong 2010), although this is likely to be a greater problem for birds and bats than reptiles, amphibians, and invertebrates.

The best way to manage dispersal in contiguous landscapes is to manage as large an area as possible, including potential dispersal routes, through an integrated landscape management approach (Richardson et al. 2014). However, it is not currently known how big a site needs to be to accommodate postrelease and natal dispersal in most species, and it will often be difficult, too expensive, or simply not feasible to protect very large sites. This currently limits the ability to translocate some species to large sites.

A variety of alternative approaches have been used to try to reduce dispersal, albeit with variable results. Holding animals in captivity at the release site (delayed release) has been tried with many taxa, and many sites, but the results have been extremely variable. They have been generally ineffective for wild to wild releases, but sometimes useful when releasing captive-reared animals (Parker et al. 2012a; Smuts-Kennedy & Parker 2013; Richardson et al. 2014, 2015; Parker et al. 2015). Supplementary feeding has also been used with success for some species at some release sites, e.g. kākā (Nestor meridionalis), pāteke / brown teal (Anas chlorotis) (Rickett et al. 2013), but has been less useful for others, e.g. hihi, (Richardson et al. 2014). Acoustic anchoring (playback of pre-recorded calls) was attempted with NI kokako (Callaeas



Figure 2. A hypothetical relationship between expected equilibrium population density and habitat connectivity mediated dispersal following translocation. The dark green areas with solid black lines are managed habitat. The pale green areas surrounded by dashed lines are unmanaged habitats. The white area surrounding the first three managed areas represents habitat with a high resistance to dispersal (e.g. open water or pasture). Resistance to dispersal decreases as connectivity increases. The managed area (dark green) on the right is within contiguous habitat (pale green) that provides no resistance to dispersal. In this case dispersal/emigration is acting as mortality. A similar shaped curve would be seen for other sources of mortality or loss to the population, e.g. increasing predator density. While it is unequivocal that dispersal is problematic and directly related to connectivity, the exact shape of the curve is unknown for most species.

wilsoni), NI toutouwai, and popokōtea / whitehead (*Mohoua albicilla*) in Aotearoa but was not effective (Leuschner 2007; Molles et al. 2008; Bradley et al. 2011).

Another option for mitigating the impact of dispersal in the establishment phase is the release of large numbers of individuals, either in one big release or in a series of smaller releases over several years. This is intuitively appealing but is rarely effective and there are many examples where large numbers of animals have been released but the translocation has failed (Miskelly & Powlesland 2013). For instance, single popokotea translocations of 40-100 birds to isolated managed sites of up to 3300 ha have typically been successful. However, the translocation of 653 birds over 12 years into a 2450 ha protected block within the 17 000 ha Waitākere Ranges appears to have been unsuccessful (KAP unpubl. data). The relationship between release group size and establishment is also unclear. This is because high-quality sites where translocations are successful following the release of large numbers of animals could have been equally successful if fewer animals were released. In contrast, managers typically release fewer animals when they have less confidence in a site, creating a reporting bias towards success with larger releases (Armstrong & Seddon 2008; Armstrong & Wittmer 2011). Translocating large numbers of animals in the knowledge that many will die also

raises significant welfare and ethical issues, and may strain relationships, especially where translocation is not essential for the management of the species in question.

Ultimately, the best way to reduce dispersal is to release animals at isolated or relatively isolated sites. However, the great challenge with managing dispersal is that we want translocated species to establish populations within large contiguous sites, and we want individuals to be able to disperse freely between sites. This will protect against the problems of populations being small and will largely remove the need for reinforcement translocations for genetic management, i.e. natural dispersal via safe dispersal corridors will essentially act as passive meta-population management. It will also provide new opportunities for populations in smaller sites. In the current environment safe corridors generally mean protection from pests but as pest control improves other habitat variables will become more important. For example, what size, shape, and structure do corridors need to be to cater for as wide a range of native species as possible? We recommend that the ability of animals to safely disperse from intensively managed areas should be a performance measure for initiatives such as Predator Free 2050. Furthermore, dispersal pathways should be incorporated into decisions about which landscapes to protect first.

(5) Will genetic management be required and how realistic is it that this will be implemented?

Genetic diversity maintains evolutionary potential by providing populations with long-term capacity to adapt to changing conditions (Frankham et al. 2017; Forsdick et al. 2022). All populations lose genetic diversity over time because of chance events, i.e. genetic drift. However, small populations are especially vulnerable because they accumulate the mutations required to replace lost alleles so slowly (Frankham et al. 2017; Forsdick et al. 2022). Inbreeding (mating between relatives) in small populations can also reduce survival and reproductive success through inbreeding depression which, in turn, threatens population persistence (Frankham et al. 2017; Forsdick et al. 2022). Translocated populations are particularly susceptible to genetic drift and inbreeding depression. They also often impose a genetic bottleneck on new populations because the founders only represent a portion of the source population's genetic diversity. This effect is further compounded because the number of founders that recruit and contribute to the new population is usually smaller than the number released. In addition, translocated populations at small sites will always be small.

Therefore, careful consideration of genetic objectives is needed to minimise the loss of genetic diversity, to select a source population or populations, to define ongoing genetic management, and to predict the genetic diversity of the translocated population (Weeks et al. 2015). It is also essential to clarify whether genetic objectives are fundamental or means based. For example, we are rarely interested in maintaining genetic diversity for its own sake, i.e. as a fundamental objective. Rather our interest in genetic diversity is usually as a means objective that contributes to the long-term persistence of the translocated population by maintaining evolutionary potential and reducing extinction risk. If this is the case, then a means objective might be to release enough animals to maximise genetic diversity in the founders and therefore the evolutionary potential of the new population.

Alternatively, there are many reasons why small (\leq 100 individuals) translocated populations are created, including because only small numbers of animals exist, ease of management, for advocacy, or simply that only small sites are available for release. In these cases, genetic means objectives might include informed reinforcement translocations to maintain genetic diversity across a metapopulation. All management involves trade-offs. For example, the best source populations are typically large, genetically diverse, and have no history of tight (< 40-100 individuals) and/or long-term bottlenecks, although bottlenecks are sometimes acceptable if they were of short duration (Boessenkool et al. 2007). However, while obtaining animals for translocation from a small, inshore island or fenced sanctuary might be relatively easy and cheap, populations from such small sites are likely to have lower genetic diversity than those obtained from a large source population. Furthermore, the ongoing maintenance of a large release site, and the translocation of a large diverse founder population, could be significantly more expensive than managing a much smaller site with ongoing reinforcement translocations, at least in the short to medium term.

One creative option is to combine populations that have low, but different, genetic diversity. This approach was used by Heber et al. (2013) who mixed SI toutouwai (*Petroica australis*) from two low diversity translocated populations, to increase diversity in a new translocated population. Similarly, all translocated populations of NI tieke are descended from the last surviving population on Taranga / Hen Island from which birds were translocated to Whatupuke, Whakau/Red Mercury or Repanga / Cuvier Island (Parker et al. 2012b). However, the Repanga lineage is overrepresented with 15 descendent populations followed by Whatupuke (7 descendent populations) and Whakau (2 populations). Therefore, recent translocations have used multiple source populations including, where possible, underrepresented lineages, to maximise the genetic diversity in both new populations and the metapopulation (KAP, Lovegrove TG, McClellend P, unpubl. data). Alternatively, if it is uncertain if animals will establish and persist, lower value individuals (e.g. males or juveniles) can be released to test a new site. If these survive, additional animals can be released to maximise genetic diversity in the medium to long-term. This approach has been used for hihi translocations where the primary founders for new sites are juveniles from Tiritiri Matangi whereas birds from the remaining wild population on Te Hauturu-o-Toi / Little Barrier Island, which are viewed as higher value by some, are reserved for reinforcement translocations to established sites. Another option could be to increase the size of the release area through improved pest control thereby enabling a larger population to establish and removing or reducing the need for reinforcement translocations.

Additional considerations include the genetic profile and history of the source population(s). For instance, will the source population(s) provide genetically diverse individuals for translocation? How many individuals are needed to capture that diversity? These questions are not easily answered because they require high resolution genetic and demographic data for source populations and species. These data are usually lacking, especially for widely distributed taxa that show significant geographic variation in genetics and demography, such as lizards and invertebrates. However, even in the absence of such data, combining knowledge of natural history, individual population history and theory allows reasonable assumptions to be made (Weiser et al. 2013; Frankham et al. 2017).

Post-release monitoring is essential to determine how many animals a release site can support. If the population remains small reinforcement translocations might be recommended, but how easy will they be to achieve? The feasibility of reinforcement translocations is often presented in a simplistic manner with little recognition of the cost and difficulties in getting additional animals to recruit into an established population. Often, very large numbers of individuals must be added to ensure that at least a few will be able to recruit and breed (Weiser et al. 2013). This is because density dependence (Armstrong et al. 2005) or behavioural barriers (Parker et al. 2010a; Parker et al. 2012b) often reduce the recruitment of immigrants. As noted, releasing large numbers of animals while knowing that only a few will survive raises welfare and ethical questions and can strain relationships.

Regardless of the method chosen to maintain genetic diversity, it is important to recognise that not every translocated population needs to have maximum or ideal genetic diversity. Overall genetic diversity can also be represented and conserved within a metapopulation connected via natural dispersal and/or management. This likely represents a more natural scenario (i.e. genetic diversity will not be equal across all natural populations, especially when moving from the core of a species range to the edges), whilst also increasing options for establishing and maintaining translocated populations that cater to a wide range of values and objectives.

(6) What do future developments mean for the management of translocated populations?

Translocations will continue to play an important role in conservation in Aotearoa. Experience and research will increase our understanding of the values driving translocations including, but not limited to, cultural and societal desires, cost, animal welfare, genetic and pathogen management, translocation techniques, and dispersal. We also need to fill the significant knowledge gaps that exist for many species, especially invertebrates, lizards, amphibians, and bats (Table 1). In Aotearoa the biggest opportunities will come about through improved control of pests over large, unfenced areas of the mainland, including forests, wetlands, dryland and braided river systems, and alpine zones (Table 1). This will provide additional habitat for species that are currently in higher threat categories, along with further options for the management and translocation of all species, especially habitat specialists such as whio / blue duck (Hymenolaimus *malacorhynchos*), kakī/black stilt, and pīwauwau/rock wren (Xenicus gilviventris), and neglected fauna, such as lizards, amphibians, bats, and invertebrates. While opinions vary on the feasibility of effective pest control over vast swathes of Aotearoa (Urlich 2015), it will clearly be a game changer if it can be achieved. However, in the short term (c. 20 years) large $(\geq 3000 \text{ ha})$ fenced sanctuaries will likely protect the greatest diversity of biodiversity on the main islands, especially if mice can be effectively controlled within them.

We also expect to see an increasing shift away from translocations for single-species recovery toward those where the fundamental objective is ecosystem restoration (Parker 2013). Pathogens and predators, such as weka (Gallirallus australis), small rails (Gallirallus spp. and Zapornia spp.), and karearea / NZ falcons (Falco novaeseelandiae) are components of Aotearoa ecosystems that are currently either not included in restoration plans or relegated to some point in the distant future once their potential prey or host species are well established (Carpenter et al. 2021). It seems logical to plan ecosystem restoration sequences in stages so that prey species are established before predators, but it is important to distinguish between a pest, against which native species have few defences, and a native predator that they have co-evolved with over 1000s of years. For example, although pests have caused the extinction of many large weta populations elsewhere, translocated Mercury Island tusked wētā (Motuweta isolata) and the giant weta / wetapunga (Deinacrida heteracantha) have established in the presence of very high densities of a natural predator, the NI tieke. Translocations of native predators require acceptance that there will be ongoing predation and possibly a reduction in the population size, alongside changes in the behaviour of prey species. This will be difficult for some people to accept and could be problematic for very small prey populations, but it is a logical objective for true ecosystem restoration. It might also require a change in thinking about the management of native predator species, and pathogens, especially where there is a perception that natural predators and pathogens must be controlled.

There has also been considerable debate about the ongoing impacts of global climate change and how translocations can be used to conserve species whose habitat will deteriorate under current climate change predictions (Hoegh-Guldberg et al. 2008; Seddon et al. 2009; Seddon 2010). In Aotearoa this would likely mean moving animals across latitudinal gradients, e.g. between the North and South Islands. For instance, climate modelling suggests that the northern South Island, where hihi have never existed, might provide higher quality habitat in the future than the North Island, to which they are currently restricted (Chauvenet et al. 2013). Any decision to undertake a translocation beyond a species' natural range will also clearly raise challenges in setting appropriate objectives, especially if it would bring closely related species into contact, although we note that this has already happened for some species.

Another interesting proposition is using close relatives of extinct species as ecological replacements in ecosystem restoration (Atkinson 1988). For example, the tutukiwi/Snares Island snipe (Coenocorypha huegeli) has been translocated to replace the extinct tutukiwi / SI snipe (Coenocorypha iredalei) and the NI kokako as a replacement for the presumed extinct SI kokako (Callaeas cinerea). SI takahē (Porphyrio hochstetteri) are also frequently translocated to the North Island (Jamieson & Ryan 2001; Parker et al. 2010b; Miskelly et al. 2012), although takahē translocations are motivated by species recovery goals rather than as a replacement for the extinct moho/NI takahē (Porphyrio mantelli). It has also been suggested that the introduced Australian brown quail (Synoicus *ypsilophorus*) could be a suitable ecological replacement for the extinct New Zealand quail (Coturnix novaezelandiae) (Parker et al. 2010b). These species, and others, might be useful for restoring ecosystem functions, known or otherwise, along with restoring generally depauperate ecosystems. In addition, genetic techniques are advancing to the point where de-extinction, the resurrection of functional proxies of extinct species, might become feasible (Seddon et al. 2014; Seddon 2017). This is a contentious issue and the objectives of any such proposal would have to be very carefully considered, including the conservation benefit of diverting funds from extant species to de-extinction proposals (Bennett et al. 2017).

Emerging genomic tools will further enhance translocation decision making (Luikart et al. 2018; Funk et al. 2019; Forsdick et al. 2022; Moehrenschlager et al. 2023). Advanced highthroughput sequencing technologies, combined with rapidly decreasing costs, increased capability and capacity in the conservation genetics community, can provide ready access to 10s to 10 000s of markers from across the entire genome, even for non-model species (Harrisson et al. 2014; Galla et al. 2019). These genome-wide markers can increase resolution for translocation questions previously answered using just a handful of neutral genetic markers. For example, genomic markers can provide more robust estimates of relatedness for pairing decisions in conservation breeding programmes that include translocations (Galla et al. 2020). Similarly, genomic markers are increasingly used to identify suitable source populations for translocations to enhance adaptive potential (McLennan et al. 2020; Rayne et al. 2022). Indeed, the promise of characterising adaptive variation has also reignited debate over how we should source, or mix, populations to enhance adaptive potential (Kardos et al. 2021). However, translating theory into practise remains difficult (Flanagan et al. 2017) despite a surge of theoretical and simulation-based papers focussed on characterising adaptive variation (Funk et al. 2019; Hoelzel et al. 2019). For many threatened species, it may prove challenging to characterise adaptive variation at all (Forsdick et al. 2022).

Recent years have also seen the rise of a new era of conservation genomics that reintegrates the structure and function of DNA (Deakin et al. 2019). For example, emerging chromosomic approaches combine genomic data with cytogenetics (chromosome architecture), epigenomics (histone

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modifications), and cell biology to reveal the mechanisms underpinning behavioural and phenotypic traits under selection (Mérot et al. 2020). Although each of these approaches come with caveats (Wold et al. 2023), genomic and chromosomic approaches are valuable additions to the translocation toolbox, particularly in the face of novel challenges such as climate change (Hoffmann et al. 2021; Wold et al. 2021).

Conclusions

The common perception that translocations are relatively easy and that success is assured is not supported by the evidence either in Aotearoa (Miskelly & Powlesland 2013), or internationally (Griffith et al. 1989; Wolf et al. 1996; Fischer & Lindenmayer 2000). The frequency of translocations is also increasing in Aotearoa (Cromarty & Alderson 2013), including calls for urban translocations (van Heezik & Seddon 2018). Furthermore, the quality of translocation proposals presented to DOC is highly variable, with some being poorly written, poorly thought out, or just a bad idea for the candidate species. The DOC approval process itself also produces variable outcomes. The authors want to see more successful translocations in Aotearoa, and we think that the six key considerations we present here will help in achieving that success.

Ultimately, our goal is to encourage careful thinking in the formulation of translocation objectives so that these capture the diverse values motivating translocations, together with appropriate performance measures for determining success. We discourage a focus on any single value. Instead, we encourage all people involved in translocations, particularly decision makers, to explicitly recognise the multiple values-based objectives associated with translocations.

Haphazard conservation translocations can cause problems at the release site, for future translocations, and in maintaining equitable relationships with mana whenua, local communities, relevant agencies, and the public. All the translocations we have been involved with have been guided by clear principles. However, the principles of good translocation practice are not currently captured in DOC policy (Parliamentary Commissioner for the Environment 2017). Furthermore, the fundamental objectives of many translocations have rarely been stated explicitly or are dominated by singular means objectives. Therefore, a clear and widely consulted translocation policy framework would enable DOC decision makers to make better decisions about all translocations. This policy should (1) specifically acknowledge that translocations are values based, (2) should be driven by an understanding of the problem at hand, (3) require informed decisions between management alternatives (including rejecting translocation as a management tool for some species/programmes), and (4) should be measured by explicitly stated objectives with appropriate performance indicators. Ultimately, being clear about what all relevant parties really want will set everyone on the right path towards the landscape of Aotearoa being one that is once again dominated by indigenous biodiversity.

Acknowledgments

We dedicate this paper to our colleague, mentor, and friend, the late Ian G. Jamieson, who contributed to an earlier version of this paper. We are grateful to the Biological Heritage National Science Challenge Project 1.4 team including Thomas Buckley, Levi Collier-Robinson, Rod Hitchmough, Michael Knapp, Roger Moraga, and Anna Santure for robust dialogue on characterising adaptive variation for translocations. We are also grateful to Jana Wold for her constructive feedback and textrelating to chromosomics. Susan Walker, David Pattemore, Anne Schlesselmann, Ron Moorhouse, and Helen O'Leary provided very helpful comments on earlier versions of this paper, along with three anonymous reviewers.

Additional Information and Declarations

Conflicts of interest: The authors declare no conflicts of interest.

Funding: KAP, ZS and DPA were funded by the Ministry of Business and Innovation (MBIE) through an Endeavour Grant (contract C09X1805) as part of the More Birds in the Bush programme.

Ethics: Ethical approval was not required for this review.

Data availability: There are no data or code directly associated with this review.

Author contributions: KAP led the writing of the MS with input from all co-authors. JGE, JI, AR, TES, PJS and DPA provided significant contributions to the overall structure. ELW, NF and DM contributed to section 5 and EP, KR and ZS to sections 2, 3 and 4. LA, TM and MM provided a management perspective throughout.

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Received: 9 July 2021; accepted: 11 July 2023 Editorial board member: David Pattemore