FORUM ARTICLE

What's the end-game for biodiversity: is it time for conservation evolution?

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Abstract: Conservation biology emerged in the 1980s to prevent extinctions by intervention and adaptive management. Despite many successes worldwide, the goal of self-sustaining populations of many threatened species without ongoing human assistance remains elusive. This is in part due to novel selection pressures overwhelming the ability of species to adapt to changing ecological circumstances. Evolution was also not considered to occur sufficiently fast to induce the recovery of many species. Recently, however, evolution has been observed in contemporary time frames, often in decades. This has stimulated discussion that evolutionary rescue could be possible for some species, leading to populations becoming self-sustaining. Evolutionary rescue is the ability of species to respond to novel selection pressures by adaptation via natural selection.

In this article, I ask whether it is possible to manipulate natural selection to facilitate the ongoing survival of some New Zealand indigenous forest bird species in the presence of introduced predators, using existing management techniques. I suggest that existing management could be reconfigured so that existing and new safe sites, which safeguard evolutionary potential, have adjoining transition zones where predator abundance is suppressed, to provide the conditions for selection of adaptive phenotypic plasticity. Natural selection is theorised to favour phenotypes with plastic behaviour or genetic mutations that enhance survival and reproduction in the face of changing selection pressures, such as introduced predators. The aim is to facilitate the long-term coexistence of some forest bird species with introduced predators, so that populations eventually require little or no human intervention, in the event a predator-free country proves to be insurmountable. I suggest this conservation evolution approach is complementary to, and extends, the current conservation predator control paradigm. This is because it remains essential to continue to protect species that are substantially maladapted to novel selection pressures for evolutionary rescue to occur.

Keywords: biodiversity goals; rapid evolution; evolutionary rescue; forest biodiversity; natural selection

Introduction

Adaptive evolution occurs in contemporary or ecological timescales, i.e. within a few hundred generations, in response to changing ecological conditions (e.g. Losos et al. 1997; Reznick et al. 1997; Grant & Grant 2002; Foster et al. 2007; Massaro et al. 2008; Galetti et al. 2013; and see reviews in Endler 1986; Thompson 1998; Hendry & Kinnison 1999, 2001; Ashley et al. 2003; Stockwell et al. 2003; Ferrière et al. 2004; Carroll et al. 2007). Microevolutionary processes have been documented in many different functional groups, such as birds (Table 1). The rate of evolution in these cases may be sufficiently fast to increase population viability in contemporary timescales (Thompson 1998; Hairston et al. 2005). Evolution is expected to have its largest effect on traits that change most quickly, and on traits that most strongly influence ecological interactions (Carroll et al. 2007).

Whether microevolutionary processes reflect the early stages of speciation over the long term (i.e. at the macroevolutionary scale) or reflect a range of adaptive states that a species can oscillate between as selection pressures fluctuate is a longstanding unresolved question (e.g. Thompson 1998; Hendry & Kinnison 2001). Estes and Arnold (2007) term these oscillations an 'adaptive zone', in which the fitness optimum can move, such that changes can be reversible or accumulate in a directional way (see also Grant & Grant 2002).

The range of adaptive states is an expression of phenotypic plasticity to changing ecological circumstances (Ghalambor et al. 2007; see Table 2 for definition of key terms). Adaptive plasticity results from developmental and behavioural responses of genotypes to environmental conditions, and operates both within and across generations. When plasticity is adaptive, as opposed to non-adaptive or neutral, it moves the phenotype towards a fitness optimum within its adaptive zone (Estes & Arnold 2007; Ghalambor et al. 2007).

In ecosystems with novel selection pressures, the adaptive zone for some species may be pushed to its extreme, resulting in a race between demography and extinction (Maynard Smith 1989). Adaptive evolution in response to novel selection pressures is therefore of much interest to conservation managers (Ashley et al. 2003; Stockwell et al. 2003; Kinnison et al. 2007). These authors collectively argue that evolutionary thinking is relevant now to conservation biology and resource management. However, conservation biology has been termed a crisis discipline, with immediate and ongoing management intervention needed to protect threatened species from further decline (Soulé 1985). In his seminal paper, Soulé acknowledged the importance of evolutionary potential in realising the long-term goal of biodiversity persistence with little or no help from humans, but considered this unrealistic for the foreseeable future. In reality, ongoing management intervention to prevent extinctions, and an adaptive evolution management

Table 1. Examples of microevolutionary processes on contemporary timescales for bird species. For a more comprehensive review, as well as a description of life-history traits hypothesised to be influenced by predation, see table 1 in Martin & Briskie (2009).

Species	Area	Natural selection driver	Microevolutionary change	Reference
Passer domesticus (house sparrow)	United States	Introduction into new environment	Colour and size	Johnston & Selander (1964)
Geospiza fortis; *Geospiza scandens* (Darwin's finches)	Galapagos Islands	Shifting climate patterns	Body size and beak traits	Grant & Grant (2002)
Sylvia atricapilla (Eurasian blackcap)	Europe	Shifting climate patterns	Migratory behaviour	Bearhop et al. (2005)
Hemignathus virens (honeycreeper aka Amakihi)	Hawaiʻi	Disease	Resistance to avian malaria	Foster et al. (2007)
Phylloscopus fuscatus (dusky warbler)	Siberia	Changing predator abundance	Change in nest selection	Forstmeier & Weiss (2004)
Anthornis melanura (bellbird aka korimako)	New Zealand	Introduced predators	Change in nest behaviour	Massaro et al. (2008)
Vermivora celata (orange-crowned warbler)	California	Introduced predator	Change in nest behaviour and placement	Peluc et al. (2008)
Zosterops lateralis (silvereye)	Islands in Australasia	Introduction into new environment	Increased body size	Clegg et al. (2002); Clegg (2010)

Table 2. Definitions of key terms used in this article.

Term	Definition	Reference
Contemporary evolution	Heritable trait evolution observed in contemporary time (i.e. less than a few hundred generations).	Stockwell et al. (2003, p. 94)
Directional selection	Individuals with trait values at one extreme have higher fitness, resulting in a directional shift in the population mean value for that trait.	Stockwell et al. (2003, p. 94)
Disruptive selection	Selection favouring the extremes at the expense of average phenotype.	Maynard Smith (1966, p. 637)
Novel ecosystems	Containing new combinations of species that arise through human action, environmental change, and the impacts of the deliberate and inadvertent introduction of species from other parts of the world.	Hobbs et al. (2006, p. 1)
Phenotypic plasticity	The phenomenon of a genotype producing different phenotypes in response to different environmental conditions.	Ghalambor et al. (2007, p. 395)
Rapid evolution	Occurs if a heritable phenotypic change occurs sufficiently quickly to alter the trajectory of an ecological process while it is still in progress.	Hairston et al. (2005, p. 1117)
Safe sites	Habitat refugia that components of biodiversity retreat to, persist in and potentially can expand from under changing environmental conditions.	Keppel et al. (2012, p. 393)

approach to enable threatened species to successfully coexist with novel selection pressures (Ferrière et al. 2004; Kinnison & Hairston 2007), may both be needed and are compatible with each other. This is pertinent as novel selection pressures have resulted in many novel ecosystems (*sensu* Hobbs et al. 2006). These authors suggest that novel ecosystems could be manipulated to a preferred state in which they retain a strong wild or natural composition.

The goal of manipulating or facilitating natural selection by conservation management is self-sustaining populations of threatened species in novel ecosystems. Ferrière et al. (2004) describe this as an 'evolutionary conservation biology' response, with the ultimate goal to foster systems that enable threatened species to persist. For that to occur, species that are not critically maladapted to novel ecosystem stresses may need to be facilitated to evolutionary rescue (*sensu* Gomulkiewicz & Holt 1995). Evolutionary rescue is essentially a resurgence of a declining population, due to sufficiently rapid adaptation in response to sudden and ongoing environmental change (Gomulkiewicz & Holt 1995; see also Gonzalez et al. (2013) and others in the January 2013 issue of *Philosophical Transactions of the Royal Society B*).

Management to facilitate evolutionary rescue has been suggested as a complementary conservation strategy for the ongoing protection of threatened populations (Ashley et al. 2003; Stockwell et al. 2003; Ferrière et al. 2004). For example, safe sites for captive populations can also be viewed as dynamic reserves of evolutionary potential (Stockwell et al.

2003). This presupposes that species of conservation interest are not maladapted enough to be caught in evolutionary traps (Gomulkiewicz & Holt 1995; Schlaepfer et al. 2002). Those species, such as the kākāpō (*Strigops habroptilus*), may well have a future confined to safe sites where novel selection pressures are absent. This is due to maladaptation characteristics such as flightlessness, reduced predator escape responses, and slow reproductive rates (Duncan & Blackburn 2004). For those species that can adapt, Estes and Arnold (2007) suggest that populations are often well equipped genetically to respond to at least short-term ecological challenges.

There are conservation management trade-offs to consider when attempting evolutionary rescue, such as loss of genetic diversity due to directional selection (Stockwell et al. 2003). These authors suggest that adaptation could lead to a loss of genetic variation as genotypes that improve fitness increase. Survival of threatened species may therefore mean prioritising future adaptation over preservation of genetic diversity, as preservation may decrease overall fitness and thereby impede adaptation in the present (Stockwell et al. 2003). The key for enabling adaptation is amelioration from novel selection pressures, sufficient for natural selection to operate. For evolutionary rescue to occur, generations of selection in intermediate or 'transition' environments, i.e. where selection pressures are reduced or continually suppressed by management, could help buffer the strength of novel selection pressures in unmanaged areas (Stockwell et al. 2003).

In this paper, I present such a system that may facilitate the adaptive evolution of indigenous forest bird species to novel predators in New Zealand forest ecosystems. This is based on a source–sink framework of population regulation at the landscape level (Pulliam 1988). I provide an example of how current conservation management could potentially be configured to facilitate adaptive evolution (in sinks), while still protecting threatened forest bird species (in sources). I show how amelioration of novel mammalian predation pressures could potentially induce adaptive evolution and evolutionary rescue of some forest bird species. The management aim is to assist forest bird species that are not critically maladapted to become resilient to novel selection pressures with little, or no, further human intervention. This is considered in the context of the current predator management paradigm. I then extend Gomulkiewicz and Holt's (1995) model of evolutionary rescue to provide a heuristic model for different forest bird species based on life-history attributes. The objective of this conservation evolution approach is to augment the current strategic framework around predator control, to achieve the goal of self-sustaining populations of some forest bird species. To support this objective, a series of potential research questions are posed.

Challenges in the current management paradigm of New Zealand forest ecosystems

In New Zealand forest ecosystems, the introduction of novel selection pressures since human arrival has been catastrophic for avian biodiversity (Holdaway et al. 2001; Duncan & Blackburn 2004). Over 70 species became extinct, including many forest birds (Holdaway et al. 2001). Populations of many remaining species are threatened by predation from introduced mammals, habitat loss, disease, competition from introduced species, and effects of climate change (O'Donnell 1996; Green & Clarkson 2005; Miskelly et al. 2008; Innes

et al. 2010; Christie 2014). Introduced predators are considered the most serious immediate risk to the survival of threatened forest bird species (Innes et al. 2010).

Goal Three of the New Zealand Biodiversity Strategy (NZBS) is [paraphrased] to halt the decline in biodiversity, and maintain and restore viable populations of all indigenous species (DOC & MfE 2000). One of the key implementation methods for the protection of threatened forest birds is ongoing predator control programmes (e.g. Parkes & Murphy 2003; Brown & Urlich 2005; Green & Clarkson 2005; O'Donnell & Hoare 2012). Conservation management techniques to protect forest bird species from predators rely on the creation and maintenance of island refuges, fenced predator-exclusion zones, translocations of threatened species, and small-scale (intensive) and large-scale (extensive) predator control.

The primary tool for extensive predator control is the aerial application of 1080 (sodium monofluoroacetate) toxin, over thousands of hectares, to cull introduced possums (*Trichosurus vulpecula*), rats (*Rattus* sp.) and stoats (*Mustela erminea*) (Brown & Urlich 2005). These operations release predation pressure on forest birds, sufficient to stabilise populations and to enable new recruitment to occur (Powlesland et al. 1999; Innes et al. 2004; O'Donnell & Hoare 2012). If these operations are discontinued, pest numbers rapidly rebuild and forest bird species decline, as in areas where predators are not culled (Elliot et al. 2010).

However, only a fraction of New Zealand's two main islands receive sustained predator control (PCE 2011), and outside these areas forest bird species continue to face unrelenting predation pressure, or contemporary extinction (see Innes et al. 2010 and references therein). The ongoing threats to forest birds outside of protected areas have led to calls to increase the aerial application of 1080 more widely (PCE 2011; Callaghan 2012 [weblink]). The Parliamentary Commissioner for the Environment stated this was necessary as: 'we cannot allow our forests to die' (2011, p. 7). Callaghan (2012) called for an 'Apollo' style mission to systematically and totally eradicate mammalian predators from New Zealand, starting with the 169,464-hectare Stewart Island. However, the Department of Conservation does not consider predator eradication from Stewart Island feasible at this time (Bell & Bramley 2013).

The outcome of successfully achieving a predator-free New Zealand (PFNZ) is the long-term protection of indigenous biodiversity (Byrom & Timmins 2012 [weblink]). Achievement of PFNZ may depend on technological advances to deliver new and innovative eradication tools (Byrom & Timmins 2012). However, even if such developments do not eventuate to enable this goal to be attained, predator control in forest ecosystems is expected to continue indefinitely. This is because preservation and protection of natural resources (i.e. species and ecosystems) is a core function of the Department of Conservation in section 6 of the Conservation Act 1987; and predator control by individuals and community groups is also likely to continue.

The PFNZ goal is likely to be dependent on this sort of social support for the widespread implementation, and the follow-up application, of new or existing eradication tools (Byrom & Timmins 2012; Bell & Bramley 2013). Success may also depend on individual consent from all landowners and occupiers to temporarily give up property rights in the form of allowing access to houses, garages, drains, buildings, factories, barns, sheds, and all manner of structures and vegetation, if toxins and/or traps are to be deployed to put every predator at

risk at similar times. Different social constraints may apply to a transmissible pathogen in the form of public health, and pet and stock welfare concerns (PCE 2000). Social agreement to ongoing biosecurity measures to prevent reinvasion of areas cleared of introduced predators will also be problematic (Bell & Bramley 2013), as some people may hide (e.g. Church 2008 [weblink]) or re-release predators because they care about them and/or they do not care for indigenous biodiversity, or a profit can be made from illicit trading (Tan 2012 [weblink]). There could also be international food safety implications depending on the pathogen or toxin used around food-producing areas; and trading partners could impose costly biosecurity measures to prevent the transmission of pathogens to areas where predators are a threatened species in their home environment (PCE 2000).

The possibility of eradicating predators from the country using existing technology is now under investigation by the Department of Conservation and Landcare Research in response to Callaghan's call (Byron & Timmins 2012). Regardless of whether this turns out to be technically and socially feasible, there is also a raft of potential ecological consequences that need careful examination and contingency planning prior to implementation. This is because eradication of introduced species that are functionally integrated in novel ecosystems may lead to unintended and undesirable outcomes, such as release of exotic mesopredators or weed expansion with adverse effects on indigenous biota (Soulé et al. 1988; Courchamp et al. 1999, 2003; Zavaleta et al. 2001; Carroll 2011). For example, Feare (1999) reported exotic crazy ant (*Anoplolepis longipes*) populations exploded on Bird Island in the Seychelles, after eradication of introduced rats, with negative consequences for indigenous bird and lizard species. However, there are many instances of successful recovery of indigenous biodiversity after eradications of island invasives (see Veitch et al. 2011). Whether that can occur on the greater scale of mainland New Zealand will depend on the success of eradicating multiple species contemporaneously (Byrom & Timmins 2012). For example, should stoats and rats be eradicated from forest ecosystems, but not mice (*Mus musculus*), population explosions of mice could ensue (e.g. Innes et al. 1995) resulting in negative effects on indigenous biota from competition or predation (e.g. Caut et al. 2007; Wanless et al. 2007).

Therefore, what ecosystems could look like if the PFNZ goal is achieved has not yet been articulated, as biodiversity recovery may not be as simple as just removing predators. Innes et al. (2012) argued that the ecological damage wrought in terrestrial ecosystems is not reversible due to extinctions, decimation of some functional groups, extensive habitat modification, the effects of climate change, and introduced predator and pest impacts. Norton (2009) also cautioned that reversing biotic thresholds is very difficult, because of extinctions and altered selection pressures caused by biological invasions. In addition, the ability of predators to adapt to changing ecological circumstances and control pressures is another significant challenge to overcome (Carroll 2011). For example, Vander Wal et al. (2012) identified rat resistance to anticoagulant poison as an example of introduced predators undergoing evolutionary rescue in contemporary time.

An alternative goal to PFNZ is the promotion of coexistence of some indigenous species with introduced predators in novel ecosystems (Norton 2009). This is premised on the idea that as predator eradication is highly unlikely on mainland New Zealand, at least in the foreseeable future except in small defendable areas, alternative strategies to facilitate long-term

biodiversity protection need to be identified. In the following section, I explore such a strategy based on the possibility that adaptive evolution can occur for some indigenous forest bird species leading to evolutionary rescue and self-sustaining populations.

Evidence for evolutionary rescue

Nothing in biology makes sense except in the light of natural selection (Dobzhansky 1973).

Evolutionary rescue is the combination of genetic and demographic conditions that enable populations to adapt successfully to changing environments (Gomulkiewicz & Holt 1995). Evolutionary rescue will be visible if the population increases and there is a rapid change in the phenotype, either by selection-induced changes in the standing genetic variation or through novel advantageous mutations (Vander Wal et al. 2012). Others have suggested that increased phenotypic plasticity occurs after sudden extreme environmental change, with subsequent genetic assimilation of the adapted phenotype (Hendry et al. 2008; Lande 2009). Regardless of the operant mechanism, evolutionary rescue will lead to a change in genetic variability as natural selection favours those variants that survive better in novel ecosystems (Stockwell et al. 2003). These might be those rare individuals at the tail of the fitness distribution who survive better in the face of environmental change (Gonzalez et al. 2013).

Evolutionary rescue is a relatively new field of study, which has focused on establishing a general conceptual basis, and has not yet developed predictive tools for gauging evolutionary success in the wild (Gomulkiewicz & Shaw 2012). These authors identify a number of properties that are likely to be involved in identifying the process of evolutionary rescue:

- Environmental change (form, rate, pattern, severity, and magnitude)
- Size of the population experiencing the change
- Rate of population growth or decline (mild, catastrophic, gradual, or sudden)
- Amount of heritable genetic variation in absolute fitness
- Manifestation under stress of traits that mediate absolute fitness
- Behavioural or phenotypic plasticity affecting fitness
- Ecological properties that affect population trajectory (density dependence, spatial heterogeneity, interspecific interactions).

The difficulties in obtaining data on both population dynamics and evolutionary changes means that evidence for evolutionary rescue in vertebrates is still sparse in the wild (Vander Wal et al. 2012). A review by these authors identified the best support was to be found in highly fecund, relatively short lived species, such as in rats exposed to toxic anticoagulant baits, and rabbits (*Oryctolagus cuniculus*) exposed to rabbit haemorrhagic disease and myxomatosis. The review was not exhaustive, however, as it did not include the evolutionary rescue of the Hawaiian honeycreeper bird, the amakihi (Foster et al. 2007). The recovery after outbreaks of avian malaria of amakihi populations at low elevations originated from resistant individuals that colonised from relict populations at similar altitudes. These examples illustrate that continued persistence of population remnants is required if evolutionary rescue is to occur (Holt 2004; Gomulkiewicz & Shaw 2012).

Safe sites and conservation evolution

If we can create persistent populations, then we expect adaptive evolution (Holt 2004, p. 2057).

The most effective way to create persistent populations is to create safe sites as refuges for biodiversity (Keppel et al. 2012). One of the key functions of safe sites in novel ecosystems is to provide threatened species with relief from incessant encounters with introduced predators (Innes et al. 2012). Outside safe sites, a species may encounter multiple, different predators (O'Donnell et al. 1996; Innes et al. 2010). The frequency and types of different predation attempts may come too often, and be too lethal, for any adaptive responses to be selected for. Safe sites therefore protect biodiversity from extinction and maintain evolutionary potential (Stockwell et al. 2003). Safe sites can also soften other selection pressures such as habitat changes from land use activities, and provide species with the opportunity to expand should environmental conditions change (Keppel et al. 2012).

A safe site can thus be thought of as an ecological 'bank' that protects biodiversity or 'capital'. As populations stabilise within safe sites, and density-dependent population pressures build, there should be ongoing dispersal of propagules (the 'interest') into the surrounding unsafe sites. There is support for this concept from the source–sink hypothesis of population regulation at a landscape level (Pulliam 1988). *Sources* are favourable habitats at a landscape scale where birth rates exceed death rates; whereas *sinks* are unfavourable or suboptimal habitats where species struggle to persist without ongoing immigration from source populations (Pulliam 1988; Holt 1996). Safe sites are, in effect, sources of biodiversity, whereas the surrounding unmanaged, or partially managed, landscapes are sinks.

The transition between sources and sinks may be too abrupt for some New Zealand forest bird species to adapt to novel selection pressures. For evolutionary rescue to occur more rapidly, a zone surrounding a safe site may be needed where dispersing propagules can be exposed to some predation or selection pressure. This 'transition' zone has less predation pressure compared with unmanaged sinks, and can be thought of as a managed environment for natural selection purposes. The regular culling of predators immediately outside safe sites, to keep populations suppressed at low abundance, buffers propagules somewhat from predation, allowing natural selection the chance to operate in transition zones (Stockwell et al. 2003).

This strategy attempts to favour those traits that confer higher fitness by directional selection to changing ecological circumstances, in this case a managed gradient in predation pressure (Stockwell et al. 2003). The goal is the eventual colonisation of unmanaged sinks by increasingly predator-savvy forest birds leading to self-sustaining populations in the forest landscape. While there is currently little empirical evidence in New Zealand for this (but see Massaro et al. 2008), there are multiple studies showing that adaptive phenotypic plasticity can reduce the strength of selection pressures on birds (see Martin & Briskie (2009) for a review). The evolution of self-sustaining populations may not be a linear or straightforward process, however. Adaptive traits could be subsumed by non-adaptive traits caused by interbreeding between forest birds in sources and sinks (Gomulkiewicz & Holt 1995; Lenormand 2002; Stockwell et al. 2003). Alternatively, co-evolutionary processes could occur as selection for adaptive traits in transition zones filters back to forest birds domiciled in

sinks (Holt 2004), although this may depend on the direction of gene flow as migrant flow is generally higher from denser to more sparsely populated environments (Lenormand 2002). In the long term, conservation managers may also need to carefully consider the desirability and implications of disruptive selection.

The premise underpinning the source–sink model is that a combination of a safe site and a transition zone should result in selection for adaptive phenotype plasticity: i.e. individual forest birds that are more phobic or 'skittery' towards novel species; or individuals that select breeding refuges that are inaccessible to predators; or that can adapt nesting behaviour to reduce predation risk (Starling 2006; Massaro et al. 2008; Martin & Briskie 2009). Starling (2006) summarised evidence that individual birds can assess the risk of predation and so adapt their feeding, flocking, or nesting preferences to increase survival and reproduction. Martin and Briskie (2009) suggest that such plasticity in these traits can be heritable as they are under selection pressure, and are therefore adaptive as they confer higher fitness (see also Price et al. 2003; Lande 2009). Starling (2006) also cautioned that loss of predator recognition in succeeding generations of birds after predator removal could make the offspring more vulnerable to predator reinvasion (see also Maloney & McLean 1995). A level of predation may therefore be beneficial to some bird species from a population evolutionary perspective, to enable them to coexist with novel predators by evolving adaptations (Carroll 2011; Lankau et al. 2011).

Predicting adaptive evolution from life-history traits

Evolutionary rescue is likely to occur at different rates for different species depending on life-history traits and phenotypic plasticity and heritable trait diversity (Gomulkiewicz & Holt 1995; Price et al. 2003; Kinnison & Hairston 2007). Figure 1 extends Kinnison and Hairston's (2007) modification of Gomulkiewicz and Holt's (1995) heuristic model of evolutionary rescue. This simple model shows five potential trajectories for forest bird populations in the ongoing presence of novel selection pressures. The trajectories range from evolutionary rescue (*a*) where the population does not fall below a critical abundance where probability of extinction is high, to extinction (*e*) where evolution does not occur sufficiently fast, or not at all. The remaining three trajectories reflect the ability of different species to adapt in the presence of predators with ongoing management. Population (*d*) is illustrative of critically maladapted species that require management and protection in safe sites; and, as such, are unlikely to attain evolutionary rescue in the presence of predators. This would include forest bird species such as the kākāpō. Evolution is evident in (*b*) and (*c*) with the start of population recovery occurring at different rates depending on life-history traits. Evolutionary rescue occurs more quickly for species that could be termed *r*-selected (*b*), than for species that are characterised as *K*-selected in (*c*). This is because evolutionary rescue is predicted to occur more rapidly for bird species with relatively large populations, high fecundity, and short generation times (cf. Vander Wal et al. 2012). However, where a species ends up within the shaded area depicted in Figure 1 may also be due to an important life-history behavioural trait, or particular suite of traits, related to time since ancestral arrival and the extent of behavioural plasticity (Price et al. 2003; Duncan &
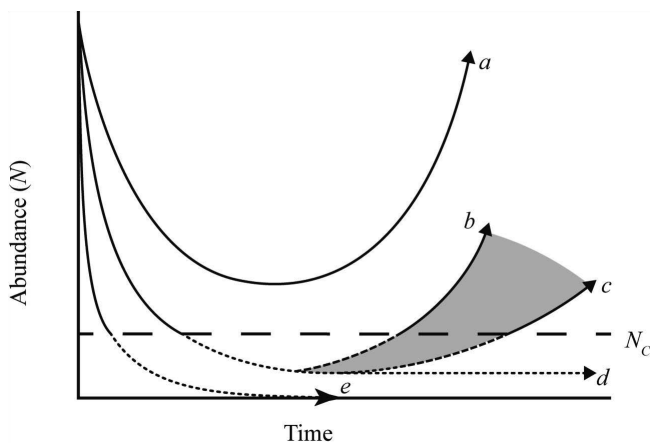
Figure 1. Population abundance (N) and extinction risk in the presence or absence of evolutionary rescue. Adapted from Gomulkiewicz & Holt (1995) and Kinnison & Hairston (2007) and modified for indigenous forest bird species in New Zealand. Growth is independent and N_c represents a threshold abundance below which the likelihood of extinction is high. Five heuristic scenarios of population trajectories in the presence of novel selection pressures, in this case introduced mammalian predators, are shown. Evolutionary rescue allows the population to avoid extinction risk (a). In contrast, population (e) is driven to extinction in the absence of evolution, or evolution does not occur sufficiently fast enough. Population (d) is illustrative of critically maladapted species that require ongoing management and protection in safe sites; as such, populations are unlikely to attain evolutionary rescue in the presence of predators and reach N_c. Evolution is evident in (b) and (c) with the start of population recovery illustrated by dashed lines. Evolutionary rescue and increased abundance occur more quickly for (b) in the equivalent time than for (c). The shaded area represents the relative adaptive plasticity of phenotypic life-history traits for different species in response to predation. This may be a key life-history trait, or particular suite or mix of traits, along the r–K spectrum related to time since ancestral arrival (see text).

Blackburn 2004; Martin & Briskie 2009). The shaded area between (b) and (c) therefore represents the relative adaptive plasticity of phenotypic life-history traits for different species in response to predation pressures. These traits may include such things as nesting preferences, nest behaviour, number of nesting attempts per year, predator avoidance or defence behaviour (Martin & Briskie 2009), and priority assigned by management (Stockwell et al. 2003).

In a review of predation driving behavioural plasticity in avian life-history traits, Martin and Briskie (2009) identified nest predation of dependent offspring as a strong source of natural selection, as it accounts for >70% of reproductive mortality in most bird species. Factors influencing sensitivity to nest predation risk included incubation activity and parental feeding activity both within and among species. Martin and Briskie (2009) suggested nest predation appeared to favour evolution of faster growth and earlier departure of offspring. Evidence of adaptation to nest predation in New Zealand comes from the work of Starling (2006) and Massaro et al. (2008) in forests in the eastern South Island. These authors found that bellbirds changed nesting behaviour in response to novel predators in an unmanaged site compared with a predator-culled area. Under high predation risk, bellbirds reduced the number of visits to nests and increased the length of time per

bout of incubation, which diminished their conspicuousness to predators. Massaro et al. (2008) suggested that some life-history traits are plastic in response to predation risk in ways they considered adaptive (see also Price et al. 2003; Forstmeier & Weiss 2004; Peluc et al. 2008; Martin & Briskie 2009). Massaro et al. (2008) proposed that conservation efforts could be more effective if managers work with this behavioural plasticity, when eradication of predators is not possible.

Due to New Zealand's prolonged isolation, evolutionary rescue could also occur more rapidly for species that are relatively recent arrivals (Miskelly et al. 2008). This is because more recent immigrants that evolved in the presence of mammalian predators may have greater latent phenotypic plasticity than species that evolved during New Zealand's isolation. In their 2008 assessment of the conservation status of New Zealand birds, Miskelly et al. identified that none of the 59 taxa that shared breeding distributions with other countries had gone extinct in New Zealand since the arrival of humans. These authors point to a correlation between levels of endemism and extinction and threat (see also Duncan & Blackburn 2004; Boyer 2008). The greater the level of endemism at the family and species level, the greater the susceptibility to the ubiquitous novel selection pressures introduced by humans. An interesting question is whether the inverse applies for the ability of a species to undergo evolutionary rescue. This is likely to be influenced by the ability of a species to increase behavioural plasticity in response to management (Lande 2009), and the types and severity of maladaptation that evolved since ancestral arrival (Duncan & Blackburn 2004).

Low levels of genetic diversity within many threatened endemic forest bird populations may also reduce the ability to evolve adaptive behaviours (Jamieson 2009). Population declines and local extinctions since human arrival to New Zealand have resulted in reduced genetic diversity, and consequently the ability to adapt to novel selection pressures (Jamieson 2009). High rates of inbreeding in threatened forest bird species and genetic bottlenecks may stall or slow the rate of evolutionary rescue, depending on which life-history traits are affected by reduced fitness (Jamieson et al. 2006). These authors caution that genetically depauperate species with slow mutation rates may go extinct, even if predation is ameliorated, due to reduced resistance to emerging disease and the effects of deleterious alleles on reproductive performance. Therefore, predicting which individual forest bird species are able to undergo evolutionary rescue, and the likely time taken, is beyond the scope of this conceptual paper.

Safe sites and predator management in New Zealand forests

The 'safest' safe sites in New Zealand forest ecosystems are predator-free offshore islands and fenced pest-resistant sanctuaries ('fences'). These require ongoing management to prevent invasion or reinvasion by introduced predators. The success of safe sites in protecting biodiversity is well documented (e.g. Innes et al. (2012) for summary). However, there is debate about the benefits of fences due to their cost and to unclear species conservation goals (Scofield et al. 2011; Innes et al. 2012; Scofield & Cullen 2012). Their utility as a source of adaptation in combination with predator control outside fences has not been part of the debate. One of the benefits of fences is that they protect species that are vulnerable to low densities of predators. The ability to keep predators at low

abundance will be important in transition zones. Low predator abundance exposes threatened species to selection pressure, which can facilitate the expression of adaptive traits (Stockwell et al. 2003; Forstmeier & Weiss 2004; Massaro et al. 2008; Peluc et al. 2008; Martin & Briskie 2009).

Some evidence of increased abundance of forest bird species outside fences has been detected, including recolonising areas where predator culling has been undertaken (Miskelly et al. 2005; Bell 2008; Innes et al. 2012). Spurr (2012) reported that threatened forest birds were recorded in urban gardens up to 25 km from safe sites. These included kākā (*Nestor meridionalis*), saddleback (*Philesturnus carunculatus*), stitchbird (*Notiomystis cincta*), and red-crowned parakeets (*Cyanoramphus novaezelandiae*). Moreover, Spurr (2012) noted that seven indigenous bird species were among the 15 most common in the percentage of gardens visited nationally between 2007 and 2011. Whether these observations collectively reflect adaptation leading to self-sustaining populations of some species is one of a number of important questions that could be addressed in a conservation evolution framework (Table 3).

Conclusions

Evolutionary rescue may not be a panacea for conservation of all threatened forest bird species (Vander Wal et al. 2012). However, the number of forest bird species that can be facilitated to evolutionary rescue is unknown without attempting it. Research as outlined in Table 3 is needed to explore this more fully. Answers to these questions are important for the development of future conservation management options, not only for forest birds, but also potentially for birds inhabiting different habitats, and also for other functional groups of species.

The time taken for evolutionary rescue may require a long horizon. The literature indicates that adaptive evolution can occur within a few hundred generations, depending on the suite of life-history traits that a species possesses. Conservation evolution is therefore a mid- to long-term strategy, which will require experimentation and adaptive management to succeed. For example, an experiment over three years to entice

saddlebacks to roost in artificial nest boxes to avoid predation by rats on Kapiti Island was unsuccessful (Lovegrove 1992). However, there was evidence that some young birds learnt to use the nest boxes. Saddlebacks also recognised avian and rat predators and exhibited a range of strategies to avoid predation (Lovegrove 1996). However, there was no safe site free from rats, or transition zone, to facilitate selection of adaptive phenotypes at a rate that recruitment exceeded the overall population decline.

Therefore, the way in which management is configured and interconnected at the forest landscape scale is important to any strategy that attempts to facilitate adaptive evolution, such as that outlined in this article. Most management scenarios will be unique given the complexities and dynamics between population size, genetic variation, gene flow, and degree of maladaptation in response to different selection pressures (Stockwell et al. 2003). Whether evolutionary rescue is desirable or achievable for all species will depend on the constraints imposed by the interplay of genetic, environmental, social, political, and budgetary factors outside of conservation management control. However, it is worth asking what theoretical and practical alternatives are available, if a predator-free country is improbable for social, technical, and ecological reasons.

This leads to the larger question of why we should bother with evolutionary rescue when so much of our biodiversity is in various stages of decline (such as birds, or 'the wreckage of an avifauna' as Diamond (1984) referred to it), when immediate action is needed to arrest declines, and we do not have enough resources to save every species. This is true; however, as evolution occurs over a range of timescales, its potential application as a long-term conservation management tool needs further investigation. If successful, it would complement current management that aims to prevent local and permanent extinctions of forest bird species, and to sustain species that are unable to adapt (trajectory (*d*) in Fig. 1).

Conservation evolution may emerge as a key strategy, alongside effective biosecurity, that could lead to the long-term sustainability of many threatened species in novel ecosystems. Conservation evolution will potentially be expensive to test and implement. However, it may help to justify management well into the future, and potentially result in more cost-effective

Table 3. Potential research questions to support the testing and implementation of a conservation evolution framework for forest bird species in New Zealand. The list is by no means exhaustive.

Conservation evolution research questions

Are micro-evolutionary processes occurring in forest bird species in response to novel selection pressures, and are these adaptive?

Is the rate of adaptive evolution sufficient to keep pace with the ongoing rate of environmental change?

Is there evidence for adaptive evolution of birds to introduced predators in response to current conservation management?

Which forest bird species are potentially able to be facilitated to evolutionary rescue, such that populations are able to sustain themselves in different ecosystems?

How can management be configured and adapted to optimise evolutionary rescue for different species?

What are the implications for current management and the ecological and economic opportunity costs involved?

How long or how many generations will it take for different species to undergo evolutionary rescue?

Are there detectable differences in micro-evolutionary processes between populations of the same species, in response to different novel selection pressures, or in the absence of those pressures? How will these manifest behaviourally and genetically?

Can individuals translocated from populations where adaptive evolution has occurred influence the survivability of receiving populations?

Does successful evolutionary rescue to novel predation pressures also increase the adaptive resilience of populations to different novel selection pressures?

Are introduced bird species colonising niches left vacant by extirpation of populations of indigenous forest bird species?

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management in the long-term, as species progressively become self-sustaining.

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