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Essay

Securing the Demographic and Genetic Future of Tuatara through Assisted Colonization

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Abstract: *Climate change poses a particular threat to species with fragmented distributions and little or no capacity to migrate. Assisted colonization, moving species into regions where they have not previously occurred, aims to establish populations where they are expected to survive as climatic envelopes shift. However, adaptation to the source environment may affect whether species successfully establish in new regions. Assisted colonization has spurred debate among conservation biologists and ecologists over whether the potential benefits to the threatened species outweigh the potential disruption to recipient communities. In our opinion, the debate has been distracted by controversial examples, rather than cases where assisted colonization may be a viable strategy. We present a strategic plan for the assisted migration of tuatara* (Sphenodon punctatus)*, an endemic New Zealand reptile. The plan includes use of extant populations as reference points for comparisons with assisted-colonization populations with respect to demography, phenotypic plasticity, and phenology; optimization of genetic variation; research to fill knowledge gaps; consideration of host and recipient communities; and inclusion of stakeholders in the planning stage. When strategically planned and monitored, assisted colonization could meet conservation and research goals and ultimately result in the establishment of long-term sustainable populations capable of persisting during rapid changes in climate.*

Keywords: assisted migration, climate change, ecological replacement, managed relocation, reintroduction, translocation, tuatara

Aseguramiento del Futuro Demográfico y Genético de la Tuatara Mediante Colonización Asistida

Resumen: *El cambio climático representa una amenaza particular para especies con distribución fragmentada y con poca o ninguna capacidad para migrar. La colonización asistida, mover especies hacia regiones donde no ocurrían previamente, trata de establecer poblaciones donde se espera que sobrevivan a medida que el clima cambia. Sin embargo, la adaptación al ambiente original puede afectar si la especie se establece exitosamente en regiones nuevas. La colonización asistida ha estimulado el debate entre biólogos de la conservación y ecólogos sobre si los beneficios potenciales para las especies amenazadas tienen más peso que la disrupción potencial a las comunidades receptoras. En nuestra opinión, el debate ha sido distraído por ejemplos controversiales, en lugar de casos en los que la colonización asistida puede ser una estrategia*

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viable. Presentamos un plan estratégico para la migración asistida de la tuatara (Sphenodon punctatus), *un reptil endémico de Nueva Zelanda. El plan incluye el uso de poblaciones existentes como referencia para comparaciones con poblaciones de colonización asistida con respecto a la demografía, plasticidad fenotípica y fenología; optimización de variación genética; investigación para llenar vacíos de conocimiento; consideración de comunidades huésped y recipientes; e inclusión de diversos actores en la etapa de planificación. Cuando es planeada y monitoreada estratégicamente, la colonización asistida podría alcanzar metas de conservación e investigación y finalmente resultar en el establecimiento de poblaciones sustentables a largo plazo, capaces de persistir durante cambios rápidos en el clima.*

Palabras Clave: cambio climático, migración asistida, reemplazo ecológico, reintroducción, translocación, traslado, tuatara

Introduction

Rapid climate change poses unusual threats to species with fragmented distributions and limited capacity to migrate or evolve. Many plant and animal species have already undergone dramatic range shifts and contractions in response to climate change and have moved to higher elevations or closer to the poles (Walther et al. 2002; Parmesan & Yohe 2003; Parmesan 2006). However, some species are simply unable to migrate, or to migrate quickly enough, to allow potential adaptation to climate change (Menéndez et al. 2006).

Moving species into regions where they have not previously occurred may help prevent extinctions if the recipient location is likely to remain climatically suitable (Hoegh-Guldberg et al. 2008). Assisted colonization (also known as assisted migration or managed relocation [Seddon 2010]) is 1 of 15 nascent global conservation issues (Sutherland et al. 2010) and has spurred debate among conservation practitioners (Hoegh-Guldberg et al. 2008; Ricciardi & Simberloff 2009; Sandler 2010). Although promising results from at least one assisted-colonization project are available (Willis et al. 2009), most of the literature on assisted colonization focuses on whether the benefits to the threatened species outweigh the potential disruptions to recipient communities (e.g., Ricciardi & Simberloff 2009). Although the debate is warranted, and in many cases is central to the conservation of species and ecosystems, we focused on examining the scientific principles that can be used to direct the experimental design and implementation of assisted colonization where potential disruptions to recipient communities are likely negligible.

Assisted colonization aims to circumvent physical barriers to migration in response to climate change, but adaptation of an organism to the source environment may affect whether species establish successfully in new regions. Translocations of threatened species, even within their native range, have had low success rates (approximately 50%) (Griffith et al. 1989; see Germano & Bishop 2009 for herpetofauna). Phenotypic differences among populations may indicate plasticity (i.e., individuals alter their responses when presented with different environmental cues). However, phenotypic differences among populations may reflect local adaptation to the source environment, and a population's response to new environmental cues cannot be predicted without understanding the cause of phenotypic differences. Information on differences among populations is often lacking for many, if not all, populations across a species' range (Jetz et al. 2009). Manipulative experiments are required to determine whether the observed differences result from phenotypic plasticity or genetic adaptation (Mitchell & Janzen 2010; Reed et al. 2011).

We considered the potential for assisted colonization to counter the effects of climate change on tuatara (*Sphenodon punctatus*), a species of reptile that was once widely distributed across New Zealand. Due to anthropogenic habitat change and the introduction of predators, many populations of tuatara have been extirpated. The species' range has contracted substantially over the last 800 years, and tuatara now occur naturally on only 31 offshore islands northeast of the North Island and in Cook Strait (Fig. 1). On the basis of International Union for Conservation of Nature definitions and recent literature, our proposals for assisted colonization of tuatara could also be described as a reintroduction (attempt to establish a species in an area that was once part of its historical range) or ecological replacement (functional equivalent) (IUCN 1987; IUCN 1998; Seddon 2010). However, we use the term *assisted colonization* due to the lack of information on whether extirpated populations of tuatara were of a different species than current populations and whether the locally adapted, extant populations would be suitable sources for the establishment of new populations outside the species' current range. We do not use the term *ecological replacement* to avoid negative connotations arising from controversial examples of the use of non-native species as functional equivalents (Seddon 2010).

Translocations of tuatara have already occurred, and the establishment of new populations in areas outside their current fragmented distribution is planned for the near future. We synthesized current knowledge of tuatara and considered the factors involved in the design of an assisted-colonization project. Our aim was to guide future assisted-colonization projects for tuatara that could offset the negative effects of climate change. The plan includes social issues and regional cultural issues surrounding guardianship and historic integrity of populations.

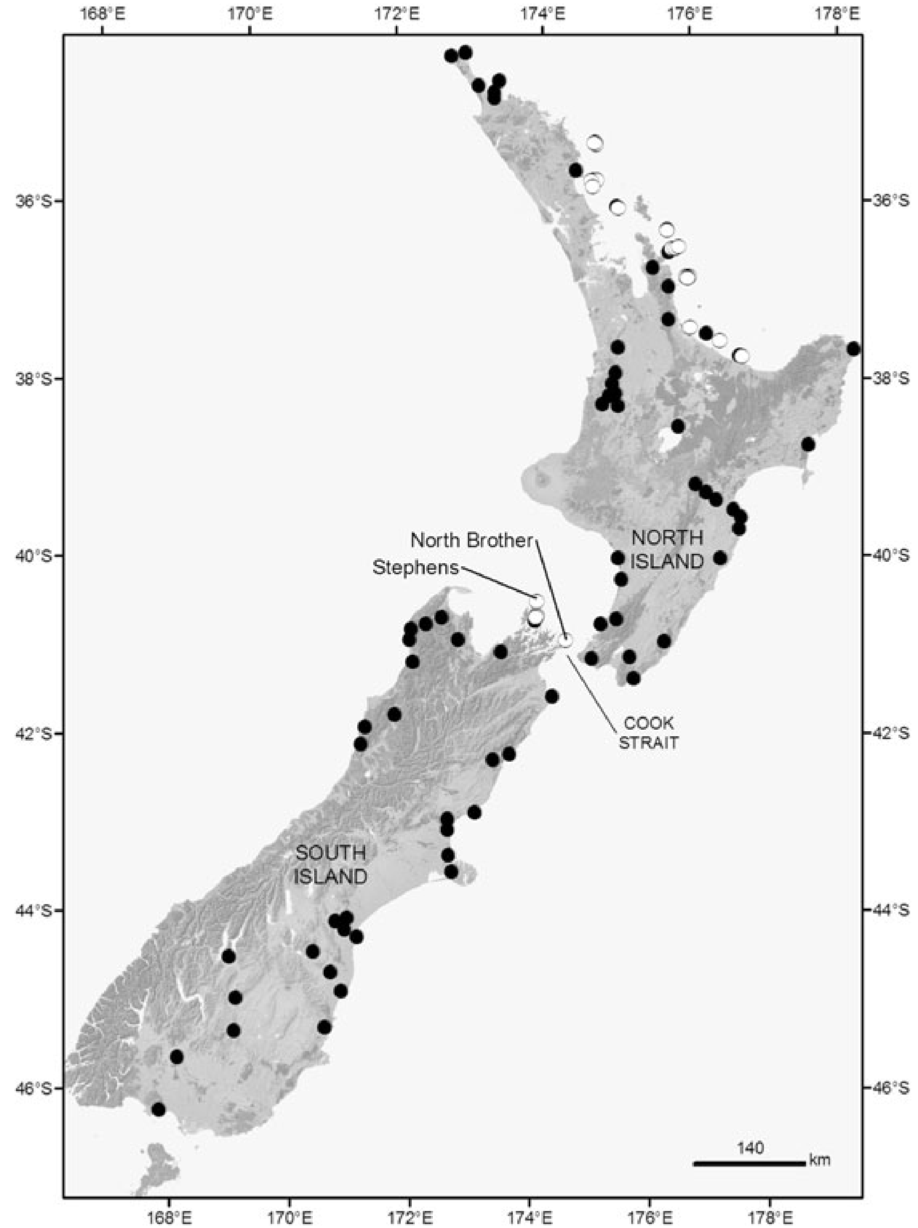

Figure 1. Sites on the North and South Islands of New Zealand where Holocene subfossil remains of tuatara (black circles) (Worthy & Holdaway 2002; Wood 2009; P. Millener, personal communication cited in Cree & Butler 1993) have been found and sites on off-shore islands where extant populations (white circles) occur. Remains were found between 35°S and 47°S, including in areas up to 500 m asl that are covered by snow throughout much of winter.

Tuatara

Tuatara are medium-sized (adults range from 300 to 1000 g) reptiles and the only living representatives of Rhynchocephalia, which diverged from other reptilian orders approximately 250 million years ago (Gaze 2001; Hugall et al. 2007). Not only is their current distribution restricted, but their current elevational range is also limited. Two of the 10 largest islands on which they occur are >300 m asl (Whitaker & Daugherty 1991). Extant populations of tuatara span 6° of latitude (approximately 30% of their latitudinal range before human settlement), are separated by up to 600 km, and differ considerably from each other in population history. Most of the islands on which they occur are small (mean 63 ha; median 6.3 ha) (Whitaker & Daugherty 1991), and tuatara population sizes are primarily in the tens to low hundreds (Gaze 2001). Thus, many populations are at a high risk of extinction through demographic and genetic stochasticity.

Contemporary climate change may threaten extant populations of tuatara because the species is cold adapted and exhibits temperature-dependent sex determination (males are produced when incubation temperatures are >21.7 °C; below this temperature females are produced) (Cree 1994; Mitchell et al. 2006). It is predicted that New Zealand's mean annual temperature will increase 0.1–1.4 °C by the 2030s and 0.2–4.0 °C by the 2080s (Hennessy et al. 2007), but the temperature difference between production of all-female and all-male hatchlings is only 1 °C (Nelson et al. 2004; Mitchell et al. 2006). In one well-studied population, a significant (60–80%) male-biased adult sex ratio is already apparent. Sex ratios are projected to become more male-biased as temperatures increase (Mitchell et al. 2008; Wilson 2010). Furthermore, predicted drought and extreme high-temperature events (Hennessy et al. 2007) may reduce recruitment through nest failure and negatively affect demographic parameters in small populations (Thompson et al. 1996).

Although the taxonomic history of the tuatara is complex (Daugherty et al. 1990; Hay et al. 2010), management of tuatara since 1990 has been conducted on an island-by-island basis. Recent taxonomic work indicates there is a single species (*S. punctatus*) and geographically distinct genetic variants (Hay et al. 2010). Nuclear and mitochondrial DNA show a substantial divergence between tuatara from the north and Cook Strait islands (Fig. 1.), and even neighboring islands appear to support genetically distinct populations (MacAvoy et al. 2007; Hay et al. 2010). It is unknown whether genetic groups of extant populations differ physiologically or ecologically and how populations across the species' former latitudinal range were related.

Extant populations of tuatara may be locally adapted to their ecological regions (adjacent areas with similar biotic and abiotic characteristics [McEwan 1987]). Given the reduced geographic range and restriction of tuatara populations to offshore islands, current levels of genetic diversity are likely to be much lower than historic levels. Life-history characteristics that could be local adaptations important for population establishment include thermal tolerance, disease resistance, timing of key life-history events (phenology), nesting behavior, body size, and the pivotal temperature for sex determination (i.e., incubation temperature that produces a 1:1 offspring sex ratio). The pivotal temperature for sex-determination appears to vary across populations; it is slightly cooler for the extant populations in the south (Mitchell et al. 2006).

The potential for differences in disease resistance between northern and Cook Strait populations is underscored by differentiation of major histocompatibility complex (MHC) genes, which play a central role in pathogen resistance (Penn et al. 2002). All populations of tuatara are highly differentiated, and Cook Strait and northern populations have very little overlap in MHC allelic diversity (Miller et al. 2010*a*). Although this pattern partly reflects genetic drift through isolation and small population size, one cannot rule out the possibility of coevolution of local populations with different suites of pathogens. Little is known about the range of pathogens present in most tuatara populations, but pathogen loads are related to climate in many species (e.g., Harvell et al. 2002), and suites of pathogens may vary among islands as a result of founder effects and extinction through demographic stochasticity.

The long-term recovery goal for tuatara is to maintain genetic diversity by returning all existing populations to natural sizes (approximately 100 tuatara/ha over half the island area) and by establishing new wild populations throughout their range before human settlement (Gaze 2001). Recent conservation efforts have focused on reintroductions and restocking (IUCN 1987) within an ecological region (often within 10 km) with individuals from one source population (Miller et al. 2009). All monitored populations involved in such efforts have succeeded in the short term; survival, growth of founders, and recruitment have been observed (e.g., Nelson et al. 2002; McKenzie 2007). However, their long-term viability will remain unclear for several decades (Miller et al. 2010*b*). Tuatara characteristics that make it difficult to detect management success include their extreme longevity (100 years) (Castanet et al. 1988), delayed sexual maturity (14 years) (Cree et al. 1992), infrequent production of offspring (every 2–9 years), low reproductive output (approximately 6–9 eggs/clutch) (Cree et al. 1992; Mitchell et al. 2010), and low detection probabilities for hatchlings and juveniles. Translocations over much greater distances and outside ecoregional boundaries are now proposed for several populations of tuatara (Fig. 2). Proposed sites include cooler locations that may mitigate some predicted effects of climate change. However, there is little information on whether tuatara were historically present at many of the proposed sites and whether the current genetic diversity of tuatara is representative of the diversity of tuatara before human settlement of New Zealand.

Management decisions in New Zealand are guided by scientific principles, but advocacy, cultural values, and economic affordability also affect decisions. Increased accessibility to threatened species is central to promoting public awareness of conservation issues, and the most recent Tuatara Recovery Plan cites this as one of the primary objectives for conservation (Gaze 2001). The sites proposed for assisted-colonization and reintroduction projects are easily accessible from urban areas and contain putative habitat for tuatara.

In addition, consideration of European and Māori cultural values regarding the historic integrity and guardianship of tuatara populations may not be reflected in recommendations driven by science. Tuatara are culturally significant to people of both European and Māori descent. Under New Zealand law, Māori retain guardianship of the *taonga* (treasures) in their *rohe* (territory), and policy makers are mandated to maintain the relationship of Māori with their taonga (e.g., Conservation Act 1987). Therefore, all research on and management of tuatara must be conducted in consultation with local Māori tribes. Although the principles of all partners in decision making may align predominantly for the good of the species, conflicting opinions arise, for example, over areas where mixing island stocks might be desirable. Lack of knowledge about local adaptations of tuatara suggests that introduction of individuals from

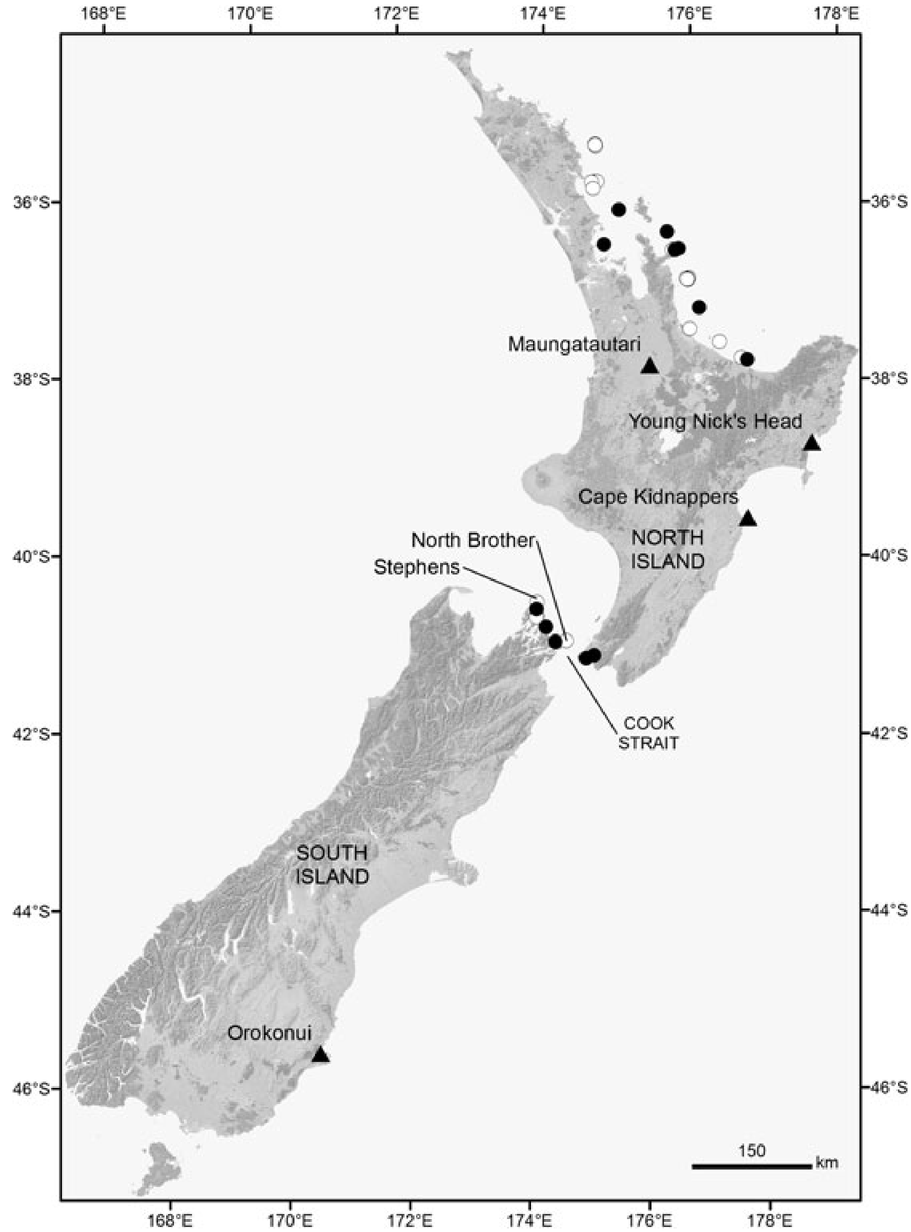

Figure 2. Current and possible future distribution of tuatara (white circles, extant island populations; black circles, reintroduced or supplemented populations; triangles, proposed translocation sites).

several populations may be optimal when proposed introduction sites are geographically between locations occupied by tuatara (Weeks et al. 2011), but mixing populations raises cultural issues related to historic integrity (*whakapapa* or genealogy or ancestry). Disruption or alteration of the whakapapa of tuatara may be considered destructive to the natural order, but an understanding of the relations among tuatara populations could address such concerns. Furthermore, the translocation of tuatara beyond the territory of one tribe may be affected by existing tribal relationships. Historic tensions or amity between tribes can result in the proposal to move tuatara between tribal territories being met with strong resistance or seen as an opportunity to heal or reinforce tribal relationships.

Assisted-Colonization Projects as Conservation Experiments

We applied the following 5 common conservation principles (McLachlan et al. 2007) to our plan: extant populations should remain in situ unless population viability is threatened, and assisted-colonization projects should optimize genetic variation, be designed as experiments to fill knowledge gaps, be considered only when recipient locations and ecological communities are appropriate, and require effective communication with stakeholders. We devised research foci to guide an assisted-colonization program for tuatara. We advocate an approach to assisted colonization in which research is aimed at understanding the potential effects of management actions, and used to inform future management actions and acknowledge that it would be ideal to know the answers to many research questions before the movement of individuals.

We consider the movement of individuals a reintroduction if the translocation is within a single ecological region, and assisted colonization if translocation is outside the ecological region of the extant population. Whether a given case is considered reintroduction or assisted colonization may change on the basis of new information on past distributions and genetic variation. The 5 principles we emphasize in our plan should be considered with the understanding that we support the medium-term goal of using reintroduction and assisted-colonization projects to reestablish tuatara throughout their former range where feasible (Gaze 2001) and that actions to fulfill this goal should not put source populations at risk.

Extant Populations

Morphologically similar remnant populations of tuatara have survived climate changes over at least 100,000 years, but the species' past physiological attributes are unknown. Extant populations can serve as a reference point for comparisons with populations involved in an assisted colonization with respect to demography (e.g., sex ratios, mating systems, and population trends), phenotypic plasticity, and phenology (e.g., Mitchell et al. 2008).

Mechanistic models may be the best tools for exploring the responses of populations to climate change in existing and novel environments (sensu Buckley 2008; Mitchell et al. 2008), but because the evolutionary consequences of assisted colonization in long-lived species will not be apparent for centuries, confirming the accuracy of predictions made on the basis of these models will take decades. Measuring responses of extant populations to climate change will be crucial for model verification.

Genetic Variation

In a newly established population, retaining moderate to high levels of genetic variation maximizes evolutionary potential (Frankham 1999) and minimizes the need for supplementation of populations in the future (Miller 2009). Therefore, source populations should have moderate to high levels of genetic diversity at neutral and functional markers, and founders should represent source-population diversity. Although this principle is intuitive, we emphasize the importance of retaining genetic diversity in populations involved in assisted colonization, given the potential novelty of the environment into which the organism will be introduced. Individuals moved outside of their local range will be exposed to a range of novel conditions (e.g., new pathogens), and high genetic variation will be essential for retaining the potential for adaptation.

The geographic location of the introduction site relative to the potential source population should be a factor in the selection of the source populations. If climate is stable, we believe current patterns of genetic diversity should be maintained where possible. For example, individuals should not be sourced from a different ecological region if individuals are available from within the same region unless there is strong evidence (e.g., from results of mechanistic models) that the climate at a translocation site will change significantly in the near future (e.g., within decades). Physiographic and climatic differences may indicate which source population is most appropriate.

It may also be appropriate to choose founders from more than one source population to maximize genetic diversity in reintroduced populations (Weeks et al. 2011). For example, on the North Island mainland, assisted colonization sites for tuatara (Young Nick's Head and Cape Kidnappers) (Fig. 2) are between remnant populations in 2 ecological regions and reintroduced populations should therefore be composed of founders from the northern and Cook Strait genetic groups (Hay et al. 2010) to provide the greatest adaptive potential for the new populations. This action may have multiple benefits and drawbacks. For example, fitness may increase as a result of greater genetic diversity and hybrid vigor (e.g., Tallmon et al. 2004), and microevolutionary responses may result in adaptation to the new local conditions. Alternatively, hybridization could result in outbreeding depression (breakdown of coadapted gene complexes [Tallmon et al. 2004, but see Frankham et al. 2011]) or maladapted phenotypes (e.g., Hatfield & Schluter 1999). Furthermore, the hybridization of animals from 2 populations exposes some founders to novel diseases introduced from the other population. Thus, before full implementation a mixed-stock approach to assisted colonization requires careful measurement of, for example, short-term survival and growth of founders, recruitment, and performance of hybrids relative to each founder stock (Weeks et al. 2011).

Understanding how the timing of events (e.g., reproduction, maturation) varies among populations at different latitudes or elevations is the first step in gauging local adaptation. To determine the effect of these differences among populations (e.g., on whether eggs are laid at an appropriate time of year for successful embryonic development in suitable environmental conditions), one needs to understand the extent of acclimation, whether patterns of neutral genetic variation reflect adaptive differences among populations, and the genetic basis of functionally important traits (e.g., traits involved in thermal adaptation), and perform common-garden or transplant experiments to assess the extent of phenotypic plasticity underlying variation in these traits (Mitchell & Janzen 2010). New genomic approaches will facilitate the identification of genes and genomic regions that may be associated with functionally important traits or traits under selection in different populations and of variation in expression patterns among locations (Ellegren 2008; Rokas & Abbot 2009).

Experiments to Target Knowledge Gaps

Assisted colonizations and reintroductions provide excellent opportunities to address questions that may not be possible to address in extant populations because manipulation is prohibited, undesirable, or unfeasible. We believe that initially assisted colonizations should be treated as experiments and research opportunities. For example, with carefully planned controls, the assisted colonization of tuatara into the Young Nick's Head and Cape Kidnappers sites could be used to evaluate local adaptations and the effects of hybridization. Another factor that can be examined experimentally on molecular, developmental, physiological, and ecological levels is the influence of temperature on sex determination. Although tuatara are the only known species in which male phenotypes develop at higher temperatures (Mitchell et al. 2006), many reptiles have temperature-dependent sex determination, and some species with sex chromosomes exhibit sex reversal when exposed to certain incubation temperatures (Quinn et al. 2007; Shine et al. 2008). It is proposed that reptiles may readily evolve from genotypic sex determination to temperature-dependent sex determination (Georges et al. 2010). Opportunities to improve understanding of the lability of the sex-determination process and of the thermal constraints on ectotherms when temperatures vary daily, seasonally, and annually are critical to predicting the evolutionary response of different species to climate change. For tuatara a key trait to investigate is the temperature threshold for sex determination across the species' latitudinal range and its influence on population viability (McGaugh & Janzen 2011).

Recipient Locations and Ecological Communities

Ecological surveys of potential assisted-colonization sites are required to assess suitability and potentially novel selective pressures, including temperature and precipitation regimes. Climate change raises new questions about site suitability, particularly whether biophysical and ecological requirements for the species can be met now and in the future. Climate change is already altering many ecosystems (Brown et al. 1997; Sanz-Elorza et al. 2003). Predictive modeling (e.g., Louis et al. 2002; Mitchell et al. 2008) can be used to assess the future conditions of a site under projected-climate scenarios and to identify locations suitable for use in assisted colonization (Hijmans & Graham 2006). Predictive modeling of habitat quality could also be used to evaluate the effects of climate change on distributions of, and hence likely interactions among, other members of the community. In the absence of an accurate understanding of optimal site requirements, assisted-colonization sites should encompass a range of vegetation types, elevations, prey composition, and climatic conditions.

The threats posed by introducing species through assisted colonization to recipient ecological communities have been used to argue that assisted colonization is inherently too risky to be feasible (Ricciardi & Simberloff 2009). Thus, ecological surveys should also aim to identify threats to the recipient communities (e.g., predation on or competition with threatened species, effects on fragile ecosystems). Although not all threats can be identified, the most obvious detrimental effects that would exclude a given site should be apparent. Monitoring of ecological communities (e.g., population trends, mortality events) should continue as part of any assisted-colonization program so that the possibility of a quick response to threats is maximized.

Microbial communities are especially important to consider because climate change is predicted to alter patterns of infectious disease occurrence as parasites undergo range shifts or expansions, changes in growth and survival rates, and form new associations within ecosystems in response to increasing temperatures and changes in precipitation patterns (Lafferty 2009; Polley & Thompson 2009). However, few empirical studies of wild animals have measured changes in disease dynamics and distribution at different sites or in response to climate change (e.g., Jepsen et al. 2008), and in many instances, the diversity and abundance of pathogens that affect particular species or occur in ecosystems are poorly known (Smith et al. 2009).

Communication with Stakeholders

For charismatic flora and fauna, assisted colonization represents a move into new cultural territory. It raises issues related to the historical integrity of populations, public perceptions of climate change, and the relationships among human communities. Society's endorsement may not be easily gained. Therefore, researchers, managers, and community members must collaborate on conservation issues related to climate change. Effective and frequent communication among all parties facilitates consensus on controversial conservation actions (Richardson et al. 2009). Early involvement of communities affected by an assisted colonization will be important for maintaining and enhancing the relationships among communities. In New Zealand, discussions on translocations of tuatara have occurred over long periods due to the community concerns with moving tuatara to other sites. Assisted-colonization proposals are further complicated by the likely distances between source and release sites and a lack of existing relationships among parties.

When strategically planned and monitored, assisted colonization programs could meet conservation, research, and policy goals and ultimately result in the establishment of self-sustaining populations capable of persisting during rapid changes in climate. If the ecological risks to recipient communities are negligible, assisted colonization is a promising tool to conserve species that are unable to adapt rapidly to climate change without intervention. Developing principles and research directions informs decision making regarding the application and success of assisted colonization, including possible reintroductions with stocks sourced from different ecological regions. The most successful interventions measure the evolutionary and ecological effects on the target species and ecosystems and incorporate human cultural values.

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