Conservation Biology

Diversity

Rapid evolution in predator-free conservation havens and its effects on endangered species recovery

Chris J. Jolly * and Ben L. Phillips
School of BioSciences, University of Melbourne, Parkville, VIC, 3010, Australia

Invasive predators are implicated in almost 60% of all contemporary bird, mammal, and reptile extinctions (Doherty et al. 2016). For many native species, the arrival of invasive predators sets up a race between the processes of adaptation and extinction, a race often won by extinction (Woinarski et al. 2015). Indeed, many native species have declined so precipitously that one of very few options has been to move them into havens (i.e., islands and fenced areas) free of invasive predators (Legge et al. 2018). This action helps threatened taxa persist because it removes the demographic burden of predation, but also blunts predator-imposed natural selection. The species may be saved; however, it appears that moving individuals to havens can also select for bold, hypercompetitive individuals, causing rapid evolutionary loss of antipredator traits (Jolly et al. 2018*a,b*). This trait loss can affect antipredator responses toward both invasive and native predators. If this maladaptive evolution is occurring in havens generally, it may dramatically undermine the value of predator-free conservation havens.

Although the evolutionary concerns associated with small, isolated populations are broadly discussed (Stockwell et al. 2003; Frankham 2008), evolution in response to predator exclusion is rarely considered by managers (Hayward & Kerley 2009; Moseby et al. 2016). Where it is considered, it is assumed (often implicitly) that antipredator traits will be lost only very slowly, over hundreds or thousands of generations. As such, the evolutionary loss of antipredator traits is not seen as a pressing management problem. There are documented cases of antipredator traits being retained over long periods in the absence of predators (Carthey & Blumstein 2018); if a trait is irrelevant to fitness, one would not expect it to disappear rapidly (Lahti et al. 2009). There are also hypotheses (e.g., multipredator hypothesis [Blumstein 2006]) that help explain why traits might be maintained in some circumstances. So, the assumption is that antipredator traits will persist in predator-free havens. This assumption, however, has rarely (if ever) been tested.

It is clear that most antipredator traits are ultimately lost following long-term isolation from predators (Blumstein et al. 2004; Blumstein & Daniel 2005; Muralidhar et al. 2019) and that in captive populations, antipredator traits can be lost quickly (McDougall et al. 2006). Recently, we documented the rapid loss of antipredator traits in an endangered population moved to an island haven (Jolly et al. 2018*a,b*). Northern quolls (*Dasyurus hallucatus*) moved to an offshore haven in 2003 had, by 2016, lost their response to a common natural predator (dingoes [*Canis familiaris dingo*]), rendering them ineffective for reintroduction programs (Jolly et al. 2018*a,b*). This trait loss, in <13 generations, was evolved: captive-reared mainland quolls respond to dingo scent, but captive-reared island quolls do not. The speed of this trait loss was surprising, but implies that there was strong selection acting to remove antipredator traits in a population conserved in isolation from its predators.

How would such selection arise? In the haven, because there was no top-down regulation by predators, the quoll population grew rapidly and overshot carrying capacity within 4 years (Griffiths et al. 2017). This population was then in a world in which predation vanished and intraspecific competition for resources was the dominant force of natural selection. Here, behaviors that might save an individual from predation (vigilance, shyness, and neophobia) are a clear disadvantage. In the absence of predators, an individual that restricts foraging time to protect against predators will be less competitive than

---

*email cjolly1@student.unimelb.edu.au

Article impact statement: *Rapid evolutionary loss of antipredator traits in predator-free havens may be undermining the recovery of our most endangered species.*

Paper submitted February 7, 2020; revised manuscript accepted April 14, 2020.

Conservation Biology, Volume 35, No. 1, 383–385

DOI: 10.1111/cobi.13521

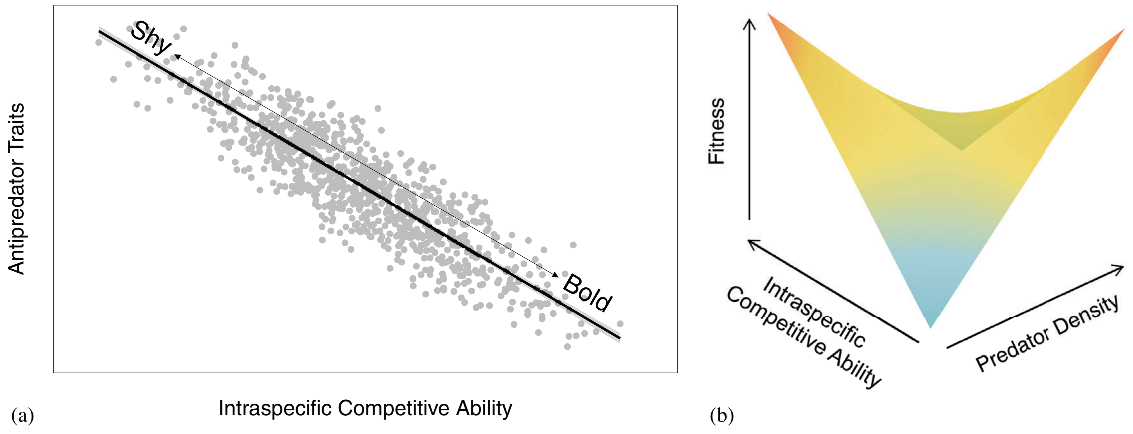

Figure 1. The hypothetical relationship between competitive ability and antipredator traits in a predator-free environment: (a) trade-off between antipredator traits and competitive ability and (b) under the scenario in (a), the relationship between fitness and competitive ability (i.e., selection gradient).

an individual that does not adopt antipredator behavior. In such a world, selection should act against antipredator traits. If correct, this mechanism is potentially a very general one that sets up a fundamental trade-off between competitive ability and antipredator traits (Fig. 1a). In the case of havens, removal of predators relaxes the selection maintaining antipredator traits, but the demographic response to predator release (i.e., high conspecific density and resource competition) sets conditions such that antipredator traits are then actively selected against. In such a scenario, the selection gradient (the relationship between fitness and competitive ability) is strongly dependent on predator density (Fig. 1b). The result is not so much relaxed selection in havens as directional selection toward predator naivete.

Alarmingly, this very scenario could be playing out globally across conservation havens (Hayward & Kerley 2009; Muralidhar et al. 2019). It is a common occurrence that populations in havens rapidly increase to high densities, to the point that haven managers have the perverse problem of too many animals in the haven (Bannister et al. 2016). Such conditions may cause active selection against antipredator traits. Despite investing large amounts of conservation funding, fundamentally important behavioral traits in the most threatened taxa may have been lost or are progressing rapidly toward being lost.

Fenced havens are financially costly to erect and maintain (Hayward & Kerley 2009). The setup costs of conservation fences vary markedly among countries, landscapes, and the taxa intended for isolation. Set-up costs of between US$8500 and 29,000/km of fence in Australia (Moseby & Read 2006; Ruykys & Carter 2019) and up to US$100,000/km (KRWSSC 1994; Hayward & Kerley 2009) in New Zealand have been reported. Maintenance costs are variable, context-dependent, and largely unknown but are required in perpetuity. The explicit objective of conserving endangered species in havens is typically to lock them away until eradication of introduced predators on a landscape or national scale becomes viable (Ringma et al. 2018). The situation in predator-free haven populations, however, may also cause populations to lose responses to native predators with which they coevolved (Jolly et al. 2018*a,b*). So, unless the ultimate aim is to remove all predators (invasive and native) from the landscape prior to reintroduction, policies need to be enacted to mitigate the loss of important antipredator traits from populations in predator-free havens. Without such management, threatened species, once conserved in isolation from predators, may require this level of human intervention forever.

Globally, the extinction crisis is accelerating. In many cases, in situ conservation is difficult, if not impossible. Isolationist conservation measures, where threatened species are removed from the threatening process, are often necessary to halt the extinction of the most critically endangered species. Thus, predator-free havens are increasingly utilized as biodiversity becomes more imperiled and the ability to ameliorate threats lags. A greater mechanistic understanding of how evolution drives the loss of antipredator traits may provide tools that improve the ability to conserve threatened species in havens without stymying their ability to return to the wild. By maintaining some level of controlled predation pressure from appropriate predatory archetypes (Blumstein 2006; Moseby et al. 2016, 2019; Carthey & Blumstein 2018; Blumstein et al. 2019) in havens, managers may be able to maintain top-down control and prevent rapid transition to systems dominated by bottom-up pressures in which invaluable antipredator traits are selected against (Fig. 1b). Alternatively, if the loss of antipredator traits is driven by intraspecific competition, reducing competition may be an alternative or complementary means of avoiding rapid antipredator trait loss in havens (Fig. 1a, b). Thus, population culling to prevent breaching carrying capacities or supplemental feeding to reduce the strength of intraspecific competition may alleviate some of the selective pressure acting on endangered species in havens (Moseby et al. 2016).

Clearly, if conservation managers continue to conserve endangered species away from threatening processes—threats that may never be possible to eradicate—evolutionary processes that act on populations in havens need to be considered to ensure these populations are one day capable of being freed from conservation interventions. In the long-term, without careful planning, safe havens may prove as significant a threat to endangered species as the threats they were intended to protect against. Integration of evolutionary theory into implementation of conservation havens is warranted to ensure that havens do not become expensive features of the conservation landscape into which threatened species are relegated in perpetuity.

Literature Cited

Bannister HL, Lynch CE, Moseby KE. 2016. Predator swamping and supplementary feeding do not improve reintroduction success for a threatened Australian mammal, *Bettongia lesueur*. Australian Mammalogy **38:**177.

Blumstein DT. 2006. The multipredator hypothesis and the evolutionary persistence of antipredator behavior. Ethology **112:**209–217.

Blumstein DT, Daniel JC. 2005. The loss of anti-predator behaviour following isolation on islands. Proceedings of the Royal Society B: Biological Sciences **272:**1663–1668.

Blumstein DT, Daniel JC, Springett BP. 2004. A test of the multi-predator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. Ethology **110:**919–934.

Blumstein DT, Letnic M, Moseby KE. 2019. *In situ* predator conditioning of naive prey prior to reintroduction. Philosophical Transactions of the Royal Society B: Biological Sciences **374:**20180058.

Carthey AJR, Blumstein DT. 2018. Predicting predator recognition in a changing world. Trends in Ecology & Evolution **33:**106–115.

Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR. 2016. Invasive predators and global biodiversity loss. Proceedings of the National Academy of Sciences of the United States of America **113:**11261–11265.

Frankham R. 2008. Genetic adaptation to captivity in species conservation programs. Molecular Ecology **17:**325–333.

Griffiths AD, Rankmore B, Brennan K, Woinarski JCZ. 2017. Demographic evaluation of translocating the threatened northern quoll to two Australian islands. Wildlife Research **44:**238.

Hayward MW, Kerley GIH. 2009. Fencing for conservation: restriction of evolutionary potential or a riposte to threatening processes? Biological Conservation **142:**1–13.

Jolly CJ, Kelly E, Gillespie GR, Phillips B, Webb JK. 2018*a*. Out of the frying pan: reintroduction of toad-smart northern quolls to southern Kakadu National Park. Austral Ecology **43:**139–149.

Jolly CJ, Webb JK, Phillips BL. 2018*b*. The perils of paradise: an endangered species conserved on an island loses antipredator behaviours within 13 generations. Biology Letters **14:**20180222.

KRWSSC. 1994. Feasibility report on the native wildlife sanctuary proposal for Karori Reservoir. Karori Reservoir Wildlife Sanctuary Trust, Wellington, New Zealand.

Lahti DC, Johnson NA, Ajie BC, Otto SP, Hendry AP, Blumstein DT, Coss RG, Donohue K, Foster SA. 2009. Relaxed selection in the wild. Trends in Ecology & Evolution **24:**487–496.

Legge S et al. 2018. Havens for threatened Australian mammals: the contributions of fenced areas and offshore islands to the protection of mammal species susceptible to introduced predators. Wildlife Research **45:**627.

McDougall PT, Réale D, Sol D, Reader SM. 2006. Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced, and wild populations. Animal Conservation **9:**39–48.

Moseby KE, Blumstein DT, Letnic M. 2016. Harnessing natural selection to tackle the problem of prey naïveté. Evolutionary Applications **9:**334–343.

Moseby KE, Letnic M, Blumstein DT, West R. 2019. Understanding predator densities for successful co-existence of alien predators and threatened prey. Austral Ecology **44:**409–419.

Moseby KE, Read JL. 2006. The efficacy of feral cat, fox and rabbit exclusion fence designs for threatened species protection. Biological Conservation **127:**429–437.

Muralidhar A, Moore FL, Easton LJ, Jamieson IG, Seddon PJ, van Heezik Y. 2019. Know your enemy? Conservation management causes loss of antipredator behaviour to novel predators in New Zealand robins. Animal Behaviour **149:**135–142.

Ringma J, Legge S, Woinarski J, Radford J, Wintle B, Bode M. 2018. Australia's mammal fauna requires a strategic and enhanced network of predator-free havens. Nature Ecology & Evolution **2:**410–411.

Ruykys L, Carter A. 2019. Removal and eradication of introduced species in a fenced reserve: quantifying effort, costs and results. Ecological Management & Restoration **20:**239–249.

Stockwell CA, Hendry AP, Kinnison MT. 2003. Contemporary evolution meets conservation biology. Trends in Ecology & Evolution **18:**94–101.

Woinarski JCZ, Burbidge AA, Harrison PL. 2015. Ongoing unraveling of a continental fauna: decline and extinction of Australian mammals since European settlement. Proceedings of the National Academy of Sciences of the United States of America **112:**4531–4540.